Environment Canada
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National Agri-Environmental Standards Initiative (NAESI)

Report No. 3-22

Habitat Suitability Model and Population Viability Analysis for the Marsh Wren (*Cistothorus palustris*) and Ovenbird (*Seiurus aurocapillus*) in Support of Habitat-based Biodiversity Standards

Technical Series 2007

Photos:
Bottom Left- clockwise

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Elk Creek, BC: Joseph Culp, National Water Research Institute, Environment Canada
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This report can be cited as follows:

> Noreca Consulting and Elutis Modeling and Consulting Inc. 2007. Habitat Suitability Model and Population Viability Analysis for the Marsh Wren (Cistothorus palustris) and Ovenbird (Seiurus aurocapillus) in Support of Habitat-based Biodiversity Standards. National Agri-Environmental Standards Initiative Technical Series Report No. 3-22. 92 p.

Prepared and published by
Environment Canada
Gatineau, QC

December 2007

NATIONAL AGRI-ENVIRONMENTAL STANDARDS INITIATIVE TECHNICAL SERIES

HABITAT SUITABILITY MODEL AND POPULATION VIABILITY ANALYSIS FOR THE MARSH WREN (CISTOTHORUS PALUSTRIS) AND OVENBIRD (SEIURUS AUROCAPILLUS) IN SUPPORT OF HABITAT-BASED BIODIVERSITY STANDARDS

REPORT NO. 3-22

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 Noreca Consulting and Elutis Modeling and Consulting Inc. 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:

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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 la biodiversité dans le cadre de l’INENA. Ce rapport a été rédigé par Noreca Consulting et Elutis Modeling and Consulting Inc. 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 :

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EXECUTIVE SUMMARY

To develop habitat-based biodiversity standards for the Eastern Ontario Model Forest (EOMF) region a set of 10 surrogate species has been identified by project team members of the National Agri-Environmental Standards Initiative (NAESI). These species and their associated habitat types are surrogates for important ecological functions, processes and services in agricultural regions of eastern Ontario. By applying a non-spatial (demographic) population model and a spatial population viability analysis (PVA) that is linked with a habitat suitability (HS) model this report aims at detecting specific landscape conditions ('thresholds') which may be critical for the persistence and stability of the marsh wren (*Cistothorus palustris*) and the ovenbird (*Seiurus aurocapillus*) in the NAESI pilot project study area in the united counties of Stormont, Dundas, and Glengarry.

Marsh Wren

For the base scenario of the demographic marsh wren population model and a simulated time of 100 years we found a final minimum viable population size (MVP) of 421 males. MVP size decreased to 182 males when the simulation time was 50 years. In the spatial model version we then used available land cover data to delineate the current distribution of marsh habitat in two 200 km^2 case study areas in the NAESI pilot project area. Based on the demographic and spatial analysis we propose the following habitat-based standards in order to achieve longer term persistence and stable population trends for the marsh wren in agricultural regions of eastern Ontario: *(1)* a minimum viable patch size of ~114 ha assuming that all individuals reside in one patch/population, *(2)* a minimum metapopulation patch size of ~1.7 ha to avoid patches being a strong population sink, *(3)* a minimum of 0.2% - 1.2% marsh habitat on a 200 km^2 landscape scale (depending on the patch size distribution), and *(4)* a maximum distance of 2-3 km to the

nearest patch to allow sufficient natal and breeding dispersal.

Ovenbird

In the second part of this report we analyzed habitat suitability and population viability of the ovenbird. By applying a demographic population model we found a MVP size of 89 adult female ovenbirds. Due to the large extent of the NAESI pilot project study area we selected three 200 km^2 case study areas. The results from the HS model and the spatial PVA indicate that all three metapopulations have a high risk of extinction and strongly negative population trends. We conclude that the current amount of forest cover and the relatively small patches of deciduous and mixed forests in the united counties of Stormont, Dundas, and Glengarry do not support persistent ovenbird populations. We propose that the entire pilot project study area may act as a population sink and is only maintained if a sufficient number of birds immigrate from outside. To find habitat-based thresholds we then generated three hypothetical landscape scenarios with higher suitable forest cover and larger patch sizes. We found that the proportion of sink vs. source population patches and the respective size distribution of source patches was a strong predictor of ovenbird viability. We propose the following habitat-based standards that need to be fulfilled in order to achieve longer term persistence and near stable population trends for ovenbirds in fragmented agricultural areas of eastern Ontario (assuming no immigration from outside): *(1)* a minimum viable patch size of ~742 ha assuming that all individuals reside in one patch/population, (2) a minimum metapopulation patch size that allows a minimum intrinsic growth rate of 1.0 (~100 ha in this study), *(3)* a minimum of 30-40% suitable forest cover on a 200 km^2 landscape scale (depending on the patch size distribution), and *(4)* for near stable population trends a minimum proportion of ~50% source patches with a minimum source patch size that facilitates 100% pairing success (250 ha in this study).

1 GENERAL INTRODUCTION AND MODELING APPROACH

A hierarchical modeling framework has been established in the first project phase of the National Agri-Environmental Standards Initiative (NAESI) (see Baldwin et al., 2006). The aim of the overall modeling strategy is to facilitate the development of habitat-based biodiversity standards based on population viability analysis (PVA) and habitat suitability modeling for a selected set of surrogate species. For this purpose a suite of 10 surrogate species has been identified by NAESI project team members representing important ecological functions and processes in the NAESI pilot project region as well as ecosystem services of the habitat types that these species are associated with. The species analyzed in this study include the marsh wren (*Cistothorus palustris*) and the ovenbird (*Seiurus aurocapillus*). The marsh wren has been identified as a surrogate species for shallow and deep marsh wetlands. This wetland obligate species depends on medium to larger sized expanses of cattail marsh with some open water. The ovenbird has been identified as a surrogate species for larger tracts of mature deciduous forests.

The methodological approach presented here comprises two major steps: a demographic population model and a spatial PVA that is linked with a habitat suitability (HS) model. The demographic model focuses on a single population, i.e. all individuals in the populations are considered to be spatially connected. Non-spatial models are useful in identifying potential demographic thresholds and minimum viable population (MVP) sizes necessary for a single population to persist for a given time period. The MVP size, in combination with observed population densities or home range sizes, can be used to identify suitable, single habitat patches that may support viable populations.

Even if it is possible to estimate the MVP size that is required to support a viable population, it is unknown whether a given metapopulation is actually viable in a spatially structured landscape. Therefore a spatial-explicit PVA is required for assessing landscape-scale effects on population viability. Although demography plays a crucial role, the probability of metapopulation persistence is also strongly affected by the amount and spatial arrangement of habitat patches (Gu and Verboom, 2004). Generally, a metapopulation experiences a higher risk of extinction if it is spatially fragmented. However, this does not necessarily apply to metapopulations that are affected by disturbance regimes or strong habitat turnover. Also, under strong environmental stochasticity spatially separated populations may be advantageous for metapopulation persistence, especially if spatial autocorrelation is low.

Divided into two major sections this reports begins with a detailed introduction to the life-cycle, habitat requirements and demography of both species. This structure aims at facilitating the understanding of how and why specific model parameters have been chosen. A non-spatial population model will be used to understand the general (demographic) behavior of the model and assess and analyze MVP for different scenarios. Subsequently, a spatial PVA with information on dispersal and metapopulation structure is used to analyze viability patterns for the current landscape.

The overall goal in this study is to detect landscape conditions which faciliate relatively stable population trends and low extinction risks for marsh wren and ovenbird metapopulations. These two population targets (i.e., stable and viable populations) will be assessed by means of three model outputs: (i) extinction risk (or extinction probability), (ii) expected minimum abundance (EMA, i.e. the minimum abundance for each simulation run averaged over all runs) and (iii) the population trend or effective growth rate (calculated as abundance in the final year divided by abundance in the initial year). The two PVA's were developed using the software package Ramas©GIS and the ArcView GIS 3.2 environment with the Spatial Analyst extension. Land cover data and background material were kindly provided by Spatialworks and the NAESI project team.

Based on these analyses we propose a set of habitat-based standards which include: (i) habitat amount (i.e., the total amount of habitat required at a certain spatial scale), (ii) distance to nearest patch (i.e., the maximum tolerable distance between two neighboring population patches), and (iii) minimum patch size needed to ensure viable and ecological functioning populations. Even though these standards are subject to a high degree of uncertainty they may serve as a target for the long term viability of both species and persistence of related ecological processes and functions in agricultural landscapes of eastern Ontario. The suggested spatial standards for both species are based on metapopulation dynamics investigated at a 200 km^2 landscape scale. In order to generalize these standards for larger management scales one option may be a GIS moving window analysis that calculates whether the recommended habitat-based standards are fulfilled in each 200 km^2 block. This technique would generate a surface map indicating areas where standards are not met and significant habitat improvements need to be done.

Uncertainty

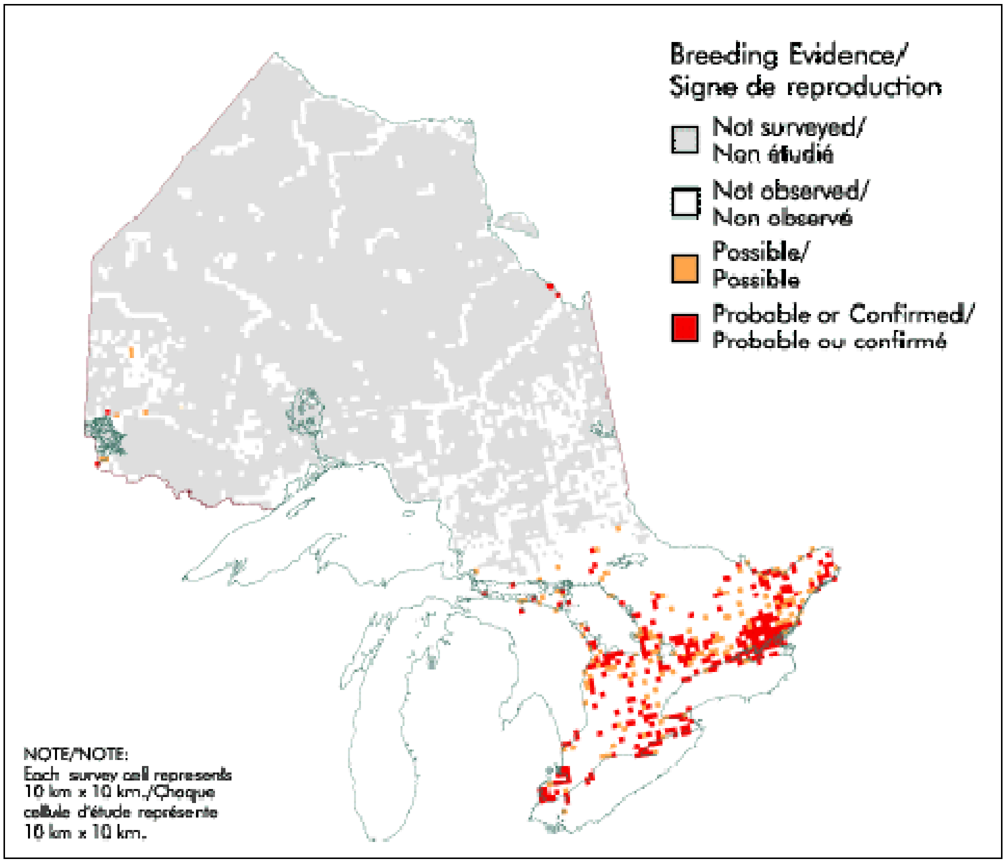
The results provided in this report are subject to an unknown degree of uncertainty. There is substantial uncertainty in the knowledge of demographic data, such as fecundity, survival and dispersal distances. There is also uncertainty in the habitat suitability models, which may be reflected in an incorrect habitat suitability map. This uncertainty and its propagation over time are partly considered in the demographic and environmental stochasticity of the population model.

Due to the stochastic nature of the population models, simulation runs were replicated up to 1000 times and results are averages out of those replicate simulation runs. Absolute numbers should be interpreted with caution. Instead trends and differences between different simulation runs (scenarios) are generally more trustworthy. All information used in this work is based upon expert knowledge and scientific, peer-reviewed literature. The work therefore represents our best possible educated “guess” based on our current knowledge of the biology, life history and habitat requirements for both species

2 MARSH WREN (*CISTHOTORUS PALUSTRIS*)

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). Marsh wrens are sexually monomorphic in appearance and eat mostly insects, and occasionally snails, both of which they glean from the surface of vegetation (Burns, 1982). Migratory populations of the marsh wren breed throughout the northern half of the United States, southern Canada, and in coastal areas as far south as Florida and winter in the southern United States and Mexico, favoring coastal areas. In southern and eastern Ontario marsh wren usually inhabit freshwater cattail marshes. In the project study area in the united counties of Stormont, Dundas, and Glengarry within the Eastern Ontario Model Forest the marsh wren is relatively common (Figure 1). To our knowledge no PVA or other population modeling efforts have been conducted for the marsh wren so far.

Figure 1: Distribution of the marsh wren in Ontario (Source: Project Wildspace, Environment Canada).



2.1 Demography and habitat

Habitat requirements

In southern Ontario marsh wrens usually return around mid May with males arriving at the breeding areas before the females. Marsh wrens usually nest in association with bulrushes, cattails, and sedges. Nests are found near standing water from several centimeters to a meter deep. Water is necessary to provide a source of food and as a defense against predators. Most studies indicate that marsh wrens use areas supporting relatively dense emergent vegetation for territories and nesting. The lowest mean percent cover of emergent vegetation recorded for territorial males in Washington was 50%. Coverage of emergent vegetation in other territories in other marshes ranged from 57% to 100% (Gutzwiller and Anderson, 1987). Marsh wrens tend to avoid areas of abundant woody vegetation. Therefore high tree or shrub densities are assumed to lower the value of a wetland for nesting marsh wrens (Gutzwiller and Anderson, 1987).

Breeding and migration period

The marsh wren is a year-round resident in some southern and coastal maritime regions where marshes do not freeze (Gutzwiller and Anderson, 1987). The timing of return of migratory populations to their breeding grounds varies across North America. Resident populations in Seattle, Washington may begin building nests as early as February while further east migratory populations at Turnbull, Washington begin nest building in April (Verner, 1965). In southern Ontario marsh wrens usually return around mid May with males arriving at the breeding areas before the females to establish territories (Environment Canada, 2005). Generally, migratory marsh wrens arrive on their breeding grounds from April to early May and depart from mid-August through October (Zimmerman et. al., 2002) (see Table 1).

Territory size

The marsh wren is a highly territorial species (Schriml, 1993) with territories including both nest sites and foraging areas. Both sexes normally remain within the territory but will occasionally forage off their territory, especially in undefended locations (Verner, 1965). Marshes smaller than 0.40 ha are usually not used by breeding marsh wrens. In Iowa, Marsh Wrens have been found to be present in all wetland size categories (<5 ha, 5-20 ha, and >20 ha). In Manitoba, Marsh Wrens were present in wetlands of all size categories studied, ranging from <1 to 19.3 ha. In Alberta, Marsh Wrens were present in wetlands ranging from 1 to >8 ha (upper size limit not given) (Zimmerman et al., 2002). In the study conducted by Metz (1991), male territories were found to be separated by distances > 30 m.

The average male territory size ranges from 0.006 to 0.17 ha, depending on the habitat and conditions of the year (see Table 1). A study conducted in Manitoba found the mean territory size of 13 males on one site to be 0.08 ha. On the other site the mean territory size of 16 males was 0.11 ha. In Minnesota, it has been suggested that marsh wren territories are about 0.03 ha. Where as, in Washington, territory size was found to vary from 0.005 to 0.34 ha (Zimmerman et al., 2002). Territory size is quite variable and no significant correlation between pairing success of males and their territory sizes has been found (Gutzwiller and Anderson, 1987, Verner and Engelsen, 1970). However, Verner (1964) suggested that there is evidence that the size of a male's territory and the total amount of emergent vegetation in it are correlated with his success in acquiring mates.

There is a trend in polygynous populations for polygynous males to defend larger territories than monogamous males or males that end up as bachelors. Bachelor, monogamous, and bigamous marsh wren territories were found to be on average 0.08 ha, 0.13 ha, and 0.17 ha respectively (Gutzwiller and Anderson, 1987). It has been suggested that bachelors may usually be first-year males that have not yet learned many of the important factors of efficient marsh exploitation, including the best nesting cover. It may follow that with experience bachelor males may gain better territories and learn that cattails provide better nest support and cover (Verner and Engelsen, 1970). It has also been suggested that the proportion of a male's territory covered by emergent plants is a criterion used by female marsh wrens for mate selection. Marsh wrens tend to use denser areas of cattails because nest structure usually requires several stems for attachment (Gutzwiller and Anderson, 1987).

There is evidence that the territory size of Marsh Wrens may be affected by interspecific competition with Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). Marsh Wren territories significantly increased in size following the departure of Yellow-headed Blackbirds from early to mid-July. Territories expanded into portions of the wetland with deeper water, which were areas formerly occupied by Yellowheaded Blackbirds (Zimmerman et al., 2002).

Site fidelity, dispersal, and return rates

It is unclear whether marsh wrens have high breeding-site fidelity or not. Since marsh wrens have a high apparent annual mortality (adults: 32% mortality, juveniles: 70% mortality) and a life span of approximately 2 years it is possible that the low site fidelity evidenced in some studies is just an indication of high mortality rates.

One report suggested that marsh wrens use the same breeding area year after year (OMNR, 2000). While studies by Leonard and Picman (1987) suggest that breeding-site fidelity is low. Zimmerman et al. (2002) provide examples that lend support to the idea that marsh wrens have low site fidelity. They found that in Manitoba, 10% of 41 marked males returned to the same wetland in the second year of the study and 7% of 28 males returned in the third year. Only one of 540 marked young returned to the banding area. In Washington, 17% of 76 adult males returned to the study site the following year. Of these 13 returning males, mean distance between breeding territories from one year to the next year was 386 m, and five males held the same territory as the previous year. Based on 10 first-year males, average distance between rearing territories and first breeding territories was 1951 m. Only one of the 10 males had its breeding territory on the same lake where it was reared (Zimmerman et al., 2002). This study found that mean dispersal distances for yearling verses adult males are significantly different (Gutzwiller and Anderson, 1987).

The low return rates of adult males and yearlings were also evidenced in a study conducted by Leonard and Picman (1987). In, 1984 they found that 10% (2/19) of marked males returned to one site and 9% (2/22) to another site. Seven percent (2/28) returned to the first site in, 1985, but no marked males were observed at the other site that year. Males that returned settled either on or within 100 m of their previous territories, with one exception. Return rates of yearlings were extremely low. Only 1 of 540 banded nestlings was observed in the study area in a subsequent year. This yearling male held two different territories in succession at one of the sites in the, 1985 season. The first was approximately 140 m from his natal territory and the second was within 40 m (Leonard and Picman, 1987). Due to the low return rates for marsh wrens it can be suggested that if the male survives the winter it will return to, or close to, its previous territory.

Nesting

Male marsh wrens build multiple domed nests out of cattail leaves on their territories which collectively comprise the "courting centers” (Metz, 1991, OMNR, 2000). Males sing and display to females from the courting center while little foraging is done there. Little singing is done in the foraging areas (Verner, 1965). Males build from 11 to 32 nests in their territory but only one is chosen by the female as a nest site and occasionally, new nests are built by females (Zimmerman et al., 2002). Another study found that male marsh wrens build between 2 and 12 nests on their territories (Metz, 1991). There does not appear to be a minimum number of nests that males need to build before attracting a mate (Metz, 1991). It is suggested, that multiple nests may increase nest success by decreasing the probability that a searching predator will find an active nest (Zimmerman et al., 2002). It has also been suggested that tall, dense vegetation and deep water may provide protection from mammalian predators. Leonard and Picman (1987) found proportionally more successful nests in the site with denser vegetation and deeper water and successful nests in both sites where there was significantly denser vegetation and deeper water than unsuccessful nests.

Usually, the number of nests a male builds far exceeds the number of females attracted to the territory. Metz (1991) notes that “according to the sexual-selection hypothesis, females gain information about male vigor and territory quality, or both, from the number of nests a male is able to build”. It also appears that bigamy and monogamy are related to sites rather than to males. Thus, a male's pairing success is related to the habitat he occupies (Verner and Engelsen, 1970). Leonard and Picman (1987) found no relationship between male quality and female choice in the population they studied. This suggests that females probably rely on features of the habitat when selecting a nesting area (Leonard and Picman, 1987).

Cattail is the preferred nesting cover as long as it still has standing water around the bases of the stalks and females tend to prefer those nests as well. Once the cattail stands dry out, the birds use bulrush stands for nesting cover (Verner and Engelsen, 1970, Verner, 1965, Gutzwiller and Anderson, 1987). A common characteristic of nest-support vegetation is several erect and closely spaced stalks or limbs that together provide the strength to support a bulky nest at least several cm above the water. Cattails and cordgrasses are commonly used by nest-building marsh wrens (Gutzwiller and Anderson, 1987). Females sometimes build the breeding nest or at least initiate its building if one of the other nests is not selected; lining of the breeding nest is usually done by the female wren (Verner, 1965). Male marsh wrens continue to build nests even after females have begun to incubate establishing a new courting center on his territory from which to attract mates (Verner, 1965, Metz, 1991).

Bigamous and monogamous males seem to nest in cattails much more frequently than if they had simply used cattails in proportion to their availability (Gutzwiller and Anderson, 1987). Permanent water through the breeding season is generally required as standing water seems to provide important protection from predators as well as abundant food resources (Verner and Engelsen, 1970, Gutzwiller and Anderson, 1987). Water depth under nests often ranges from a few centimeters up to a meter (5 cm to 91 cm) (Zimmerman et al., 2002).

In Ontario, Marsh Wrens most commonly nest in stands of cattail. Elevated nests were most often found in cattail (38% of 476 nest records) and less often in bulrush, grass, sedge, horsetail (*Equisetum sp*.), burreed, loosestrife (*Lythrum salicaria*), spiraea (*Spiraea*) or willow (*Salix*) (Zimmerman et al., 2002). The height of nests ranges from 0.2 to 1.5 m above water and the vegetation supporting nests is usually dead (Zimmerman et al., 2002). Another study found nest height to be at least 38.1 cm above ground with an average above ground height of 83.8 cm. Mean nest heights have also been found to vary from 76.2 to 92.7 cm above the marsh floor in cattails and bulrushes and other study found nest heights to range from 0.5 m to 2.0 m above the marsh (Gutzwiller and Anderson, 1987). Nests are sometimes adjacent to open water or located some distance away (Zimmerman et al., 2002).

There is conflicting evidence about whether having more nests attracts more females. Metz (1991) found that dummy nests did not appear to attract females or reduce predation in the study area. They note that “female Marsh Wrens did not preferentially nest on territories with more dummy nests or with high-density courting centers” (Metz, 1991). Contrary to this study, Verner and Engelson (1970) found a positive relationship between the number of nests built by male marsh wrens and the number of females to whom they were mated.

Table 1: Summary of demographic parameters for the marsh wren.

Parameter / Characteristic	Observation / Parameter range	Reference
Breeding period (ON)	Arrival on breeding grounds: April - early May; Depart: mid-August – October Southern Ontario return: mid May	Zimmerman et al., 2002, Environment Canada, 2005
Clutch Size (mean, variation)	Clutch size and number of clutches per year vary with latitude and climate 4.5; 6.0±0.19SD; 5.8±0.8SD	Leonard and Picman, 1987, Metz, 1991, Environment Canada, 2005
Broods/year	In southern and eastern Ontario usually 1-2	Environment Canada, 2005
Incubation period	2 weeks	Kale, 1965, Verner, 1965
Fledging period	2 weeks (nestling period) age of fledging 12-14 days	Kale, 1965, Verner, 1965
Maturity	Both sexes usually commence breeding in the first year following hatching; age of sexual maturity 1 year	Leonard and Picman, 1987
Life Span	Adult marsh wrens life span of ~ two years, usually breed for one season due to high over winter mortality	Schriml, 1993
Parasitism	Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) is rare due to the Marsh Wren's characteristic dome-shaped nest and small entrance hole; High rates of intraspecifc nest destruction by male and female marsh wrens have been demonstrated; Red-winged blackbirds aggressively suppress the singing activities of marsh wrens	Zimmerman et al., 2002, Environment Canada, 2005, Schriml, 1993, Gutzwiller and Anderson, 1987
Fledging Success	0.8-1.5 mean number of fledglings (Reproductive success, 1992, 1993); 0-3.38 mean number of fledglings (Reproductive success, 1979, 1982); number of fledge/active nest 3.4±3.4SD; # fledge/successful nest 4.5±1.3SD, 5.1±1.2SD; Fledging success for sedge wrens (number of young fledged per number of eggs laid) has been reported at 0.67 in Minnesota	Schriml, 1993, Leonard and Picman, 1987
Nesting Success	in three out of four over 50% of the active nests were depredated while less than 35 % of the active nests were successful; Sedge Wren: Nest success (nests with at least one egg hatching) was reported at 68% (n = 31 nests) and 69% (n = 18 nests)	Schriml, 1993, Burns, 1982

Table 1: Summary of demographic parameters for the marsh wren.

Parameter / Characteristic	**Observation / Parameter range**	**Reference**
Population density / Carrying capacity	For Canada (Manitoba) mean territory size for males was 0.08 ha and 0.11 ha respectively; in other regions varying densities have been recorded: 48.3±5.3SD pairs/ha; densities up to 238 wrens per 40 ha in prime cattail/bulrush habitat along the Colorado River; Densities as high as 120 adult birds per hectare	Kale, 1965, Verner, 1965, Zimmerman et al., 2002, Leonard and Picman, 1987
Stage/Age classes	2 (juvenile, adult)	-
Annual survival for adults, juveniles	Annual mortality rates (percent): adult: 32%, juvenile: 70%	Kale, 1965
Dispersal/ Migration	Short distance and neotropical migrant; Mean distance between breeding territories from one year to the next year was 386 m for adult males; Average distance between rearing territories and first breeding territories was 1951m; If males did return they settled either on or within 100 m of their previous territories; Fledglings move about in small groups until migration occurs	Environment Canada, 2005, Zimmerman et al., 2002, Leonard and Picman, 1987
Average Territory Size/population density	0.006 to 0.17 ha; mean = 450 m^2; 0.5 ha – Territory; 0.5 ha - home range; Male territories were separated by distances > 30 m; average male population density of 0.27 ha/male for cattail marsh in Manitoba	Leonard and Picman, 1987, Verner and Engelsen, 1970, Environment Canada, 2005, Metz, 1991
Polygyny	Males mate with between 2 and 3 females; the proportion of polygynous males may be up to 50% in southern Canada	Metz, 1991, Schriml, 1993
Sex ratio	1.00:1.09; Ratio skewed in favor of females (1979 (1:1.62), 1982 (1: 1.37), 1993 (1: 1.6)); polygny was found to be common but the sex ratio did not differ significantly from unity (1.00:1.09)	Verner and Engelsen, 1970 Schriml, 1993, Verner and Engelsen, 1970
Known trends in population size for Eastern Ontario?	unknown	-

Clutch size, nesting and fledging success

Clutch size and number of clutches per year vary with latitude and climate. Clutch size tends to range between 4 and 6 eggs (Metz, 1991, Environment Canada, 2005) (Table 1). Eggs are laid at a rate of one per day until the clutch is complete (Verner, 1965). Marsh wrens can have 2 to 3 broods per year, but in places with shorter breeding seasons, like Ontario, they usually only have one (Environment Canada, 2005). Verner (1965) found that birds in Seattle, Washington can easily rear 3 broods in a season while birds at Turnbull, Washington (225 km due east of Seattle) were limited to 2.

Both male and female marsh wrens commonly destroy the eggs and kill the nestlings of conspecifics and other marsh-nesting passerines (Leonard and Picman, 1987). Re-nesting after the failure of an initial clutch and after fledging young are common (Burns, 1982, Zimmerman et al., 2002). Marsh Wrens will use one of their multiple nests for re-nesting after the destruction of the initial nest (Zimmerman et al., 2002).

The incubation period lasts about 2 weeks, as does the nestling period. Verner (1965) observed that incubation is done solely by the female. Most reports indicate that male marsh wrens provide little or no parental care (Schriml, 1993, Burns, 1982). Nest-building and continual defense by male wrens of territories with abundant food may compensate females for a lack of male parental care of offspring.

In a study of the sedge wren (a similar species) nest success (nests with at least one egg hatching) was reported at 68% (n = 31 nests) and 69% (n = 18 nests). This relatively high nest success is expected for passerines nesting in enclosed nests. Sources of nest loss include predation, infertile clutches, heavy rainfall, trampling by grazing cattle, and nest destruction by other sedge wrens (Burns, 1982) Of nests lost to all causes for marsh wrens, Leonard and Picman (1987) found 44% were lost due to mammalian predators, 27% due to other wrens, 11% due to weather, 8% due to nest abandonment, and 13% unknown. Most (79.9%, 373/468) mortality occurred during the egg stage with egg predation accounting for 50.4% (188/373) of all egg mortality (Leonard and Picman, 1987). Gutzwiller and Anderson (1987) found that nesting success in marsh wrens improves with increased distance between marsh wren breeding nests and the nearest red-winged blackbird nest (red-winged blackbirds aggressively suppress the singing activities of marsh wrens). Thus, the predator density, breeding marsh wrens, and red-winged and yellow headed blackbirds in a marsh may significantly influence habitat suitability for marsh wrens (Gutzwiller and Anderson, 1987).

Fledging success for sedge wrens (number of young fledged per number of eggs laid) has been reported at 0.67 in Minnesota. Fledging success depends strongly on nest location; nests in denser vegetation and over deeper water are less vulnerable to predation (Leonard and Picman, 1987). Fledglings often move about in small groups until migration occurs. They will also frequently roost as a brood in the breeding nest or in one of the male's courting nests for several nights after fledging (Verner, 1965). Verner (1965) found that "most broods remain close to the breeding nest until completely independent, at which time small groups of juveniles, combined from various nests, move throughout the marsh." For Delta, B.C. Schriml (1993) found a high variation in the number of fledglings per nest. For example, for the years 1979 and, 1982 fledglings per nest were 2.24 (SD 2.3) and 1.05 (SD 1.75) for a harem size of 1 and 2.64 (SD 2.3) and 0.99 (SD 1.62) for a harem size of two, respectively. In this study fledging success increased significantly with harem size. In the study of Leonard and Picman (1987) number of fledglings per nest attempt was 3.4.

Mating system, polygyny and sex ratio

Polygamy is especially common in the genus *Cistothorus*, reaching its peak with the marsh wren. Marsh wrens exhibit polygyny at levels ranging from 30-50% (Burns, 1982,Verner, 1964).

Verner (1965) suggested that all males attempt to become polygamous but not all are successful. About one-third of the breeding males have more than one mate and several cases of trigamy have been reported for marsh wrens (Burns, 1982). It has also been suggested that the shape of territories may influence the mating system; long, narrow territories may reduce polygyny because the male must continually fly back and forth between the ends of his territory (Verner, 1964).

Marsh wrens frequently mate polygynously, although the proportion of polygynously mated males in a population varies from marsh to marsh (Metz, 1991). Some males mate with between 2 and 3 females in a season. The degree of polygyny in marsh wrens has been found to vary greatly among populations: 2.4 % in Georgia salt marshes 12.5% in Washington State, and 44 % in Delta, Manitoba (Schriml, 1993). Schriml (1993) notes that males need to maximize their effort in one breeding season due to low survival rates.

Generally, a female skewed sex ratio may increase the likely hood of polygyny and even sex ratios and high population densities may decrease polygyny (Schriml, 1993). Schriml (1993) found female-skewed sex ratios varying from 1.37 to 1.62 over three years. In contrast, in a study conducted by Verner and Engelsen (1970) polygny was found to be common but the sex ratio did not differ significantly from unity (1.00:1.09).

2.2 Non-spatial population model

Data on demography and population biology of the marsh wren have been compiled on the base of published data. Table 2 shows the parameter values used for the non-spatial version of the population model where only a single, hypothetically isolated population is considered. As density dependence type we chose the ceiling type in Ramas©MetaPop where the growth rate *R* decreases below 1.0 when the carrying capacity *K* is reached (Figure 2). Each simulation run starts with an initial population size equal to the carrying capacity *K*. We used four stage classes to account for the polygynous mating system of the marsh wren (juvenile and adult stages for each sex). In terms of the number of fledglings per female we chose the data set provided by Schriml (1993) from marshes in Delta, BC. Average fledgling rates for monogamous and polygynous females in this study were reported to be 1.76 fledglings per female. As expected for the polygynous mating system of the marsh wren Schriml (1993) found a biased sex ratio of 62% females. In the model the fecundity in the stage matrix is then calculated as the product of the average number of broods per year, the average number of fledglings and the proportion of female vs. male in the population. This calculation results in an adult fecundity of 1.64 for juvenile females and 1.0 for juvenile males (see Table 2). Both fecundity and survival rates were assigned a high standard deviation based on known variations from empirical data.

Figure 2: Change in the growth rate *R* with population size based on the stage matrix. The ceiling type density dependence assumes that *R* equals 1.0 once the carrying capacity K has been reached.

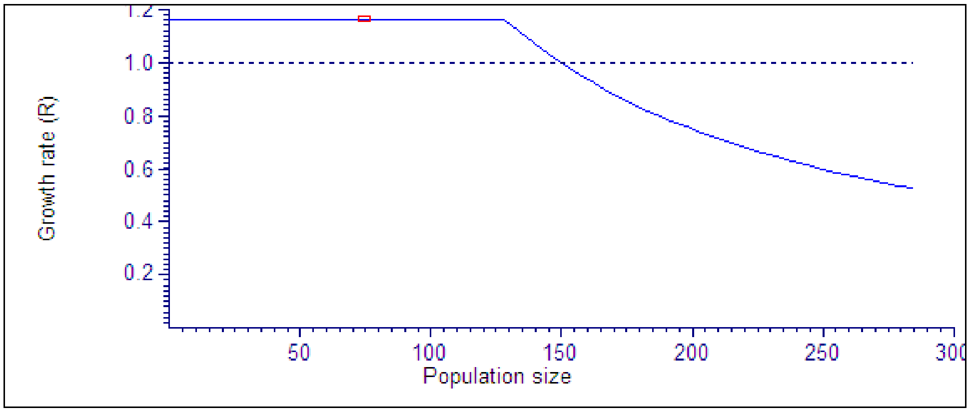


Table 2: Model parameters for the non-spatial marsh wren population model.

Parameter	Value/Range	Comments
Stage classes	4 (female and male juveniles; female and male adult)	Due to polygyny and female-skewed sex ratio 2 stage classes for each sex
Polygyny	3	Each male can mate with up to three females at each time step
Fledglings	1.76	Average number of fledglings per female for 1979 (good year) and, 1982 (poor year) for different harem sizes from Delta, BC (Schriml, 1993)
Proportion of females	0.62	Average value based on three years from Delta, BC (Schriml, 1993)
Adult fecundity (female juveniles per female adult)	1.64 (SD 0.82) (=50% CV)	1.5 * (broods) *1.76 (fledglings) * 0.62 (sex ratio)
Adult fecundity (male juveniles per female adult)	1.0 (SD 0.5) (=50% CV)	1.5 * (broods) *1.76 (fledglings) * 0.38 (sex ratio)
Juvenile survival	0.3 (SD 0.075) (=25% CV)	Kale (1965)
Adult survival	0.68 (SD 0.17) (=25% CV)	Kale (1965)
Initial abundance	10-100	Number of individuals at t=1
Carrying capacity	Same as initial abundance	Number of individuals at which the carrying capacity is reached
Density dependence type	Ceiling type	-
Simulated years	10-100 years	-
Replications	1000	-
Demographic stochasticity	yes	Number of survivors and dispersers (emigrants) to be sampled from binomial distributions, number of young from a Poisson distribution.
Environmental stochasticity	lognormal	statistical distribution to be used in sampling random numbers for vital rates
Dispersal	No	-
Disturbance	No	-

A typical simulation run and the average predicted population abundance for a population that is viable for a time frame of 100 years are shown in Figures 3 and 4, respectively. Figure 4 shows stable population dynamics with many outliers, due to the high standard deviation of the fecundity and survival rates. The MVP size for different simulation times (with 95% confidence, i.e. less than 5% of the simulation runs may result in population extinction) is given in scenario 1 in Figure 5. Final MVP for 100 years was 421 males (initial MVP of 680 individuals, i.e., 340 males and females, respectively). This final MVP size decreased to 182 males when the simulation time was 50 years.

However, as both fledgling rate and sex ratio have been reported to vary highly among years we analyzed additional model scenarios as shown in Figure 5. Final MVP size changed from 421 males in the base scenario (scenario 1) to 246 and 1377 final males for a 10% higher and lower fledgling rate, respectively. MVP increased dramatically when a 10% lower fledgling rate was accompanied by an equal sex ratio and no polygyny. This is largely due to the fact that with equal sex ratio less female can produce offspring and the advantage of males mating up to 3 females is offset.

Figure 3: Typical simulation run with an initial population size of 680 individuals (340 males) over a time frame of 100 years

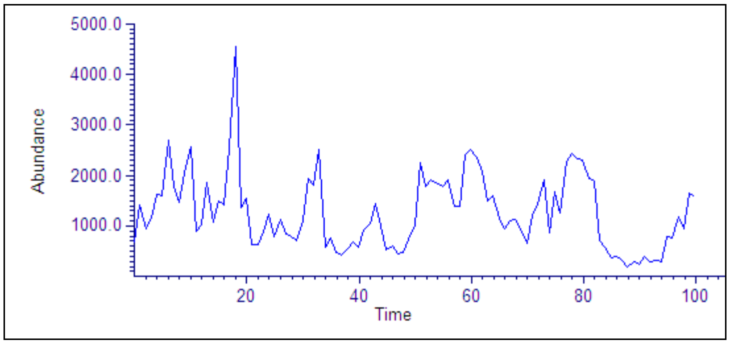
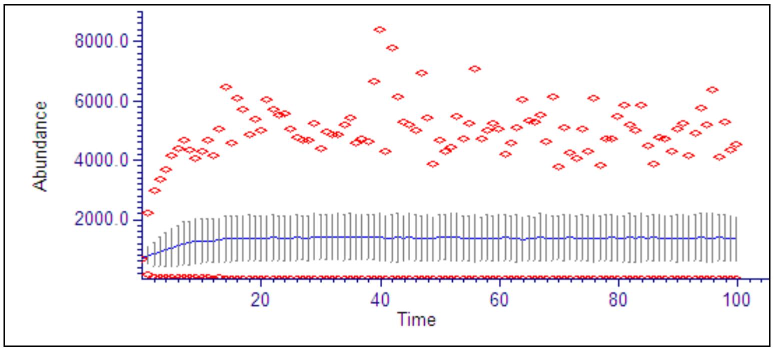
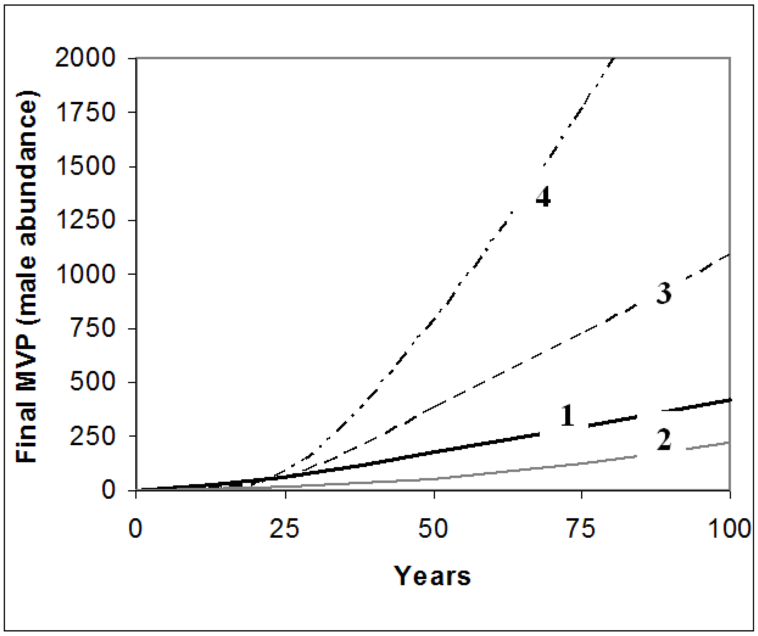


Figure 4: Average predicted population abundance over 100 years for 1000 replicates based on an initial population size of 680 individuals.



The vertical lines indicate the range of the standard deviation and the red trapeziums show the observed maximum and minimum values. A total of 680 initial individuals (340 males) generate a population that is viable with 95% confidence over a time frame of 100 years. Final sex structure after 100 years for this scenario is 421 males and 694 females

Figure 5: Final minimum viable population (MVP) size (number of males) for the marsh wren with 95% confidence (i.e., the MVP needed to ensure an extinction risk of less than 5%). Four scenarios are shown.

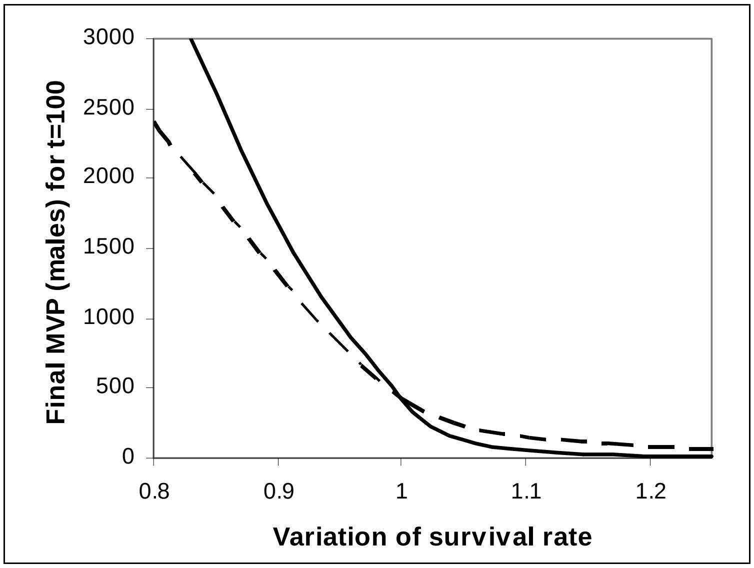


The bold solid line (1) indicates the base scenario with 1.76 fledglings per female on average and a female-skewed sex ratio of 1:1.53. The lower solid line in gray (2) shows MVP for a 10% higher fledgling rate (i.e., 1.94). The dashed line above the base scenario (3) shows MVP for a 10% lower fledgling rate. The uppermost dashed line (4) shows MVP size for a 10% lower fledgling rate with an equal sex ratio and no polygyny. All lines show abundance as the final number of males after X years.

We also evaluated the MVP size with respect to changes in survival rates (Figure 6). In the base scenario of the model juvenile survival is estimated at 30% and adult survival at 68% (see data from Kale, 1965). These high mortality rates reflect the short life span of marsh wren. As mentioned earlier, mortality rates in the marsh wren model reflect the actual proportion of individuals returning to the metapopulation breeding sites after migration. MVP (only males) changed from 421 in the base scenario to 110 when juvenile survival was increased by 15 percent. Changes in adult survival rates showed a threshold-like, non-linear response and were significantly higher: for the same increase MVP decreased to approximately 20 males.

By assessing average population densities the results from the non-spatial model can be used to estimate the amount of breeding habitat required to maintain a single population over a certain time frame. Male territory size is not a useful measure as males use multiple and overlapping territories. Based on a study from cattail marshes in Manitoba we applied an average population density of 0.27 ha/male which is similar to densities reported from eastern Ontario (Leonard and Picman, 1987; see also Table 1). Assuming an average population density of 0.27 ha/male for cattail marshes and a MVP size of 421 males for a time frame of 100 years (with an extinction risk of less than 5%) we can calculate a <u>minimum ‘viable’ patch size of 114 ha</u>. Taking into account the high variability in annual territory size and vital rates this figure is only a very broad estimate and should be used with caution.

Figure 6: Final MVP (only males) for the marsh wren with 95% confidence for a time frame of 100 years. The dashed and solid lines show the response of relative changes in juvenile and adult survival rates for the MVP, respectively. For example, a rate of 1.1 refers to a 10% increase in the adult survival rate from 0.68 to 0.748. The base/standard scenario is where both lines meet.

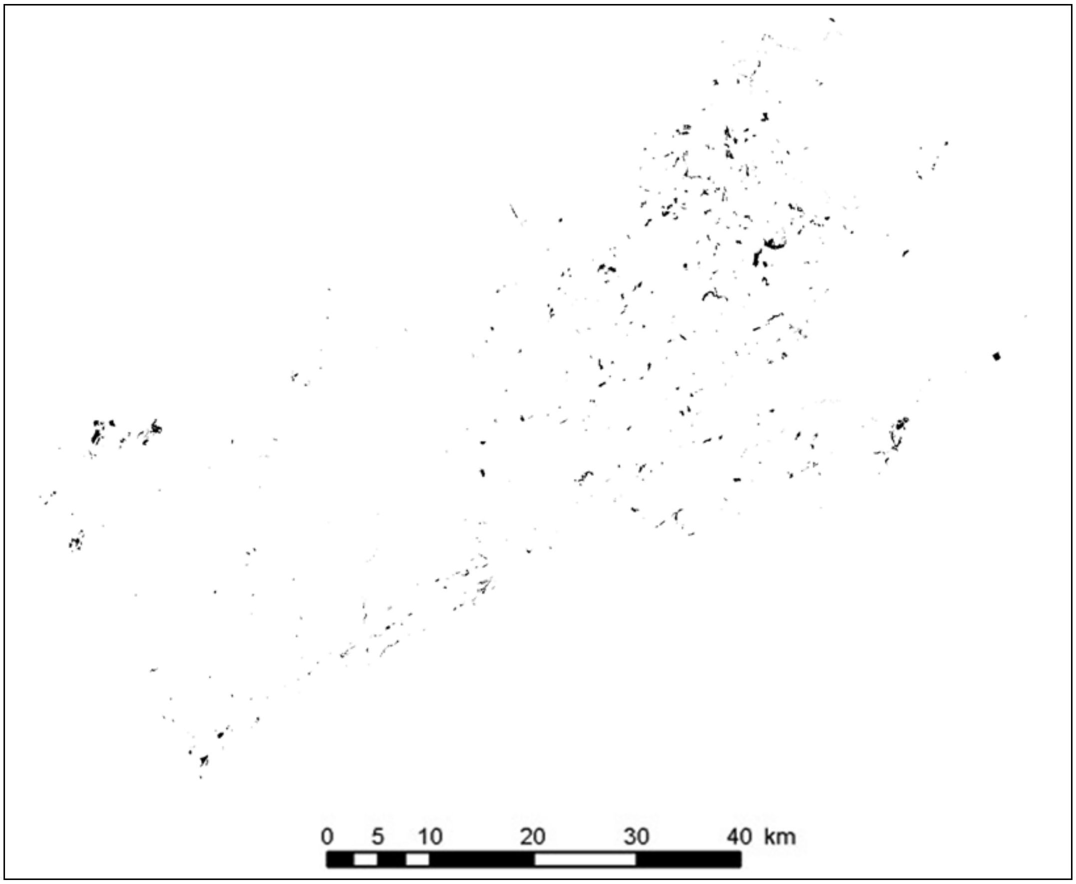


2.3 Habitat suitability model and spatial population viability analysis

The following section deals with the application of a habitat suitability model (HSM) and a spatial PVA to determine habitat-based standards for the marsh wren based on the distribution of marshes in the NAESI pilot project study area in the united counties of Stormont, Dundas, and Glengarry in Eastern Ontario. In a first step we used the land cover data set provided by the Eastern Ontario Model Forest to delineate the distribution of marsh habitat. Marshes cover approximately 0.84% of the NAESI pilot project area. Figure 7 shows an assessment of the spatial distribution of marshes in the NAESI pilot project study area in the easternmost portion of Ontario. Generally, marsh habitat is relatively scattered across the study area. Even though marsh wren habitat quality may be determined by small-scale habitat features such as water levels or cover of emergent vegetation the provided land cover classification did not allow for a finer scale

HSM. We therefore classified habitat as either suitable for the marsh wren when marsh was present and unsuitable when absent.

Figure 7: Scattered distribution of marshes in the NAESI pilot project study area.



2.3.1 *Case study areas and model parameterization*

Due to the aim to analyze a reasonably sized metapopulation structure (and computational constraints of Ramas©MetaPop) we decided to select two case study areas within the overall pilot project area. Study areas 1 and 2 are shown in Figure 8 and have an approximate size of 14.8 * 13.5 km (equivalent to approx. 20,000 ha). Area 1 represents a highly scattered and low density distribution with 8 smaller patches of marshes several kilometers apart. Study area 2 is characterized by a relatively high density of differently sized marsh habitats typical for the north-eastern portion of the united counties of Stormont, Dundas, and Glengarry.

Figure 8: Location of marsh wren case study areas 1 and 2 within the NAESI pilot project study area in the united counties of Stormont, Dundas, and Glengarry (marshes are indicated in black). The NAESI pilot project study area is located in the easternmost portion of Ontario, Canada. Outside of both areas black land cover types indicate urban areas and water bodies. Both study sites are approximately 14.8 * 13.5 km in size (~200 km2).

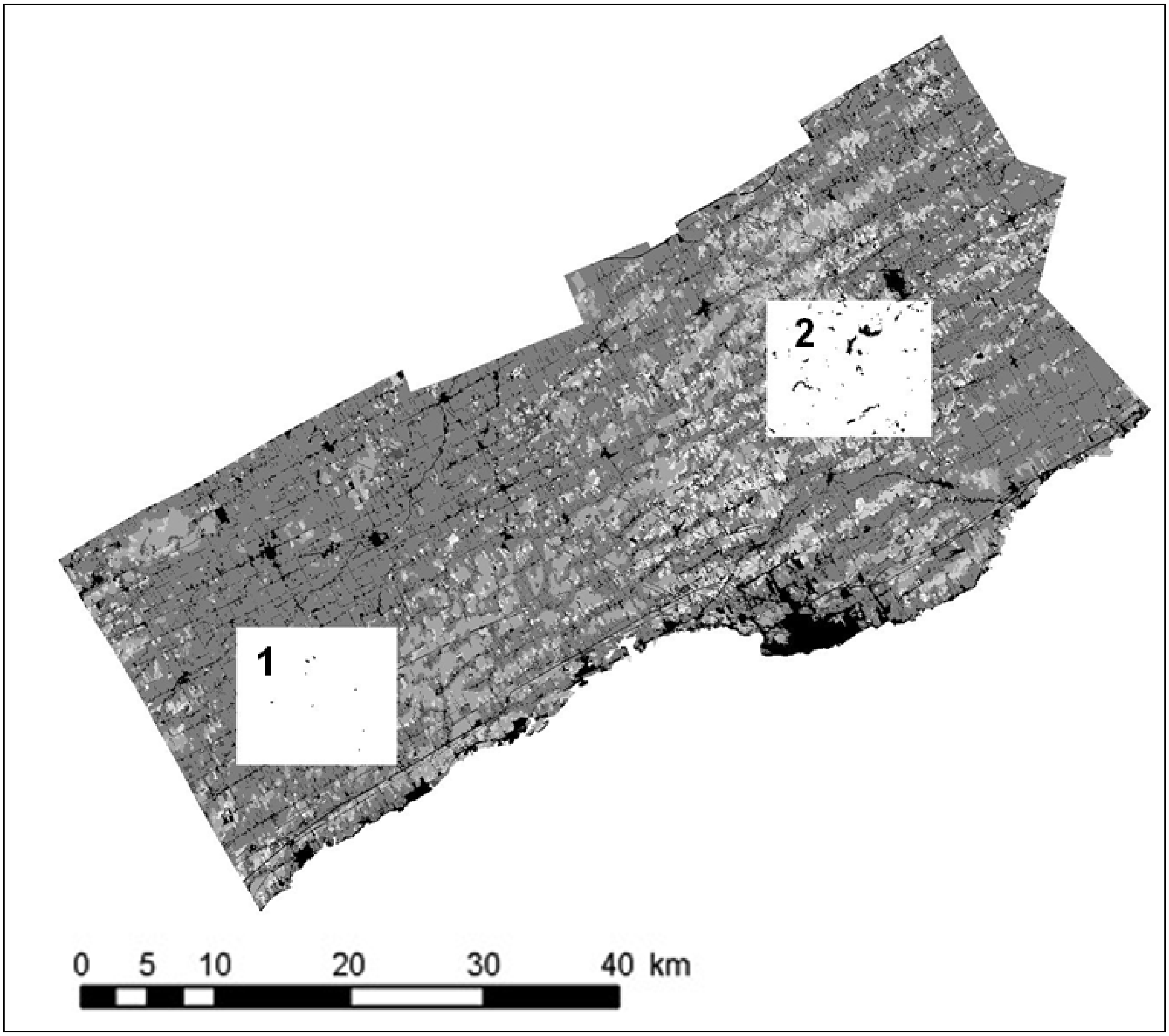
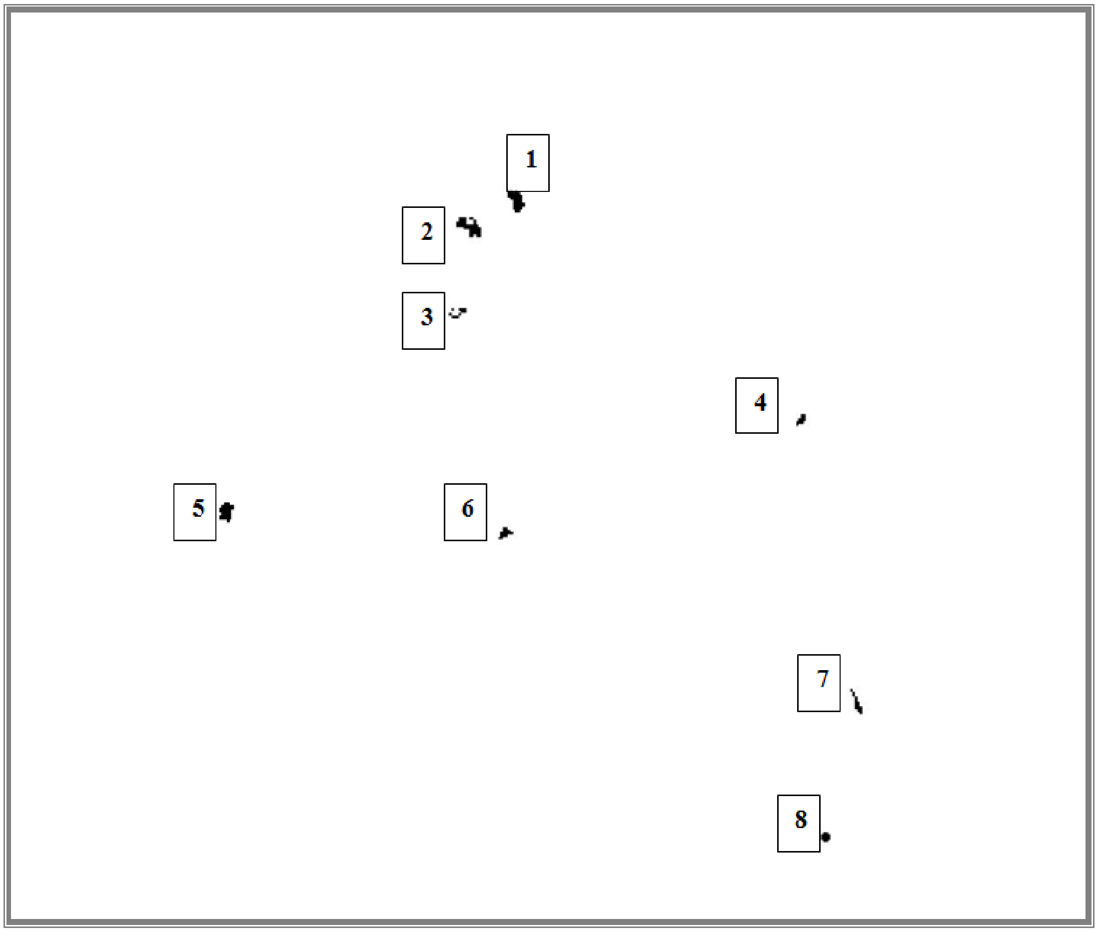


Figure 9: Patch distribution for study area 1. Each ID represents a marsh wren population patch. The spatial extent of study area 1 is approximately 14.8 km * 13.5 km.

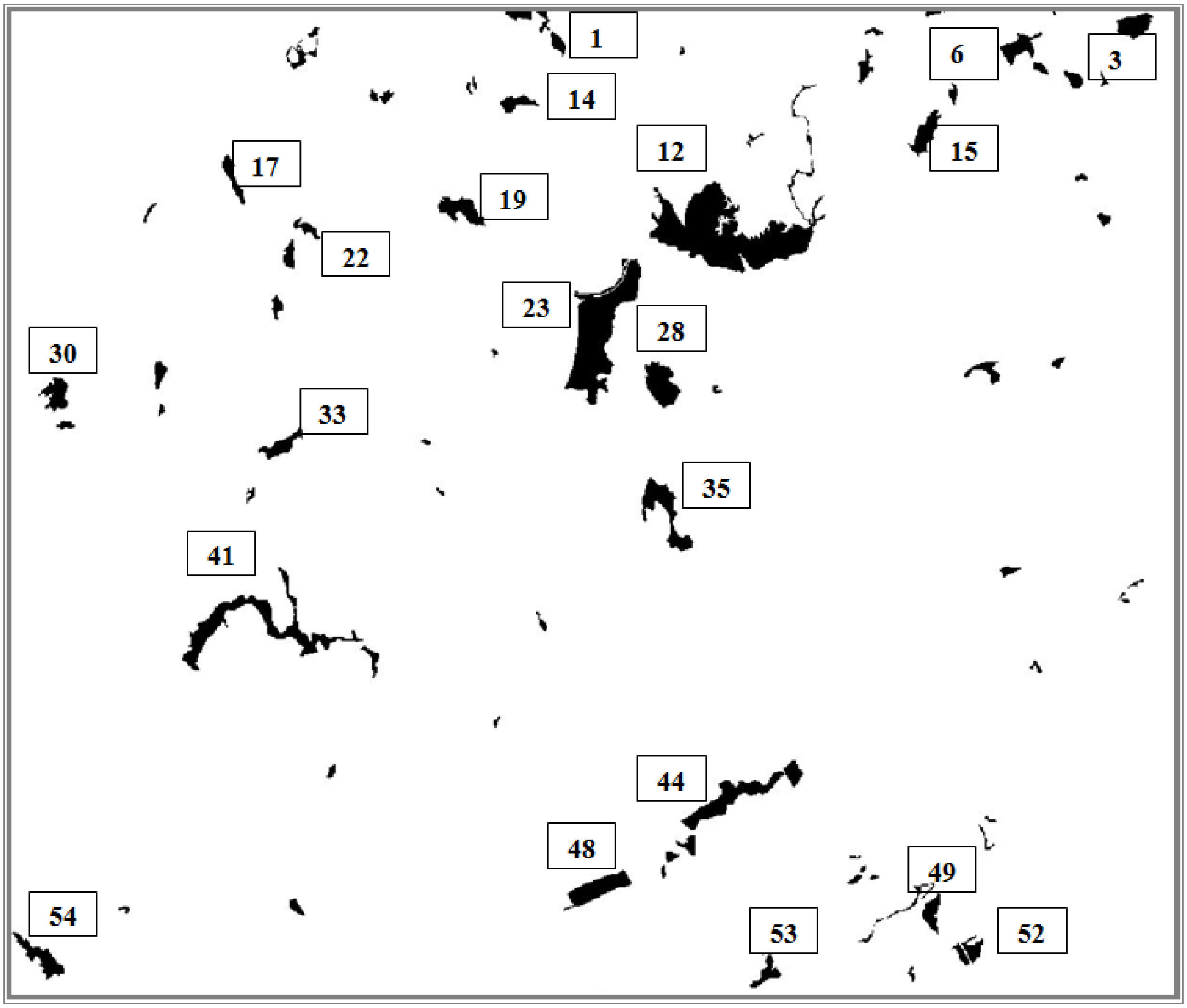


According to Wildspace™ (Envionment Canada, 2005) marsh wren occurrence for most of the NAESI pilot project study area is either confirmed or probable (Figure 1). Based on occupancy data from published studies we assumed that all marsh patches larger than 0.4 ha are potentially occupied (Bent, 1948). For both case study areas we ran a Ramas©GIS analysis that delineates population patches based on the assumption that two distinct marsh wren populations should be separated by at least 300 m of matrix habitat. This assumption is reasonable based on known seasonal movement ranges and territory sizes (Zimmerman et al., 2002).

For study area 1 and 2 we classified 8 and 56 marsh wren population patches, respectively (Figures 9 and

10). Study area 1 comprises approximately 18.46 ha of marshes with an average patch size of 2.31 ha, an average distance to the nearest patch of 2.56 km, an average inter-patch distance of 5.15 km and a total amount of 0.11% marshes (Table 3).

Figure 10: Patch distribution for study area 2 (note that IDs are only given for population patches that are larger than 5 ha). The spatial extent is approximately 14.8 km * 13.5 km.



For study area 2 with approximately 484 ha of marshes we calculated an average patch size of 8.22 ha, an average distance to the nearest patch of 0.54 km, an average inter-patch distance of

6.79 km and a total amount of 2.67% marshes in the landscape (Table 3). Average inter-patch distance is directly related to the spatial scale of a given metapopulation and the total number of patches as the inter-patch distance is the average distance between one patch and all other population patches. This can bee seen in a higher average inter-patch distance for case area 2 with more population patches present in the landscape. The frequency distribution of patch size classes shows that both areas have the highest frequency in the size class of 1-2.5 ha (Figures 11 and 12). However, case study area 2 has a significant amount of patches larger than 5 ha which are absent in the low density region of area 1. Here, patches 12 and 23 cover the largest area (Figure 10).

Table 3: Landscape indices and spatial statistics for study area 1 and 2.

Study area 1	
Total patch area (ha)	18.46
Average patch size (ha)	2.31
Average distance to nearest patch (km)	2.56
Average inter-patch distance (km)	5.15
Amount of patches in landscape (%)	0.11
Study area 2	
Total patch area (ha)	483.9
Average patch size (ha)	8.22
Average distance to nearest patch (km)	0.54
Average inter-patch distance (km)	6.79
Amount of habitat patches in landscape (%)	2.67

Figure 11: Patch size distribution for study area 1.

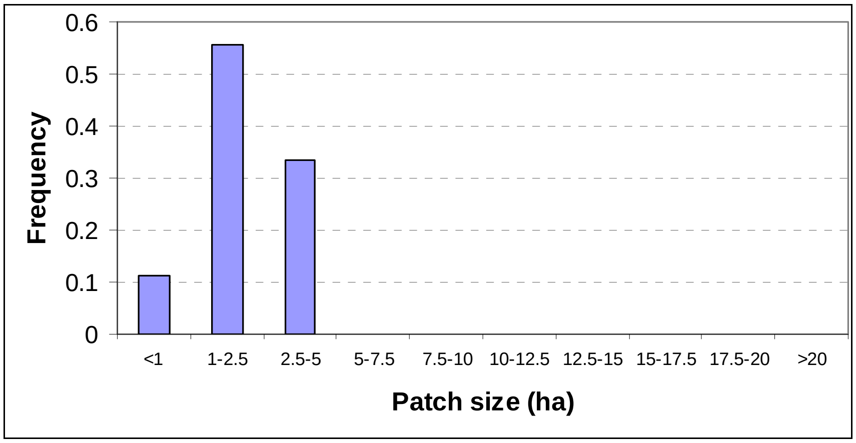
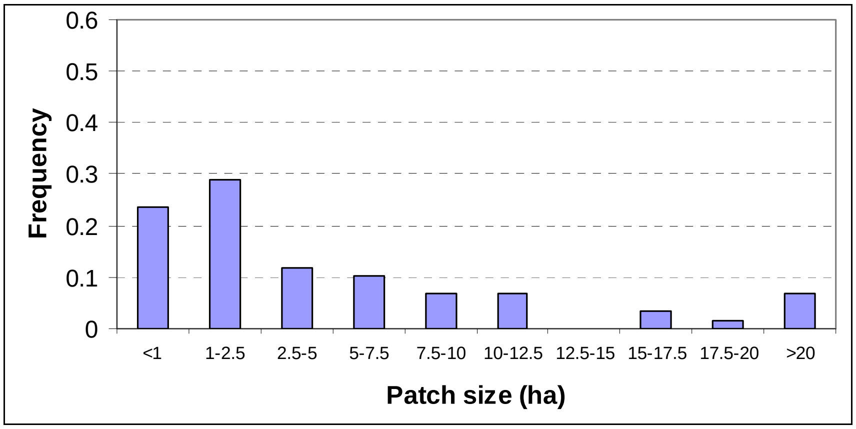


Figure 12: Patch size distribution for study area 2.



Based on the demographic model we included additional model parameters for the spatial model version (Table 4). For both case study areas and each marsh wren population patch we calculated the initial population abundance and the carrying capacity *K* based on the average observed population density for both male and female marsh wrens (Tables 5 and 6). For study area 1 and 2 total calculated carrying capacity *K* for all patches were 173 and 4533 individuals, respectively (Table 5). Initial population density in year 1 in each simulation run was equal to *K*. We also assumed a coefficient of variation (CV) for *K* of 10% taking into account annual variations in the habitat quality (e.g., imposed through changes in water levels).

Table 4: Model parameters for the spatial marsh wren PVA.

Parameter	Value/Range	Comments
Carrying capacity	9.43/ha (3.73 males/ha; 5.7 females/ha)	Average male population density (female density is based on estimated sex ratio of 1:1.53); see Table 1 and 2
CV of *K*	10%	Own estimation; coefficient of variation around which the carrying capacity varies;
Initial abundances	=Carrying capacity	Initial abundance of juveniles and adults in year 1 based on the stable age distribution from the stage matrix
Dispersal rate	0.25	Own estimation; maximum dispersal rate (nearest cell); decreases towards 0 up to the maximum dispersal distance; note that adult dispersal rate is multiplied by 0.5 to account for higher dispersal rates of juveniles
Maximum dispersal distance	3.0 km	Maximum dispersal distance among population patches (Zimmerman et al., 2002, Verner, 1971); non-linear dispersal kernel is assumed
Correlation	Function parameters: *a*=1.0; *b*=1.9; *c*=1.0;	Correlation among the vital rates of populations; represents the similarity of environmental fluctuations; empirical data not available, own estimate is based on a negative exponential function ranging from 1.0 (nearest patch) to 0 (maximum edge to edge distance in study area 1 and 2)

Table 5: Area and estimated carrying capacity *K* for population patches in study area 1.

Population	Area (ha)	Area (% total patch area)	*K* (males)	*K* (total)
1	3.99	21.31%	15	37
2	4.51	24.04%	17	42
3	1.13	6.01%	4	11
4	1.13	6.01%	4	11
5	3.38	18.03%	13	32
6	1.54	8.20%	6	14

Table 5: Area and estimated carrying capacity *K* for population patches in study area 1.

Population	Area (ha)	Area (% total patch area)	*K* (males)	*K* (total)
7	1.54	8.20%	6	14
8	1.23	6.56%	5	12
	18.46	100.00%	68	173

Table 6: Area and carrying capacity *K* for population patches in study area B. Patches larger than 5 ha are indicated in bold and shown in Figure 10.

Population	Area (ha)	Area (% of total patch area)	K (males)	K (total)
1	9.1	1.89	34	85
2	2	0.41	7	19
3	9.7	2	36	91
4	4.9	1.02	18	46
5	1.2	0.25	4	11
6	10.5	2.17	39	98
7	3.8	0.78	14	36
8	3.1	0.64	11	29
9	0.7	0.15	3	7
10	1.2	0.24	4	11
11	1.8	0.36	7	17
12	113.4	23.4	420	1062
13	2.6	0.54	10	24
14	5.2	1.08	19	49
15	9.6	1.98	36	90
16	0.9	0.18	3	8
17	5.5	1.14	20	52
18	1	0.21	4	9
19	11.1	2.3	41	104
20	1.2	0.24	4	11
21	1.7	0.36	6	16
22	6.9	1.42	26	65
23	67.7	13.97	251	634
24	2.4	0.5	9	22
25	0.5	0.11	2	5
26	1.4	0.28	5	13
27	3.5	0.72	13	33

Table 6: Area and carrying capacity *K* for population patches in study area B. Patches larger than 5 ha are indicated in bold and shown in Figure 10.

Population	Area (ha)	Area (% of total patch area)	K (males)	K (total)
28	16.1	3.32	60	151
29	4.8	0.99	18	45
30	10.2	2.1	38	96
31	0.7	0.14	3	7
32	0.9	0.18	3	8
33	7.3	1.52	27	68
34	0.6	0.12	2	6
35	18.2	3.74	67	171
36	1	0.21	4	9
37	0.5	0.1	2	5
38	1.8	0.36	7	17
39	1.4	0.29	5	13
40	1.1	0.23	4	10
41	45	9.27	167	422
42	1	0.2	4	9
43	0.5	0.11	2	5
44	32.2	6.64	119	302
45	1.2	0.24	4	11
46	1.4	0.29	5	13
47	2.5	0.51	9	23
48	16.1	3.31	60	151
49	9.7	2	36	91
50	2	0.42	7	19
51	0.6	0.13	2	6
52	11	2.27	41	103
53	6.8	1.4	25	64
54	5.4	1.1	20	51
55	0.8	0.17	3	7
56	0.5	0.1	2	5
	483.9	100.0	1793	4533

The annual rate at which juveniles and adults from a given population may disperse into an adjacent habitat patch is determined by the respective distance from the source to the target patch (up to a maximum distance of 3 km), the dispersal rate, and the stage class (we assumed that juveniles have higher dispersal rates). The dispersal parameterization of the marsh wren model results in a dispersal kernel that shows a decrease in dispersal rate with increasing distance from the source population (Figure 13). The distance between each population patch can be seen in Table 7. The resulting annual dispersal rates between each population (based on the dispersal kernel) are shown in Table 8. We also included a correlation-distance function that represents the similarity of environmental fluctuation which is indicated by differences in vital rates among populations (Figure 14). Due to the lack of empirical data (e.g., time series in fecundity and survival rates among different populations) we assumed a negative exponential function ranging from 1.0 (adjacent cell) to 0.0 (maximum distance between edges).

Figure 13: Dispersal kernel for the spatial marsh wren PVA based on maximum dispersal distance (km) and dispersal rate.

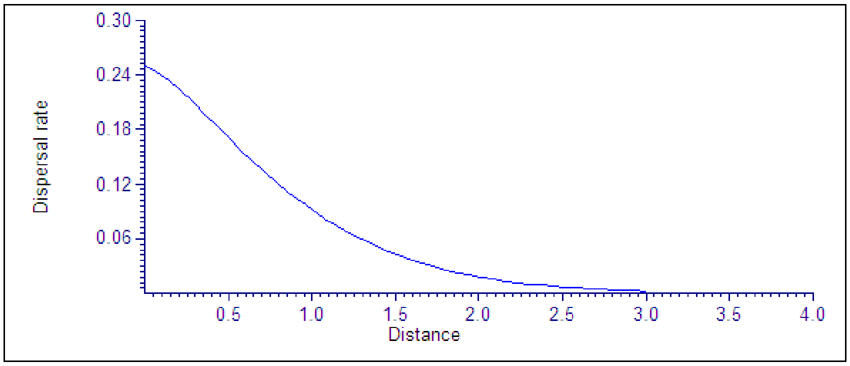


Table 7: Distance matrix (km) for 9 marsh patches in study area 2.

	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5	Patch 6	Patch 7	Patch 8
Patch 1		0.69	1.64	4.69	5.5	4.32	7.91	9.21
Patch 2			1.12	5.01	4.88	4.01	8	9.2
Patch 3	0			4.7	3.99	2.93	7.28	8.34
Patch 4	0	0	0		7.62	4.15	3.75	5.43

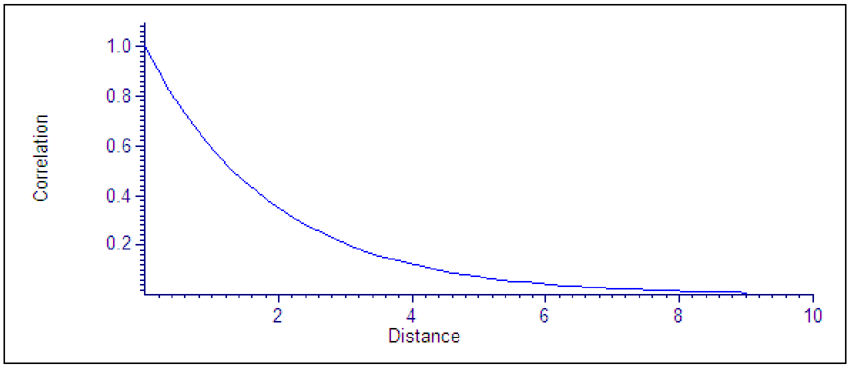
Table 7: Distance matrix (km) for 9 marsh patches in study area 2.

	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5	Patch 6	Patch 7	Patch 8
Patch 5	0	0	0	0		3.65	8.63	8.91
Patch 6	0	0	0	0	0		5.11	5.76
Patch 7	0	0	0	0	0	0		1.78
Patch 8	0	0	0	0	0	0	0	

Table 8: Matrix of annual dispersal rates for 8 populations in study area 1 based on the dispersal kernel and the distance matrix. The matrix element at the 1st row and 2nd column is the annual dispersal rate from population 2 to population 1.

	Pop 1	Pop 2	Pop 3	Pop 4	Pop 5	Pop 6	Pop 7	Pop 8
Pop 1		**0.136**	**0.033**	0	0	0	0	0
Pop 2	**0.136**		**0.076**	0	0	0	0	0
Pop 3	**0.033**	**0.076**		0	0	**0.003**	0	0
Pop 4	0	0	0		0	0	0	0
Pop 5	0	0	0	0		0	0	0
Pop 6	0	0	**0.003**	0	0		0	0
Pop 7	0	0	0	0	0	0		**0.026**
Pop 8	0	0	0	0	0	0	**0.026**	

Figure 14: Correlation-distance function for the spatial marsh wren PVA (distance in km).



2.3.1 Results from the spatial PVA

The results from the spatial analysis of study area 1 (low density) and 2 (high density) are shown in Figure 15. Extinction risk of the metapopulation was 25.4% and 0%, respectively. The expected minimum abundance (EMA) was 40 and 2579 individuals and the population trend (abundance at time step 100 divided by abundance in the first year) was 0.6 (negative) and 0.95 (nearly neutral), respectively. The metapopulation occupancy rates (i.e., the number of patches occupied over time) given in panel B show that on average 5 patches become unoccupied over a time frame of 100 years. For area 1 this is significantly less as well as the number of time steps a patch is occupied. Panel D shows the interval extinction risk, i.e. the average probability for abundance thresholds. Here, final marsh wren metapopulation abundance for case study area 2 was rarely below 1000 individuals and, therefore, extinction risk was zero. The strong difference in persistence patterns are also indicated in panel E.

To cover a wider range of hypothetical metapopulation structures within the overall NAESI pilot project study area, we decided to use these two case study areas for a more in-depth analysis as opposed to selecting additional sample study areas. For area 1 and 2 we therefore varied the carrying capacity *K* for each patch as well as maximum dispersal distances. In Ramas©MetaPop the carrying capacity for each patch determines the actual size of the habitat patch. For example, by doubling the *K* value in each patch of area 1, the total amount of habitat in the sample landscape would increase from 18.46 ha (i.e., 0.11%) to 36.92 (i.e., 0.22%) (see Tables 3 and 5), based on the estimated male population densities and sex ratios (note, the average sex ratio was used to calculate average female population densities). This procedure also modifies (here doubles) average patch sizes, however it does not change the spatial configuration of patches. The latter will be later dealt with by modifying maximum dispersal distance.

Figure 16 shows the extinction risk, EMA and the calculated population trend for increases (area 1) and decreases (area 2) of *K*. By respectively increasing *K* in the low density area and decreasing *K* in the high density area it is possible to assess the amount of habitat when marsh wren population dynamics are relatively stable and viable (here <5% extinction risk) for different patterns of marsh habitat. The population trend was calculated as the abundance in time step 100 divided by the initial abundance in year 1. We used the population trend as an additional model output to assess under which changes in the *K* value a metapopulation over time might show relatively stable population dynamics. This is of importance when considering that viable population may not necessarily be stable (and ecologically 'healthy') over a certain time frame.

For study area 1 in the left panel of Figure 16 extinction risk decreased when *K* was increased. For example, an increase of 75% (equivalent to 32.8 ha) generated an extinction risk of ~5% and an EMA of ~125. For this *K* value the population trend appeared to be stable (~1.0, i.e., initial and final population size where similar). Interestingly, when *K* was decreased population trends in study area 2 were always negative (i.e., <1.0), even though total habitat amount in that sample landscape was significantly higher than in area 1. When *K* was decreased by -55% for study area 2 extinction risk was approximately 5% for a time frame of 100 years. This reduction in the current amount of habitat in area 2 (via *K*) is equal to ~218 ha of marsh habitat. The question that arises is why is there such a difference in the amount of marsh habitat that a metapopulation requires in order to support similar levels of persistence?

Figure 15: Results for the base scenario for study area 1 (left) and 2 (right). Panel A show the trajectory summary for 500 simulation runs over 100 years; B shows the metapopulation occupancy; C the local occupancy; D the interval extinction risk, and E time to extinction. Extinction risk is 25.4% and 0% for case study are A and B, respectively. Expected minimum abundance (EMA) is 40 and 2579, respectively

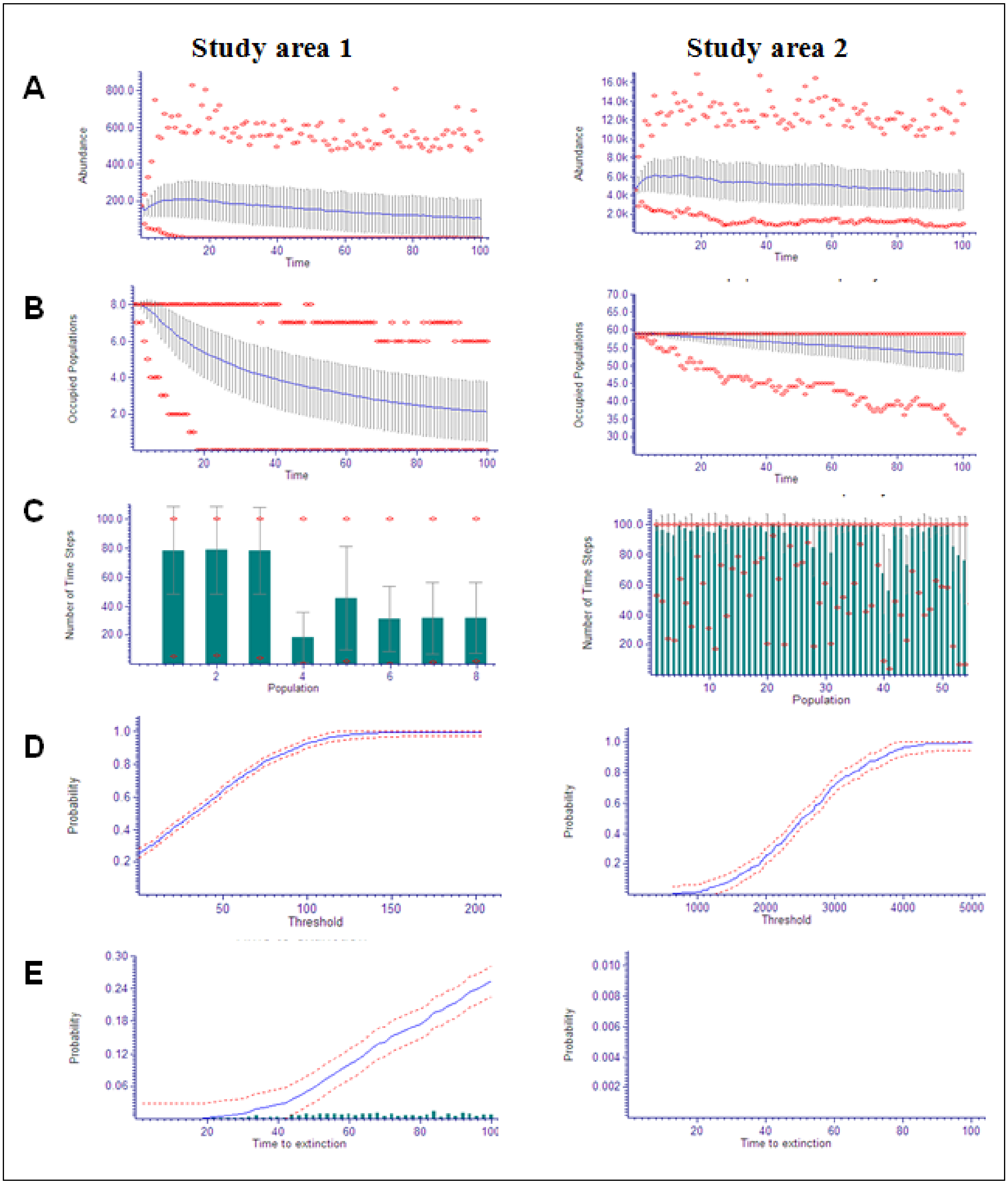
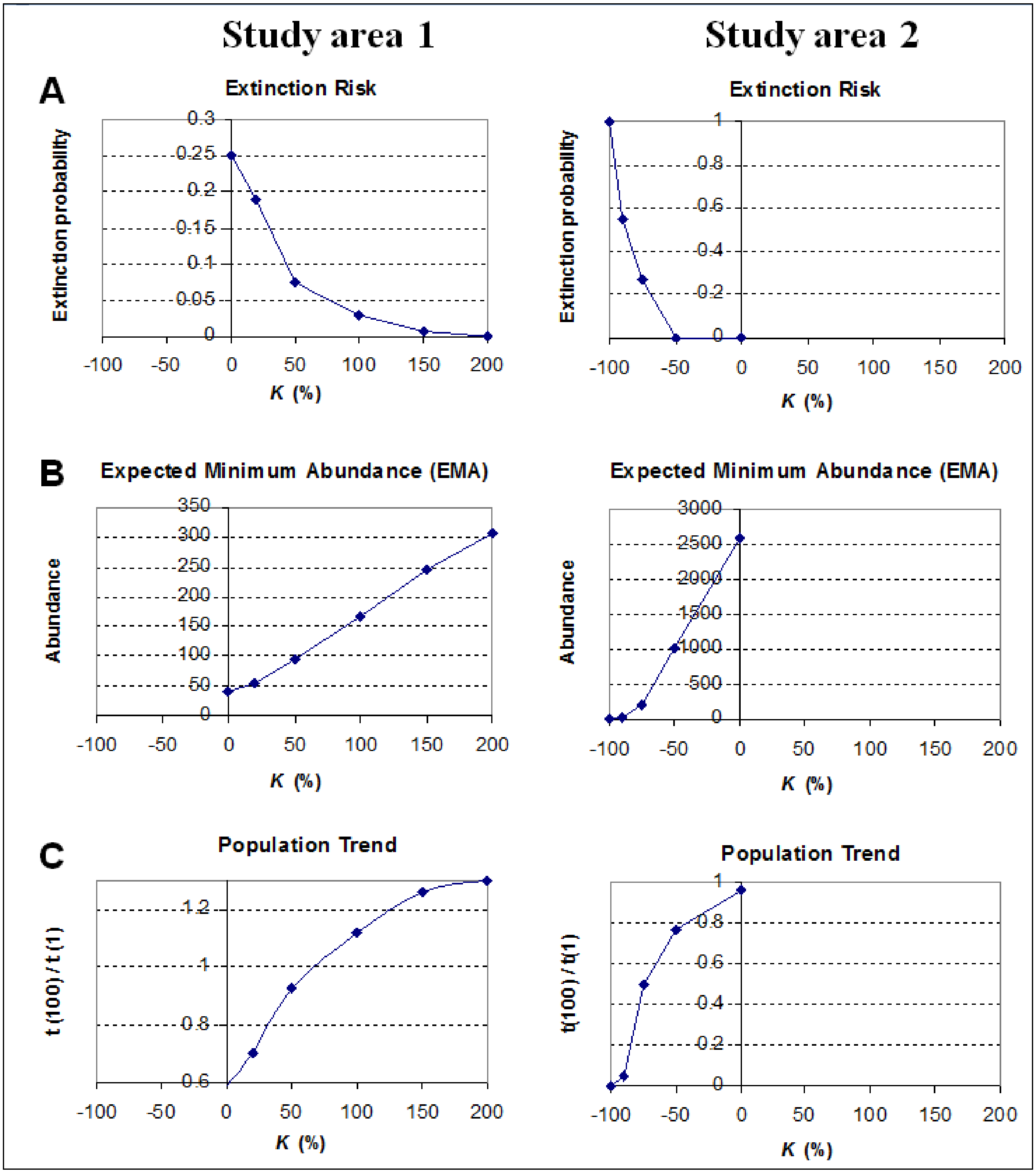


Figure 16: Extinction risk (A), EMA (B) and population trend (C) for modified carrying capacities (*K*) for study area 1 and 2. The population trend as. the effective growth rate was calculated as abundance in year 100 divided by abundance in year 1.



To answer this question we evaluated the size class distribution of marsh habitat patches in area 2. Figure 17 shows the average projected population trajectory and the time to extinction for two different scenarios for study area 2. In the first scenario on the left hand side the *K* value for all 56 patches was reduced to 10% of the original amount (from a total of 4533 to 453 marsh wrens, equivalent to a decrease from 483.9 to 48.4 ha marsh habitat) and evenly distributed among all population patches, i.e. each habitat patch received 8 individuals on average. For this scenario the extinction risk increased to 94%, compared to 55% generated in the base scenario (Figure 16). However, when the same carrying capacity of 453 marsh wrens was distributed among 29 randomly selected patches (remaining patches were deleted) with 16 individuals per patch on average the extinction risk decreased dramatically to 14%. Surprisingly, this was so even though connectivity decreased due to the lower density of patches.

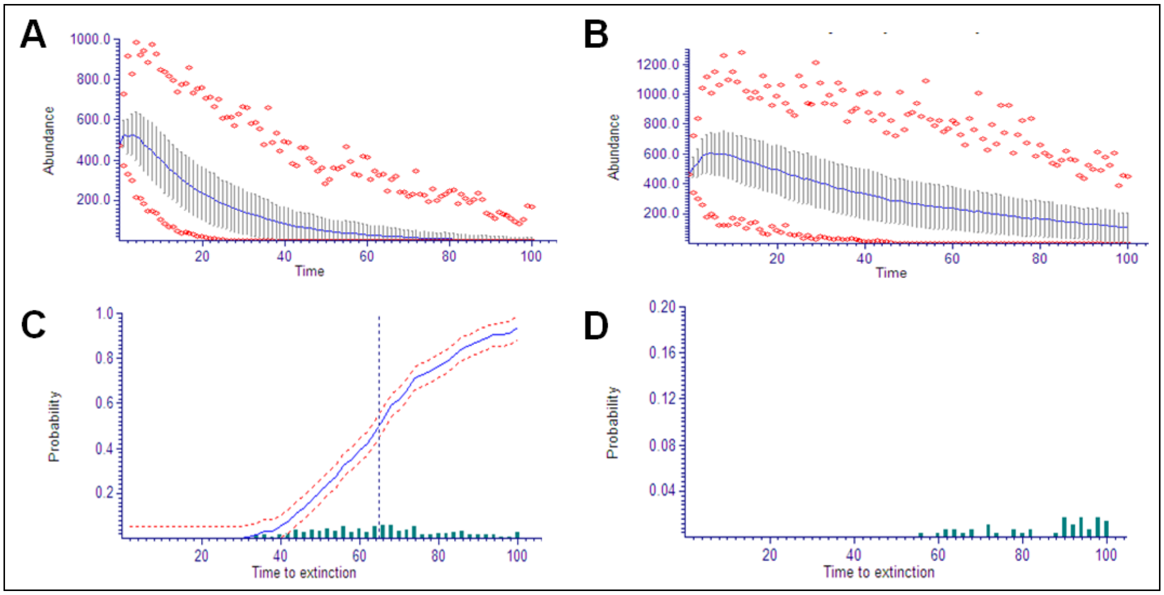
These results highlight two major dependencies. Firstly, the distribution of patch sizes within a landscape appears to be important. Both base scenarios resulted in different thresholds regarding the amount of habitat needed in order to facilitate persistent populations. For the low and high density study area 32.8 ha and 218 ha were needed, respectively. The latter habitat amounts are equivalent to 0.19% and 1.2% marsh cover on the case study area scale. The calculated proportion of 0.84% of marsh habitat within the entire NAESI pilot project area lies within that range. However, the spatial distribution of marshes on the regional scale is very heterogeneous and may not be directly compared to metapopulation processes on the landscape scale. Surprisingly, for the non-spatial model minimum viable patch size was higher than for the modified low density case study area, i.e. 114 ha compared to 32.8 ha (even though required habitat amounts are usually higher for spatially structured populations due to lower connectivity). This pattern resulted from high annual variability in fecundity rates (50%) for marsh wrens: the more variability in fecundity the lower the advantage of inhabiting a single larger patch. That is, due to lower correlations of vital rates spatially structured populations spread the risk of extinction from environmental and demographic fluctuations.

Secondly, as we can see in the two simulation experiments of Figure 17, marsh patches with a size of 0.85 ha (supporting 8 individuals, i.e. 1 adult male on average given the known sex ratio and stable age distribution) are too small to contribute to metapopulation persistence due to the nature of environmental and demographic stochasticity. Interestingly, this changed dramatically if at least 2 adult males were present in a local patch. Based on the simulation results we therefore conclude that the size of a marsh patch should be at least 1.7 ha in order to contribute to the species' persistence on the metapopulation level (unless a smaller patch represents a crucial stepping stone between larger patches). However, it is important to denote that these numbers have to be dealt with great caution, due to regional and annual variations in habitat quality and territory size of adult males. Moreover, there is some evidence of area-sensitivity in marsh wrens and that occupancy rates are higher for marsh patches larger than 5 ha (see e.g., Naugle, 1997, Bird Studies Canada, 2004). However, non-occupancy of (smaller) habitat patches does not necessarily mean that these habitat patches have lower habitat quality. In many cases non-occupancy may be due to the impact of environmental stochasticity and dispersal barriers: if a patch is too small and may only support a few males, a poor year with low fecundity and/or survival may result in local extinction and weak connectivity may inhibit the re-colonization of such patches.

We also evaluated changes in the maximum dispersal distance for both case study areas (Table 9). Increases in the maximum dispersal distance resulted in lower extinction risks, higher EMA and population trends when applied to the base scenario of case study area 1. This result is to be expected as the greater the distance to which birds may disperse and the greater the proportion of dispersing birds the better the connectivity within the metapopulation (note, that in Ramas©Metapop increasing the maximum dispersal distance and keeping all other dispersal parameters constant leads to an increase in the proportion of dispersing birds). However, the opposite emerged when the maximal dispersal distance was changed for area 2. Here, with increase in distance (and increase in the proportion of individuals dispersing from a patch) EMA and population trend both decreased (while extinction risk was still 0%). Intuitively, one would expect that increasing dispersal distances are of benefit for the metapopulation (as for area 1). However, here, due to the higher number of small marsh patches (13 patches <1ha) and the already sufficient connectivity, a larger number of dispersing birds in concert with a higher connectivity results in the loss of additional dispersers because of the carrying capacity of smaller patches. Therefore, smaller patches act as a population sink because of the restricted carrying capacity.

Based on the model results and the known dispersal distances of marsh wrens we recommend a maximum distance of 2-3 km to the nearest marsh wren population patch in order to allow for sufficient natal and breeding dispersal. However, as seen with the two different outcomes of changes in maximal dispersal distance for case area 1 and 2, lower distances between nearest patches (or higher maximum dispersal distances including higher dispersal rates as simulated) may not necessarily increase persistence if neighboring patches are very small, have a limited carrying capacity and therefore act as a population sink.

Figure 17: Average population trajectory (A and B) and time to extinction (C and D) for two scenarios of study area 2.



For the left scenario (A and C) the total carrying capacity of all 59 population patches was reduced to 10% of the original amount (i.e., a total of 457 instead of 4573 marsh wrens) and evenly distributed (i.e., 8 individuals on average). For the right scenario (B and C) this amount was distributed evenly across 29 patches (resulting in approximately 16 individuals per patch). For the left and right scenario extinction risk was 94% and 14%, respectively. EMA was 1.6 and 67 individuals.

Table 9: Simulated dispersal scenarios for case study area 1 and 2.

Study area	Maximum dispersal distance	Extinction risk	EMA	Population trend (effective growth rate t_{100}/t_1)
1	2 km	0.31	37	0.55
1	3 km	0.25	40	0.59
1	4 km	0.24	42	0.62
1	5 km	0.24	50	0.70
2	2 km	0.0	3328	1.32
2	3 km	0.0	2579	0.96
2	4 km	0.0	1896	0.67
2	5 km	0.0	1576	0.55

2.4 Conclusions

For the base scenario of the demographic marsh wren population model and a simulated time frame of 100 years we found a final minimum viable population size (MVP) of 421 males (with 95% confidence, i.e. less than 5% of the simulation runs resulted in population extinction). Note that the marsh wren model was a ‘male only’ model due to polygyny in this species. MVP size decreased to 182 males when the simulation time was 50 years. Based on these results we then estimated the amount of breeding habitat required to maintain a single population over a certain time frame. Based on an average reported population density of 0.27 ha/male and a MVP size of 421 males we calculated a minimum ‘viable’ patch size of 114 ha. However, due to the high variability in annual territory size and vital rates this is only a very broad estimate and should be used with caution.

In the spatial model version we then used available land cover data to delineate the current distribution of marsh habitat in the NAESI pilot project study area. We classified habitat as either suitable when marsh was present and unsuitable when absent. We selected two case study areas, approximately 200 km^2 in size, one in an area with a higher density of marshes and one in a low density area. The low density area comprises approximately 18.46 ha of marshes with an average patch size of 2.31 ha, an average distance to the nearest patch of 2.56 km, and a total amount of 0.11% marshes. For the high density area 2 with approximately 484 ha of marshes we calculated an average patch size of 8.22 ha, an average distance to the nearest patch of 0.54 km, and a total amount of 2.67% marshes in the landscape. Overall, marshes cover approximately 0.84% of the NAESI area. For these two case study areas metapopulation extinction risk over 100 years was 25.4% and 0%, respectively (8 and 56 populations, respectively). The population trend (effective growth rate between year 1 and 100) was 0.6 (negative) and 0.95 (nearly neutral), respectively.

We then increased and decreased patch sizes in each case study area to simulate the effect of habitat amount. We also modified maximum dispersal distances and analyzed when populations exhibit significant sink dynamics. Based on the demographic and spatial analysis we propose the following habitat-based standards in order to achieve longer term persistence and stable population trends for the marsh wren in agricultural regions of eastern Ontario:

- (i) a minimum viable patch size of ~114 ha assuming that all individuals reside in one patch/population,
- (ii) a minimum metapopulation patch size of ~1.7 ha to avoid patches being a strong population sink,
- (iii) a minimum of 0.2% - 1.2% marsh habitat on a 200 km2 landscape scale (depending on the patch size distribution), and
- (iv) a maximum distance of 2-3 km to the nearest patch to allow sufficient natal and breeding dispersal.

3 OVENBIRD (*SEIURUS AUROCAPILLUS*)

The ovenbird (*Seiurus aurocapillus* L.) is a common long-distance neotropical migratory passerine that breeds across North America from northeast British Columbia to the island of Newfoundland and south to North Carolina. Wintering grounds include southern Florida, Mexico, the Caribbean, and Central America (Van Horn and Donovan, 1994). Ovenbirds are sexually monomorphic (Bent, 1953) and typically breed in large, mature forests where they build a domed nest of leaves and grass on the ground. In both breeding and wintering areas, ovenbirds feed primarily on arthropods which they pick from the surface of leaf litter (Stenger, 1958, Lack and Lack, 1972). Ovenbirds segregate ecologically from similar warblers of the forest floor by using uplands and moderately sloped areas. For the NAESI pilot project study area ovenbird occurrence has been either confirmed or assessed as possible (Figure 18). Based on literature and knowledge of previous modeling efforts (e.g., Larson et al., 2004) data availability for the ovenbird appears to be relatively good. A PVA on the ovenbird has already been conducted by Larson et al. (2004) using the Ramas©GIS software environment and the landscape simulator LANDIS for hardwood forests in southern Missouri. The main difference between this study and the Larson et al. (2004) PVA is that the latter is based on a single population for a large continuous forest landscape whereas eastern Ontario is characterized by fragmented forest patches and separated ovenbird populations.

3.1 Demography and habitat

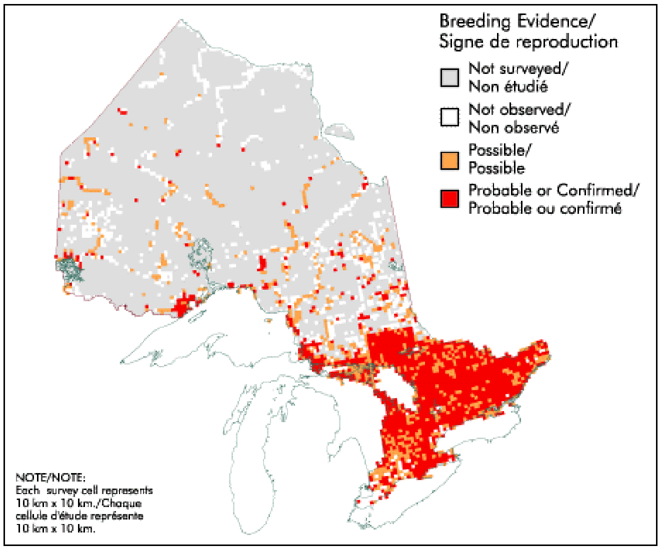
Habitat Requirements

Of primary importance to ovenbirds across the breeding range is a large area of contiguous, interior forested habitat (Bond, 1957, Robbins, 1979, Whitcomb et al., 1981, Hayden et al., 1985, Robbins et al., 1989, Villard, 1991, Burke and Nol, 1998). A minimum of 500 ha has been suggested as the minimum area required for maintaining source populations in southern Ontario (Burke and Nol, 1998). Minimum patch sizes for ovenbird occurrence have been reported at 4ha (Galli et al., 1976) and 6 ha (Robbins et al., 1989).

Given large tracts of non-fragmented forests, breeding ovenbirds have a broad tolerance for different plant communities. Mature forests used by ovenbirds are typically deciduous hardwood stands, but they also nest in mixed-wood boreal forests in Canada. In Ontario, ovenbirds breed in maple-ash (Lee et al., 2002, eastern Ontario), maple-beech (Jobes et al., 2004, central Ontario; Burke and Nol, 1998, southern Ontario), and jack pine forests (Venier and Pearce, 2005, northern Ontario).

While general habitat use varies in different parts of their range, ovenbirds consistently place their territories in mature forests (tree height 16 m – 22 m; Collins, 1983, Burke and Nol, 1998) with high levels (60% – 90%) of canopy cover (Smith, 1981, Sweeney and Dijak, 1985, Robbins et al., 1989), a relatively sparse understorey (Smith and Shugart, 1987, Flaspohler et al., 2000), and deep leaf litter (Van Horn and Donovan, 1994, Burke and Nol, 1998, Betts et al., 2006). Breeding ovenbirds select nest sites in moderately-sloped areas characterized by lower ground cover, larger trees (Smith and Shugart, 1987), and thicker leaf litter (Hann, 1937, Van Horn and Donovan, 1994, Burke and Nol, 1998) relative to random sites. In southern Ontario, nest sites are typically found on mid- to upper slopes characterized by low percent cover of bare ground (< 7%), moderate levels of herbaceous and sapling cover, low seedling and shrub cover, high canopy cover, deep litter layer, and at distances of 3 m from the nearest tree (Burke and Nol, 1998). Throughout their range, ovenbirds place their nests at least 30-50 m from the forest edge (Hann, 1937, Van Horn and Donovan, 1994, Burke and Nol, 1998, Bayne and Hobson, 2001, Larson et al., 2004).

Figure 18: Distribution of the ovenbird in Ontario (source: Project Wildspace, Environment Canada, 2005).



Recent studies suggest that habitat use by ovenbirds may change as the breeding season progresses. While interior forest is required for nesting, family groups in Virginia were frequently captured in regenerating clearcut areas in the post-fledging period (Marshall et al., 2003). Furthermore, habitat used by independent fledglings has been shown to be substantially different from that of breeding adults. In New Hampshire, juveniles (n = 41) used habitat non-randomly and selected areas characterized by significantly fewer large trees and denser understorey than nest sites (King et al., 2006).

Territory Size

Territories are established by males upon arrival on the breeding grounds, and are used to attract mates, build nests, and feed adults and young (Smith and Shugart, 1987). Regional variation in territory size has been documented to range from 0.2 ha – 1.8 ha in Michigan (Hann, 1937), 0.9 ha – 1.4 ha in Missouri (Wenny, 1989), 0.61 ha – 1.6 ha in Ontario (Stenger, 1958), and 1.9 ha in Saskatchewan (Mazerolle, 2001) (see Table 10). These differences are likely due to regional variation in vegetation structure and corresponding invertebrate abundance (Smith and Shugart, 1987, Van Horn and Donovan, 1994) and conspecific density (Mazerolle, 2001). In central Ontario, average territory size decreased from 0.83 ha to 0.489 ha during a spruce budworm outbreak (Zach and Falls, 1975). In Missouri, mean territory size was larger (1.40 ha versus 0.88 ha) and conspecific density 50% lower in small tracts of forest relative to large tracts (Wenny, 1989). In Saskatchewan, territories were slightly larger in contiguous forest (2.0 ha) than in forest fragments (1.7 ha). Territory size is also reported to increase from copulation to nestling stages (Van Horn and Donovan, 1994). Caution must be used, however, when comparing territory sizes among studies because estimates are highly sensitive to the method used to delineate territory boundaries (Börger et al., 2006).

Ovenbirds may adjust the spatial arrangement of their territories given changes to landscape structure. In eastern Ontario, ovenbird territories were only found nesting at least 50 m from the forest edge (Lee et al., 2002). Lambert and Hannon (2000) found evidence that ovenbirds elongated their territories in response to the creation of edges due to forest harvesting. Ovenbirds were observed to overlap their territories with neighbors to adjust for changes in landscape structure (Mazerolle and Hobson, 2004). Bayne et al. (2005) observed significantly larger territories in forests containing narrow/low-impact seismic lines than in those with wider areas cleared for the lines. Females may be more likely to select territories based on features that enhance reproduction (nest-site availability and food abundance), whereas males may be more likely to select territories based on features that enhance territory defense or mate attraction (e.g., song perch availability; Burke and Nol, 1998)

Table 10: Summary of demographic parameters for the ovenbird.

Parameter / Characteristic	**Observation / Parameter range**	**Reference**
Breeding period (ON)	Arrives southern Ontario 10 May; Arrives northern Ontario 22 May; Anecdotal reports of departure from southern Ontario early Oct; In Michigan, adults depart breeding area when young are independent; young depart late Sep-early Oct	Saunders, 1947; Environment Canada, 2005 ONTBIRDS Website, 2004 Hann, 1937
Clutch Size (mean, variation)	Ranges from 3-6; 4.43 ± 0.06 (mean ± 1 S.E; n = 218)	Bent, 1953 Manolis et al., 2002
Broods/year	1/pair/year; Will attempt to renest if first nest is destroyed 3 reports (1 from Ontario) of a pair raising a 2nd brood	Bent, 1953 Bent, 1953 Zach and Falls, 1976, Van Horn and Donovan, 1994
Incubation period	12 days	Van Horn and Donovan, 1994; Hersek et al., 2002
Fledging period	8-10 days	Hann, 1937, Ellison, 1985
Maturity	Both sexes commence breeding in the 1st year following hatching	Quay, 1985, Van Horn and Donovan, 1994

Table 10: Summary of demographic parameters for the ovenbird.

Parameter / Characteristic	Observation / Parameter range	Reference
Life span	Mean 2.7 years (males, 2.8 yr; females, 2.4 yrs; n = 38); Longevity record: 9 yr	Hann, 1937 Klimkiewicz et al., 1983
(Cowbird) parasitism	Adults do not recognize adult cowbirds as enemies, or cowbird eggs or young as alien; Parasitism rates influenced by forest size and isolation; higher levels of parasitism in fragmented forests southern Ontario: 0% parasitism in contiguous forest versus 29.3% in small forest fragments (93 ha); significantly reduced nest and fledging success; 2-4% nests in contiguous forest parasitized compared to 19-67% in fragmented forest; Massachusetts: mean 1.4 fewer young sucessfully fledged in parasitized compared to non-parasitized nests;	Van Horn and Donovan, 1994 Friedman et al., 1977, Brittingham and Temple, 1983, Porneluzi and Faaborg, 1999 Burke and Nol, 2000 Donovan et al., 1995 Hersek et al., 2000
Fledging success	Michigan: mean 2.9 fledglings per pair; Minnesota: mean 3.79 fledglings per pair; 1.4 female fledglings per female	Hann, 1937 Manolis et al., 2002; Donovan et al., 1995
Nesting success	eastern Ontario: higher pairing success (60%) in contiguous forests (> 200 ha) than in forest patches (< 125 ha; 30% success rate); southern Ontario: pairing success increased from 0% in small forest fragments (< 20 ha core area) to 100% on large fragments (> 20 ha core area); eastern Pennsylvania: nest success greater in larger forests (59%) than fragments (<10%); Wisconsin: mean success rate of nests < 300 m from forest edge was 0.44 ± 0.08 (n = 47); mean success rate > 300 m from edge was 0.69 ± 0.09 (n = 49);Saskatchewan: daily nest success ranged from 95.8 ± 1.1% – 97.9 ± 0.8%	Lee et al., 2002 Burke and Nol, 1998 Porneluzi et al., 1993 Flaspohler et al., 2001 Bayne and Hobson, 2002
Stage/Age classes	adult/juvenile stages only	Van Horn and Donovan, 1994
Annual survival rates for adults, juveniles	Adult annual survival = 0.623 Juvenile annual survival = 0.31; Highest reported adult survival rate: 0.845; On wintering grounds in Puerto Rico, annual survival of first-year birds: 0.32-0.42; after first-year birds: 0.53-0.63	Donovan et al., 1995 Roberts, 1971 Dugger et al., 2004

Table 10: Summary of demographic parameters for the ovenbird.

Parameter / Characteristic	Observation / Parameter range	Reference
Knowledge on dispersal/migration of juveniles/adults	Neotropical migrant Saskatchewan: site fidelity of unpaired males (11%) significantly lower than paired males (41%), which was not different from return rates of males that had nests destroyed (29%); Missouri: no difference in site-fidelity between paired, successful and unpaired males (54% vs 41%) but only 9% of unsuccessful males returned; Juvenile dispersal distances unknown; Females migrate at different times and winter in different areas than males	Van Horn and Donovan, 1994 Bayne and Hobson, 2002 Porneluzi and Faaborg, 1999 Villard et al., 1993 Lee et al., 2002
Average territory size	Ontario: 0.61 ha – 1.6 ha; Michigan: 0.2 ha – 1.8 ha; Missouri: 0.9 ha – 1.4 ha; Saskatchewan: 1.1 – 1.6 ha; Alberta: 1.3 ha – 1.8 ha; Regional variation likely due to differences in food supply and conspecific male density	Stenger, 1958 Hann, 1937 Wenny, 1989 Mazerolle and Hobson, 2004, Lambert and Hannon, 2000, Smith and Shugart, 1987, Mazerolle and Hobson, 2004
Abundance/Density	Abundance during breeding season is positively related to food supply and amount of contiguous forest available eastern Ontario: mean 0.12 males /ha; southern Ontario: significant effect of woodlot size on density; 0.033 males/ha in fragments, 0.83 males/ha in contiguous forest	Smith and Shugart, 1987, Mazerolle, 2001 Lee et al., 2002 Burke and Nol, 1998
Sex ratio	Likely biased in favor of males	Gibbs and Faaborg, 1990, Burke and Nol, 1998
Known trends in population size for Eastern Ontario?	Significant ($p < 0.1$) increase and decrease in provincial population size from, 1966-1979 ($n = 61$ routes) and from, 1980-2005 ($n = 126$ routes), respectively.	Sauer et al., 2005

Density/Abundance

Ovenbird density and abundance during the breeding season is positively related to food supply (Smith and Shugart, 1987) and the amount of contiguous forest available (Mazerolle, 2001). In southern Ontario, ovenbird densities ranged from 0.033 male/ha on smaller woodlots (80 ha) to 0.83 male/ha in contiguous forests (Burke and Nol, 1998). In eastern Ontario, mean density was reported at 0.12 male/ha (Lee et al., 2002) (see Table 10). For Pennsylvania, estimates range from 0.51 male/ha (Mancke and Gavin, 2000) to 0.69 male/ha (Porneluzi et al., 1993). In Saskatchewan, densities were greater in contiguous forest (1.1 male/ha) than in forest fragments (0.59 male/ha), and there was a positive association between arthropod biomass and density of territorial males (Mazerolle, 2001). Maximum densities in other areas have been reported near 1.0 male/ha (e.g., Holmes and Cherry, 2001).

Along with food supply, ovenbird abundance is dictated by elements of landscape structure. The relative amount of edge-to-interior, patch size, proximity to roads, and the amount of regional forest cover are important predictors of ovenbird abundance (Bayne and Hobson, 2001). Throughout their range, ovenbird abundance has been found to decrease significantly with isolation of a forest fragment from surrounding woodland (Whitcomb et al., 1981, Lynch and Whigham, 1984, Askins et al., 1987, Robbins et at., 1989). In eastern Ontario, Lee et al. (2002) found that landscape forest cover explained the most variation in ovenbird abundance. In New Brunswick, occurrence and reoccurrence of ovenbirds were positively correlated with canopy cover, basal area of deciduous trees, and leaf litter. Abundance also depended on forest characteristics at spatial extents greater than the individual territory. Ovenbirds were less likely to occur in small patches (< 50 ha), but only when those patches were in landscapes containing relatively small amounts of forest cover (< 50%; Betts et al., 2006). These results led Betts et al. (2006) to conclude that the greater importance of surrounding forest cover on ovenbird abundance contradicted reports that stress patch size or core area were primary predictor of bird abundance (e.g. Freemark and Collins, 1992, Burke and Nol, 1998, Bender et al., 1998). A number of other studies have reported greater likelihood of Ovenbird occurrence in contiguous forest than in small, isolated patches (e.g., Hannon and Schmiegelow, 2002, Nol et al., 2005). In Pennsylvania, densities were inversely related to woodlot size and distance to nearest edge (Mancke and Gavin, 2000). Nesting ovenbirds have a tendency to aggregate, and patterns of clustering occur independent of local habitat structure (Betts et al., 2006, Bourque and Desrochers, 2006).

Pairing/Nesting Success

The reproductive success of ovenbirds is influenced by local vegetation structure and the regional level of habitat loss and fragmentation. The proximate causes of nest failure due to forest fragmentation include reduced rates of pairing success (up to 75 %; Wander, 1985, Gibbs and Faaborg, 1990, Villard et al., 1993), and increased rates of nest predation (Wilcove, 1985, Robinson et al., 1995) and brood parasitism by brown-headed cowbirds (*Molothrus ater*; Brittingham and Temple, 1983).

Competition to attract female ovenbirds is intense and may result in strong selection by females for high-quality males or males having high-quality territories (Villard et al., 1993, Van Horn et al., 1995, Lambert and Hannon, 2000; Bayne and Hobson, 2001). Studies have shown higher pairing success in older birds (e.g., Saether, 1990, Bayne and Hobson, 2001; but see Habib et al., 2007). Pairing success has also been positively correlated with complexity of territory structure (Habib et al., 2007).

In intact forests, pairing success can range from ~50% to ~100% (Rodewald and Yahner, 2000). However, fragmentation of available habitat can have significant impacts on ovenbird pairing success across their range. In fragmented forests of eastern Ontario, Lee et al. (2002) observed significantly higher pairing success (60%) in contiguous forests (> 200 ha) than in forest patches (< 125 ha; 30% success rate). In southern Ontario, Burke and Nol (1998) found that pairing success increased most significantly with woodlot core area, increasing from 0% on smallest fragments (< 20 ha core area) to 100% on largest fragments (> 20 ha core area). In southwestern Quebec, Villard et al. (1993) found mean pairing success was 80% for ovenbirds in contiguous forests and ranged from 24% to 59% in forest patches. Similarly in Maine, ovenbirds holding territories in forest stands adjacent to clearcuts suffered lower pairing success than those in unharvested areas (Hagan et al., 1996), and in Vermont pairing success was lower within 150 m of gravel roads relative to forest interiors (Ortega and Capen, 1999). Western breeding populations are also affected by fragmentation. In Saskatchewan, pairing success was significantly lower in agricultural and silvicultural patches than in contiguous forest (Bayne and Hobson, 2001).

Nesting success can decline up to 5 years post-harvesting (Bourque and Villard, 2001). In southern Ontario, nest predation was the major factor influencing nest success and predation and brood parasitism rates were significantly inversely related to core area (Burke and Nol, 2000). In Pennsylvania, rate of nest success was greater (59%) in larger forests than fragments (< 10%; Porneluzi et al., 1993). Flaspohler et al. (2001) observed a significant effect of distance from forest edge on nest success rates in Wisconsin; nests located < 300 m from the edge had a mean success rate of 0.44 ± 0.08 (n = 47) while mean success rate of those > 300 m from the edge was 0.69 ± 0.09 (n = 49). In Minnesota, rates of nest success significantly increased with distance from clearcut edge, ranging from 0.20 at nests 0-100 m from the edge, to 0.54 at nest located > 500 m from the edge (Manolis et al., 2002). In Saskatchewan, daily nest success was greatest in contiguous forests (97.9 ± 0.8%), intermediate in forest fragments (96.7 ± 1.3%), and lowest in farm fragments (95.8 ± 1.1; Bayne and Hosbon, 2002)

Reproductive success of ovenbirds in small forest tracts may be lower than in contiguous forest due to inadequate foraging and nesting sites (Wenny, 1989). Internal humidity levels necessary to sustain invertebrate food supplies in the leaf litter may not be reached in small fragments (Wenny, 1989). Elevated levels of light and desiccation of leaf litter in small fragments are likely to have reduced densities of litter fauna, which in turn may support lower densities of Ovenbirds (Gibbs, 1988).

Fledging Success

Based on 91 nests monitored in Minnesota, Manolis et al. (2002) reported a mean of 3.79 young successfully fledged per pair (90% C.I.; 3.6, 3.99); mean fecundity (annual number of female young per female) was estimated at 1.18 (90% CI; 1.06, 1.28). In Michigan, ovenbirds averaged 2.9 fledglings per pair per breeding season (Hann, 1937). Mean female fledglings per adult female per year was 1.32 to 1.35 in contiguous forests and 0.74 to 0.59 in fragments, respectively (Donovan et al., 1995).

Cowbird Parasitism

Levels of brood parasitism by brown-headed cowbirds vary across the ovenbird’s breeding range and are most influenced by the level of forest fragmentation. There is no apparent recognition or defense against cowbirds (Hann, 1937, Rothstein, 1975). Fragmentation of contiguous forest habitat preferred by breeding ovenbirds causes higher levels of parasitism (Brittingham and Temple, 1983, Friedman et al., 1977, Donovan et al., 1995, Robinson et al., 1995, Porneluzi and Faaborg, 1999). Of 68 nests found in one study on parasitism in Saskatchewan, 17% of nests in farm fragments were parasitized, but none in the continuous forest or forestry fragments were

(Bayne and Hobson, 2002). Similarly, Donovan et al. (1995) recorded that 2%-4% of nests in contiguous were parasitized compared to 19%-67% in fragmented forests, and parasitized nests fledged fewer young. In Massachusetts, the main effect of parasitism was brood reduction; an average 1.4 fewer young successfully fledged in parasitized compared to non-parasitized nests (Hersek et al., 2002). However, there was no significant effect of parasitism on incubation period or the number of nests depredated, abandoned, or fledged (Hersek et al., 2002). In southern Ontario, nest success significantly declined with increasing levels of parasitism (Burke and Nol, 2000). Here, the number of young fledged was significantly reduced (by 50%) in parasitized nests, and parasitism rate was significantly greater (29%) within 100 m of the forest edge relative to nests in the forest interior (0%). However, Burke and Nol (2000) concluded that parasitism rates in south-central Ontario have not “seriously reduced ability to fledge at least one young.”

Site fidelity and breeding/natal dispersal

Both pairing success in the previous year and the amount and type of forest fragmentation can influence nest-site fidelity in adult male ovenbirds. In the southern boreal mixed-woods of Saskatchewan, unpaired males were significantly less likely to return in a subsequent year (11% of 28 males) than were paired males (41% of 136 males). The probability that a male would return in a subsequent breeding season when his nest was destroyed (29% of 21 males) was not significantly different from that of males with successful nests or that were observed with young (46% of 50 males; Bayne and Hobson, 2002). A similar study conducted in Missouri found that 54% of males observed with fledglings and 41% of unpaired males returned the next year, but only 10% of unsuccessful males returned (Porneluzi and Faaborg, 1999). The amount and type of fragmentation (agricultural versus silvicultural) can also influence adult dispersal rates. In Saskatchewan, males recruited into fragments in an agricultural landscape were more likely

(90%) to be first-time breeders than in forestry fragments (74%) or continuous forest (64%; Bayne and Hobson, 2002). The authors suggested that increased dispersal of males from small farm fragments was due to low reproductive success and was likely driven by high levels of nest predation. No information was found on breeding dispersal distances (i.e., how far males move away from previous nesting sites); natal dispersal distances (i.e., how far juveniles move away from hatching sites) are unknown (Villard et al., 1993).

The ability of ovenbirds to move across the breeding grounds is influenced by elements of landscape structure. In a translocation study on the homing capabilities of male ovenbirds, Gobeil and Villard (2002) found that males returned significantly faster to their territories in naturally patchy and harvested landscapes compared to in an agricultural landscape. The probability of return within 24 hours increased significantly with increasing amounts of forest cover in the landscape. Similar results were obtained in a homing study of ovenbirds in Quebec (Belisle et al., 2001), where the configuration of forest patches as well as the amount of forest cover significantly influenced return rates. Gobeil and Villard (2002) suggested that the relationship between forest cover and return rates by males may also hold for dispersing juveniles.

Annual survival rates for adults, juveniles

Reported rates of adult annual survival calculated on the breeding grounds range from 0.623 – 0.845 (Roberts, 1971, Donovan et al., 1995, Burke and Nol, 2000). Based on return rates of ovenbirds to wintering sites in Puerto Rico, adult annual survival varied from 0.53-0.63 over the period, 1989-2003 (Dugger et al., 2004). In Saskatchewan, forest fragment size was positively correlated with apparent annual survival (Bayne and Hobson, 2002). The best-fit model of apparent survival indicated that survival was significantly lower in small (< 15 ha) farm fragments (34%) in an agricultural landscape than in forest fragments (56%) or continuous forest (62%). Given that ovenbirds are monogamous, unpaired males are not uncommon, and unpaired females are rarely seen, it is likely that female survival is lower than male survival (Villard et al., 1993, Marra and Holmes, 1997, Bayne and Hobson, 2001). In a study of juvenile survival rates, King et al. (2006) observed that fledgling survival was positively significantly related to vegetation structure. Of 41 independent juvenile ovenbirds in New Hampshire, 12 were depredated and 3 succumbed to severe weather (King et al., 2006). Almost half of the dead fledglings were found buried in chipmunk burrows, while the rest were killed by accipiters. Most deaths occurred 0-3 days post-fledge, and sites where living fledglings were located had significantly greater vegetation structure than sites where dead fledglings were located (King et al., 2006). Annual survival rates of first-year ovenbirds based on recaptures on the breeding grounds range from 0.32-0.42 between, 1989 and 2003 (Dugger et al., 2004). In Michigan, only 1.6 of an average 2.9 fledglings per pair per season survived to independence (Hann, 1937).

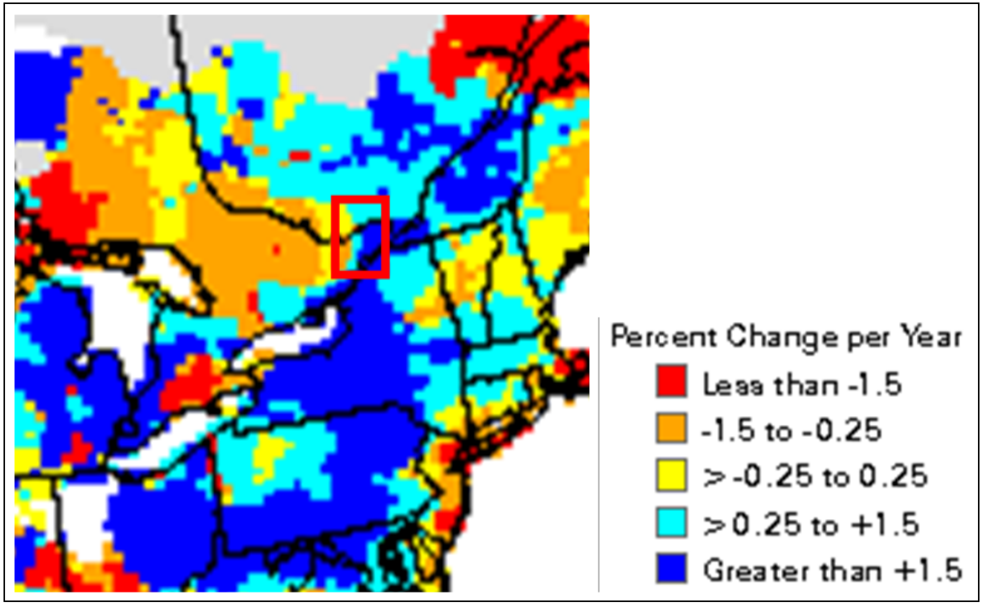
Sex Ratio

Sex ratios are thought to be biased in favor of males because there are few records of unpaired female ovenbirds on breeding grounds (Gibbs and Faaborg, 1990, Villard et al., 1993, King et al., 2000). In eastern Ontario, Lee et al. (2002) documented a high proportion of unmated males and suggested that because females migrate at different times and have different overwintering grounds than males, they may be subjected to environmental or temporal stresses that males avoid. The male-biased sex ratio may also be due to high rates of predation of females on the nest (Gibbs and Faaborg, 1990).

Population Trends

The global population of ovenbirds is predicted to decline due to habitat loss on the wintering grounds (Rappole, 1995). Based on North American Breeding Bird Survey data, Sauer et al. (2005) concluded that ovenbird numbers in Ontario significantly ($p < 0.1$) increased over the period, 1966-1979 ($n = 61$ routes), and significantly declined over the period, 1980-2005 ($n = 126$ routes). However, banding records from Long Point Bird Observatory in southern Ontario indicate no significant decline in ovenbirds in the region (Dunn, 1998). For the NAESI pilot project area the North American Breeding Bird Survey indicates a population increase greater than 1.5% during, 1966-2003 (Sauer et al., 2005) (Figure 19).

Figure 19: Population trends for the period, 1966-2003 based on the North American Breeding Bird Survey (modified from Sauer et al., 2005). The red rectangle indicates the approximate location of the NAESI pilot project area in eastern Ontario, Canada.



3.2 Non-spatial population model

Data on ovenbird demography and population biology have been compiled on the base of published data and peer-reviewed scientific studies. Table 11 shows the parameter values used for the non-spatial model. As density dependence type we chose the ceiling type in Ramas©MetaPop (see Figure 1). The ovenbird population model is a “female only” model, i.e. fecundity is calculated for female only and the results are based on the number of females. As noted in the previous section, sex ratios are believed to be slightly biased in favor of males (Gibbs and Faaborg, 1990, Villard et al., 1993, King et al., 2000, Lee et al., 2002). However, since this is likely due to lower female survival probabilities we did not consider an uneven sex ratio for the calculation of the fecundity otherwise the model would underestimate the fecundity of the population resulting in conservative results with respect to population viability. Each simulation run starts with an initial population size equal to the carrying capacity *K*. We used two stage classes: adult and juveniles. For fecundity we chose the value already implemented into a previous ovenbird PVA (see Larson et al., 2004) (see Table 11). Data on juvenile and adult survival rates are based on the study by Donovan et al. (1995) and have been used in the PVA by Larson et al. (2004). Ranges for standard deviations of fecundity and survival rates are equivalent to the ones used in the PVA by Larson et al. (2004).

Table 11: Model parameters for the non-spatial ovenbird population model.

Parameter	Value/Range	Comments
Stage classes	2	juveniles and adults; Van Horn and Donovan, 1994
Fledglings	2.8 (fledglings per female)	Donovan et al., 1995; Larson et al., 2004
Proportion of females	0.5	Own estimation; likely biased in favor of males, however this may be due to higher rates of predation of females on the nest (see p. 40); Gibbs and Faaborg, 1990, Burke and Nol, 1998
Adult fecundity (female juveniles per female adult)	1.4 (SD 0.42) (=30% CV)	1.0 * (broods) *2.8 (fledglings) * 0.5 (sex ratio) * 1.0 (pairing success); CV based on Larson et al., 2004
Juvenile survival	0.31 (SD 0.046) (=15% CV)	Donovan et al., 1995; Larson et al., 2004
Adult survival	0.623 (SD 0.093) (=15% CV)	Donovan et al., 1995; Larson et al., 2004

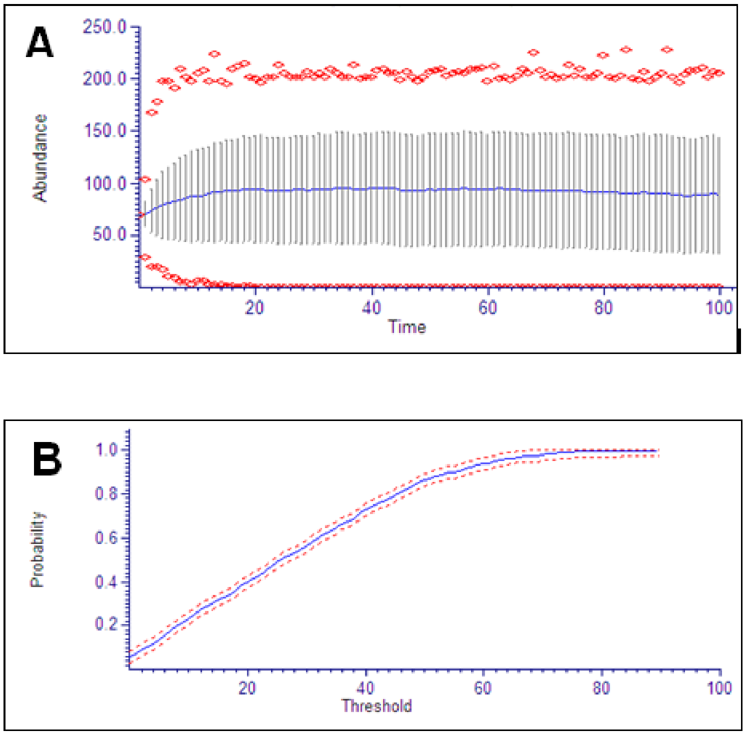
Table 11: Model parameters for the non-spatial ovenbird population model.

Parameter	Value/Range	Comments
Initial abundance	10-100	Number of individuals at t=1
Carrying capacity	Same as initial abundance	Number of individuals at which the carrying capacity is reached
CV of *K*	10%	Own estimation; coefficient of variation around which the carrying capacity varies;
Density dependence type	Ceiling type	-
Simulated years	10-100 years	-
Replications	1000	-
Demographic stochasticity	yes	Number of survivors and dispersers (emigrants) to be sampled from binomial distributions, number of young from a Poisson distribution.
Environmental stochasticity	lognormal	statistical distribution to be used in sampling random numbers for vital rates
Dispersal	No	non-spatial version
Disturbance	No	-

Figure 20 (panel A) shows the average population trend for a single ovenbird population (adult females only). A total of 69 initial adult females and 91 juvenile females (based on the stable age distribution) generate a population that is viable with 95% confidence over a time frame of 100 years. Final MVP after 100 years is ~89 adult females. The interval extinction risk for a final MVP size of ~89 adult females is given in Figure 20 (panel B). Each point in the curve shows the probability at which population abundances will fall below a certain threshold at least once during the next 100 time steps. With increase in simulation time the size of the MVP increases (Figure 21). The two lines in Figure 21 show that an initial population size of ~69 adult females (equivalent to approximately 69 breeding pairs) would increase during 100 years to a final population size of about 89 breeding pairs. The proportion of simulation runs that resulted in an extinction event for this population size was less than 5%.

By using the MVP size as model output we conducted a sensitivity analysis for juvenile and adult survival rates as well as fecundity (Figure 22). As indicated in Figure 21 initial population size was always lower than the final population size (i.e., the population experienced a positive population trend). Depending on the sensitivity of the parameter analyzed this changed when survival or fecundity were reduced. Here, initial population size had to be several orders of magnitude higher than the resulting final population size. Based on the initial model assumptions, adult survival appeared to be most sensitive, followed by juvenile survival and fecundity (Figure 22). The pattern of parameter sensitivity from this study is equivalent to the results presented in the Larson et al. (2004) study. The latter PVA was based on a single population inhabiting an area of approximately 711 km^2 of southern Missouri continuous forests and the assumption that all habitat was potentially available to all individuals (i.e., no dispersal barriers).

Figure 20: Average predicted population abundance over 100 years for 1000 replicates based on an initial population size of 69 adult female ovenbirds (panel A). Panel B shows the interval extinction risk for the non-spatial ovenbird PVA for a final minimum viable population size of ~89 adult females (100 years simulation time).



The vertical lines indicate the range of the standard deviation and the red trapeziums show the observed maximum and minimum values. A total of 69 initial adult females and 91 juvenile females (based on the stable age distribution) generate a population that is viable with 95% confidence over a time frame of 100 years. Final MVP after 100 years is ~89 adult females.

Figure 21: Final (squares) and initial (diamonds) minimum viable population size for different time spans (for <5% extinction risk).

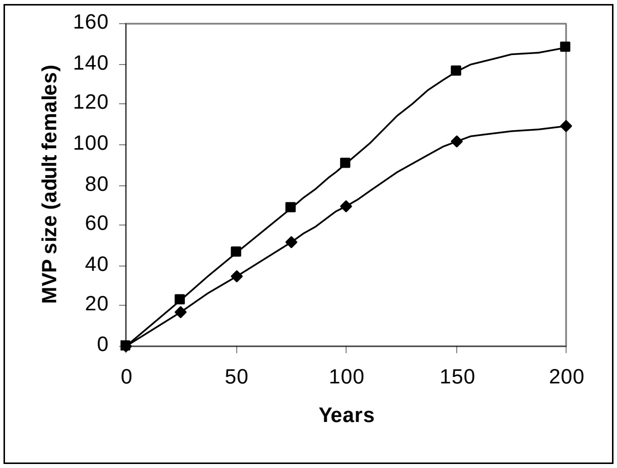
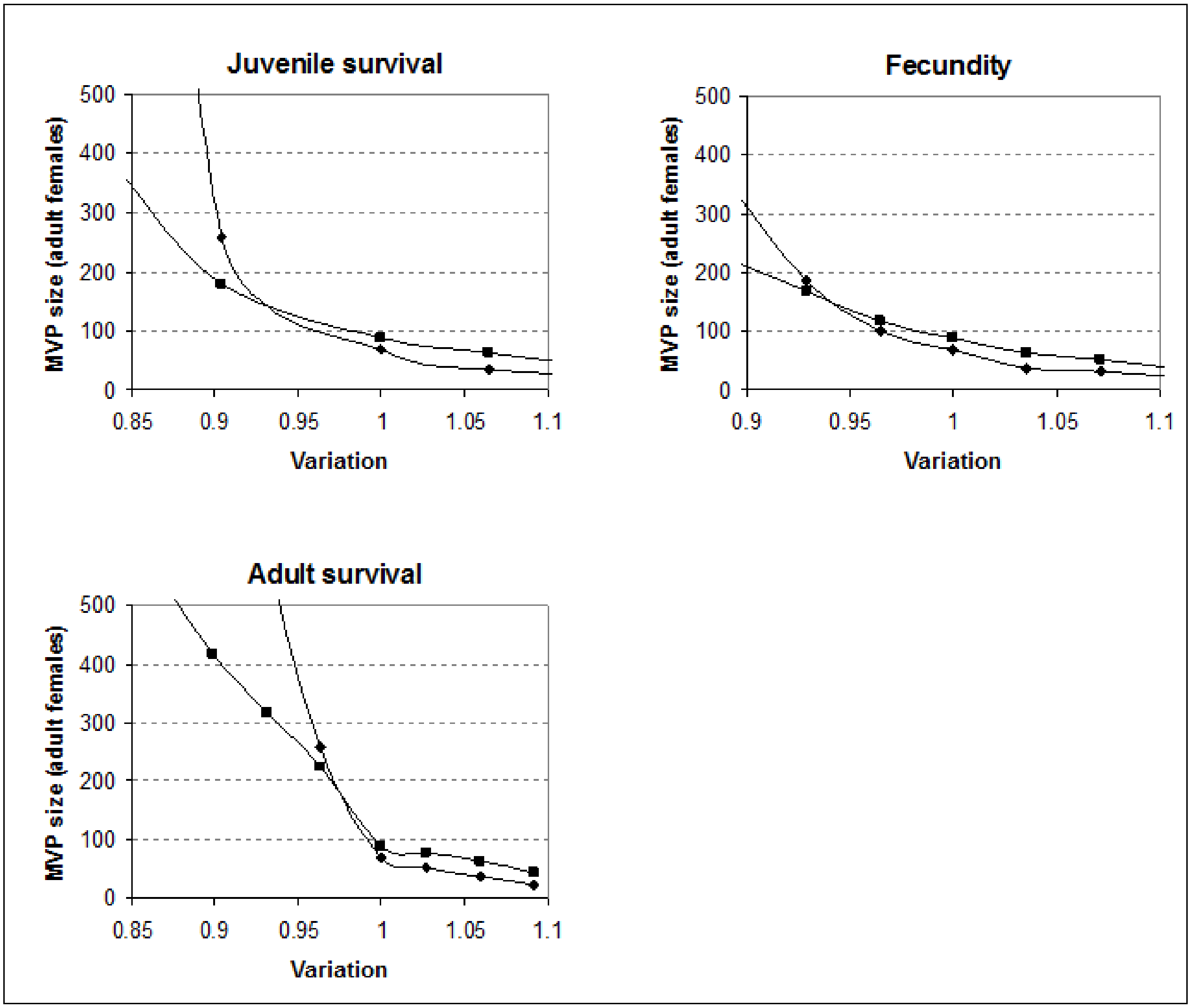


Figure 22: Final (squares) and initial (diamonds) minimum viable population size for relative changes in juvenile and adult survival rates and fecundity for ovenbirds (simulation time is 100 years with <5% extinction risk). Results are averages of 1000 replicate simulation runs.



By assessing average population densities the results from this demographic analysis can be used to estimate the amount of breeding habitat required to maintain a single population over a specific time frame. Based on the model we found that in order to achieve an extinction risk of less than 5% over 100 years a MVP size of 89 adult females is needed. In southern Ontario, ovenbird densities range from 0.033 male/ha on smaller woodlots (80 ha) to 0.83 male/ha in contiguous forests (Burke and Nol, 1998). For eastern Ontario in the vicinity of the NAESI pilot project study area, average densities for occupied patches are reported at 0.12 male/ha (SD=0.14) or 8.3 ha/male (Lee et al., 2002) which is within the reported range for other breeding areas (see Table 10). Based on these estimates and an even sex ratio we calculated a minimum viable patch size of ~742 ha for an ovenbird population to be persistent over 100 years with a confidence of 95%.

However, it has to be denoted that this number may be strongly variable due to the model assumptions and the high standard deviations for estimated population densities in eastern Ontario. In addition, this figure will be higher if pairing success is less than 100%. Despite these uncertainties our estimated minimum patch size corresponds well with assumed minimum patch sizes based on expert knowledge (e.g., Burke and Nol, 1998). For example, Burke and Nol (1998) suggested 500 ha as the minimum size for a source population in southern Ontario (i.e., where the intrinsic growth rate $\lambda>1.0$).

3.3 Habitat suitability model and spatial population viability analysis

Prior to conducting the spatial ovenbird PVA we developed a habitat suitability index (HSI) model that describes the relationship between habitat features and ovenbird habitat suitability and demography. As opposed to the binary suitability in the marsh wren model, land cover availability, knowledge on habitat requirements and autoecological response patterns allowed a continuous suitability index for each cell on the landscape.

3.3.1 Habitat suitability model

The HSI value for each cell in the spatial ovenbird model is determined by multiplying the HSI value of forest type by forest age and reducing this value by 50% if a habitat cell is located at an edge to an open or near-open habitat (Figure 23).

Edge and core habitat

Frequency of nest parasitism by brown-headed cowbirds has been reported as lower in contiguous forested tracts than in forest fragments (Donovan et al., 1995). In fragmented landscapes ovenbirds raise more brown-headed cowbirds than in contiguous forest landscapes (Porneluzi and Faaborg, 1999). However, habitat suitability was not reduced near edges with forested land cover types because edges between forest or woodland types have not been shown to affect habitat suitability for ovenbirds (Larson et al., 2004).

Forest type

With respect to different forest types, we assigned deciduous forest types an HSI value of 1.0 and mixed forests a value of 0.75 (coniferous forests were assumed to be unsuitable) as ovenbirds are known to tolerate certain proportions of coniferous trees in eastern Ontario (Lee et al., 2002) (Figure 23). Another option may be to increase the habitat suitability value with increase in the proportion of deciduous trees as done in the HS model of Romito et al. (1999).

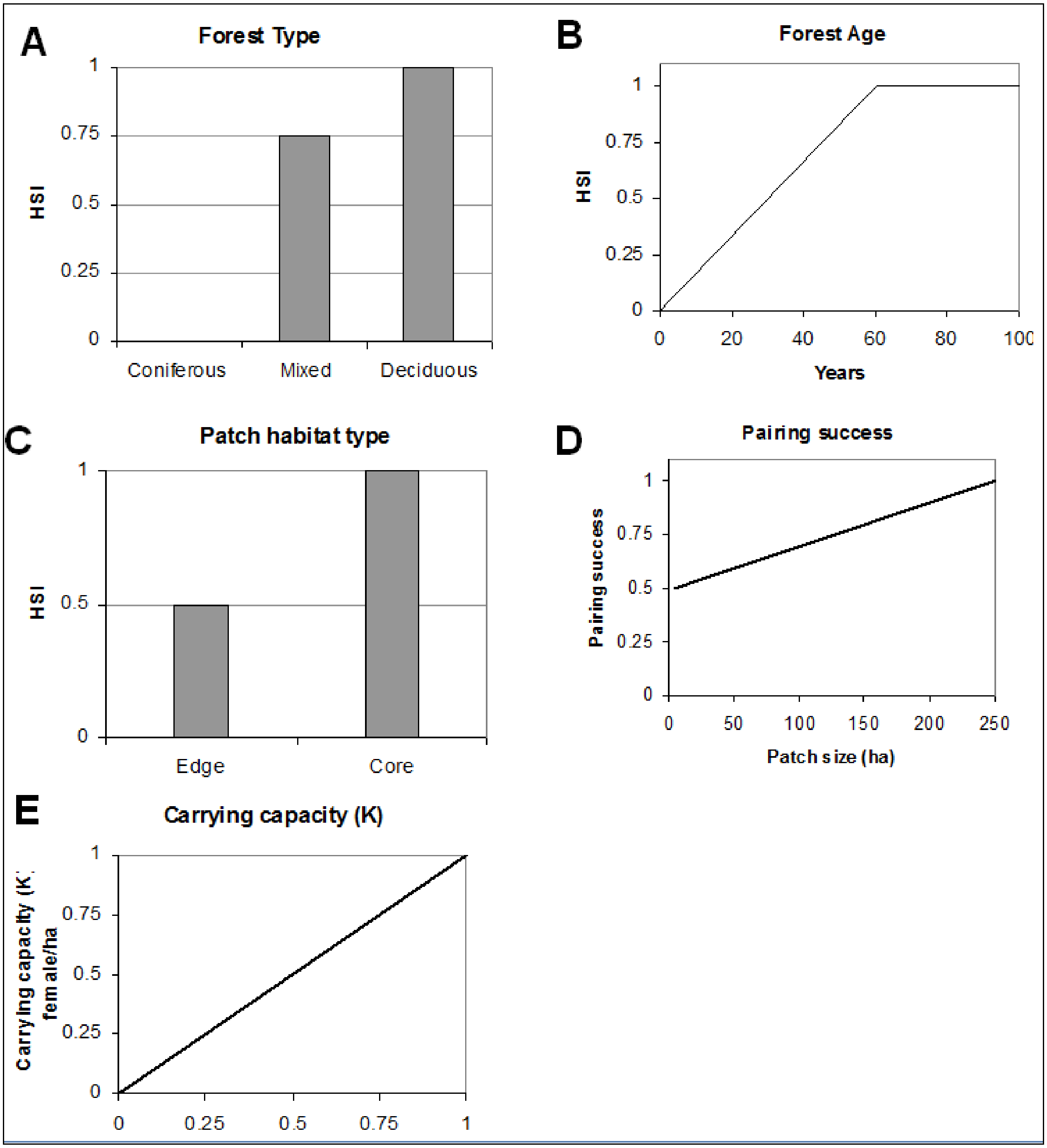
Forest age

Habitat suitability as a function of forest age reached 1 at a threshold age of 60 years (considered as mature). In the HS model forest age is based on the, 1991 inventory data. Since the majority of forest stands are relatively young and have not reached a climax stage we added 15 additional years to account for the current age strucuture.

Habitat suitability threshold

In Ramas©GIS the user defines a habitat suitability threshold for patches as the minimum HSI value below a species cannot reproduce (even though it can disperse through). Technically, this value is used to delineate suitable cells, which are then connected according to the neighborhood distance parameter to form ovenbird population patches. We chose an HSI value of 0.51 which is realistic for two reasons. Firstly, ovenbirds usually do not breed within 30 m of forest edges and the HSI value for edge habitat in the model is reduced by 50%. That is, edge habitat would be assigned a maximum value of 0.5 for a deciduous, mature forest. Secondly, this threshold value allows mature mixed forest patches to be assigned a population, as ovenbirds may generally reproduce in mixed forests. The estimated neighborhood distance in the model is one cell due to the high association of ovenbirds with interior habitat and the known variation of fecundity with patch size. In other words, each suitable forest patch in the spatial model will be assigned a separate population.

Figure 23: Habitat suitability model and functional relationship between habitat suitability and two demographic parameters.



Forest type (A), forest age (B) and patch habitat type (C) govern the habitat suitability index value for each cell in the habitat suitability map. Core habitat is defined as habitat with a distance of >30 m from adjacent open or near-open habitat (e.g. agriculture). Pairing success (D) is a function of the size of a patch, i.e. fecundity increases with patch size. Carrying capacity (E) for each ovenbird population patch depends on its respective size and the average habitat suitability index value for that patch.

Habitat suitability and carrying capacity

The suitability values that were calculated for the habitat suitability map were then used to determine the carrying capacity *K* for each ovenbird population patch in the initial year of a simulation run (Figure 23). Note that incorporating dynamic landscape change (e.g., forest succession) is beyond the scope of this study and habitat suitability values implemented into the PVA are constant over time. Based on maximum reported male densities (e.g., Holmes and Sherry, 2001, Mazerolle and Hobson, 2004) (and assuming an equal sex ratio), *K* values in each patch may range from 0 to 1.0 females/ha depending on the HSI value (Table 12 and Figure 23). This average value is then multiplied by the respective size of each patch to account for larger patches having larger carrying capacities.

Patch size and pairing success

Pairing success has been shown to increase with patch size (e.g., Gibbs and Faaborg, 1990, Lee et al., 2002). However, a recent meta-analysis showed that the proportion of paired ovenbird males increased with conspecific density after accounting for forest cover. That is, populations with higher densities seem to attract ovenbird females, suggesting that the female choice of breeding habitat is likely driven at least in part by male population density (Bourque and Desrochers, 2007). However, In Ramas©GIS it is not possible to make pairing success of a population partly dependent on its annual population density. Therefore pairing success in the model is a function of the size of a patch, i.e. fecundity increases with patch size. Pairing success reached 100% for patches larger than 250 ha (largest deciduous and mixed forest patches in the NAESI pilot study area). Forest patches smaller than 5 ha were considered to be unsuitable (Galli et al., 1976, Robbins et al., 1989).

Further parameters used in the spatial model version are shown in Table 12. To facilitate the comparison of our results with the Larson et al. (2004) PVA we assumed a coefficient variation of 10% for the carrying capacity and 15% for adult fecundity. Unfortunately, empirical data on breeding and natal dispersal are lacking and we therefore made assumptions with respect to the maximum dispersal distance and the rate of dispersal (see Table 12). Due to data unavailability we also assumed the same correlation distance function as in the marsh wren PVA.

Table 12: Model parameters for the spatial ovenbird PVA.

Parameter	Value/Range	Comments
Carrying capacity *K*	0-1.0 females/ha	Based on maximum reported male densities (Table 10) *K* was assumed to increase linearly from 0 to 1.0 for a habitat suitability index value of 0.0 to 1.0
CV of *K*	10%	Own estimation; coefficient of variation for the carrying capacity;
Initial abundances	=Carrying capacity	Initial abundance of juveniles and adults in year 1 based on the stable age distribution from the stage matrix
Female adult fecundity (female juveniles per female adult)	0.7-1.4 (15% CV)	1.0 * (broods) *2.8 (fledglings) * 0.5 (sex ratio) * 0.5-1.0 (pairing success); model assumes that pairing success increases linearly from 0.5 to 1.0 between patch sizes ranging from 5 (minimum patch size) to 250 ha; CV based on Larson et al., 2004; (see Figure 24)
Dispersal rate	0.1	Own estimation due to unknown dispersal characteristics of ovenbird; maximum dispersal rate (nearest cell); decreases towards 0 up to the maximum dispersal distance;
Maximum dispersal distance	5.0 km	Own estimation; assumed max. distance for natal dispersal; non-linear dispersal kernel is assumed
Correlation	Function parameters: *a*=1.0; *b*=1.9; *c*=1.0;	Own estimation; correlation among the vital rates of populations; represents the similarity of environmental fluctuations; empirical data not available, estimate is based on a negative exponential function ranging from 1.0 (nearest patch) to 0 (maximum edge to edge distance in study area 1 and 2)

3.3.2 Case study areas

The NAESI pilot project study area is located in the easternmost portion of Ontario, Canada. Due to the large extent of the NAESI pilot project area we selected three case study areas (Figure 24). The three case study areas selected for the metapopulation analysis are indicated by red squares. The areas are approximately 14.8 * 13.5 km in size (ca. 20,000 ha). A HS map with a 30m*30m cell size was created for each of these areas based on the assumption made in the HS model. The size of each case study area is approximately 20,000 ha and equivalent in size to the ones selected for the marsh wren. Area 3 has the highest amount of forest cover and the largest average patch size within the NAESI area. Figures 25 and 26 show a smaller sample of area 3 (high density area). Figure 26 shows the final HS map based on the location of edge and core habitat, forest age, and forest type. A summary of the landscape characteristics for each case area is presented in Tables 13 and 14. Area 1, 2 and 3 have an amount of 5.1%, 11.8% and 20.8% of deciduous and mixed forest cover, respectively. However, after applying the HS model and the minimum patch size of 5 ha amounts of suitable habitat were reduced to 1.8%, 5.8% and 12.3%, respectively. Average size of all patches larger than 5 ha was 10.2, 13.5 and 19.2, respectively (Table 14). All areas have a high proportion of smaller forest patches whereas larger patches are rare. For example for the low density area 1 nearly 75% of all patches are smaller than 5 ha and only 2% are 25-49 ha in size (Figure 27).

Figure 24: Distribution of coniferous (blue), mixed (red) and deciduous (green) forests in the NAESI pilot project counties of Stormont, Dundas, and Glengarry.

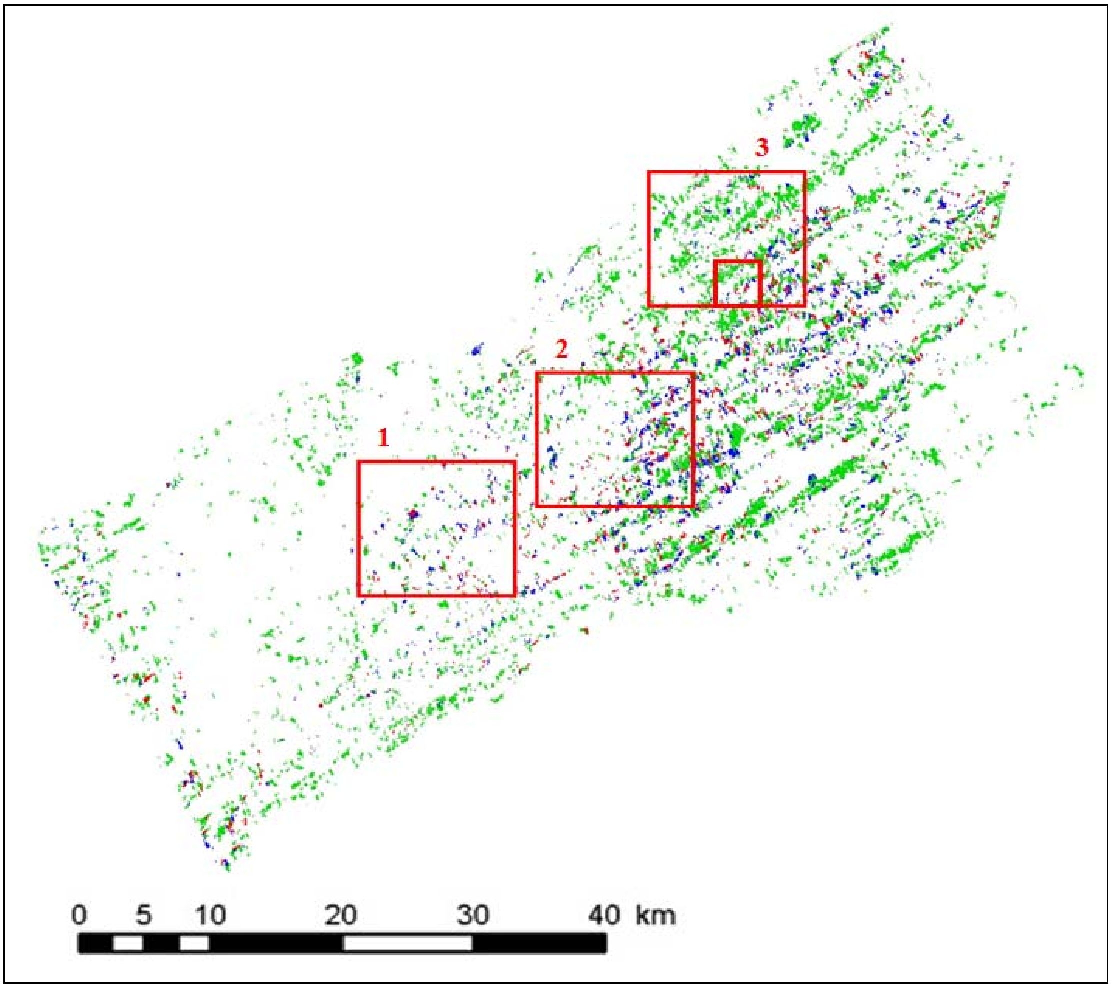


Figure 25: Pattern of edge vs. core habitat for the spatial ovenbird HS model (small sample area within area 3).

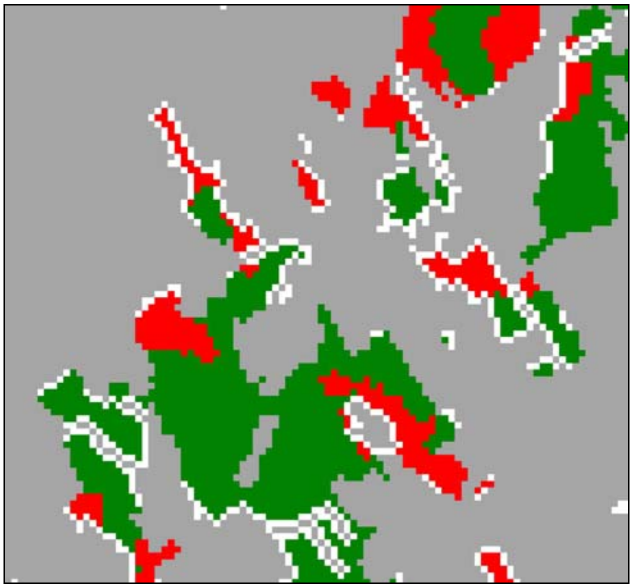


Figure 26: Ovenbird habitat suitability map of the same sample area as shown above (within area 3).

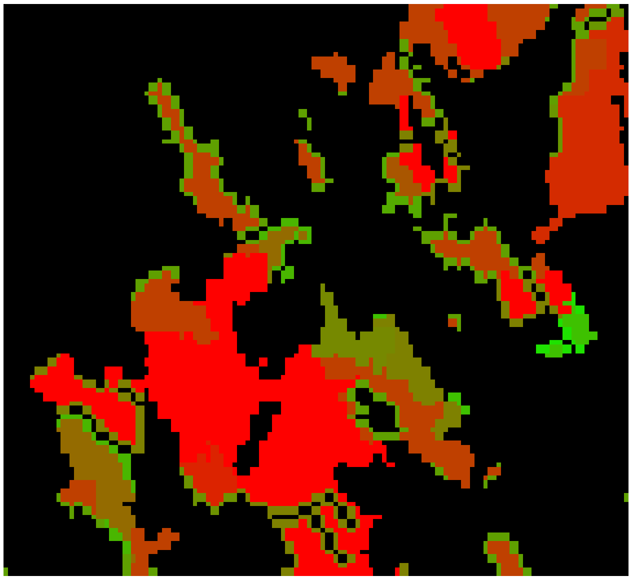


Table 13: Distribution of forest types, edge and core habitat and ages classes for three ovenbird case study areas and the NAESI pilot project region.

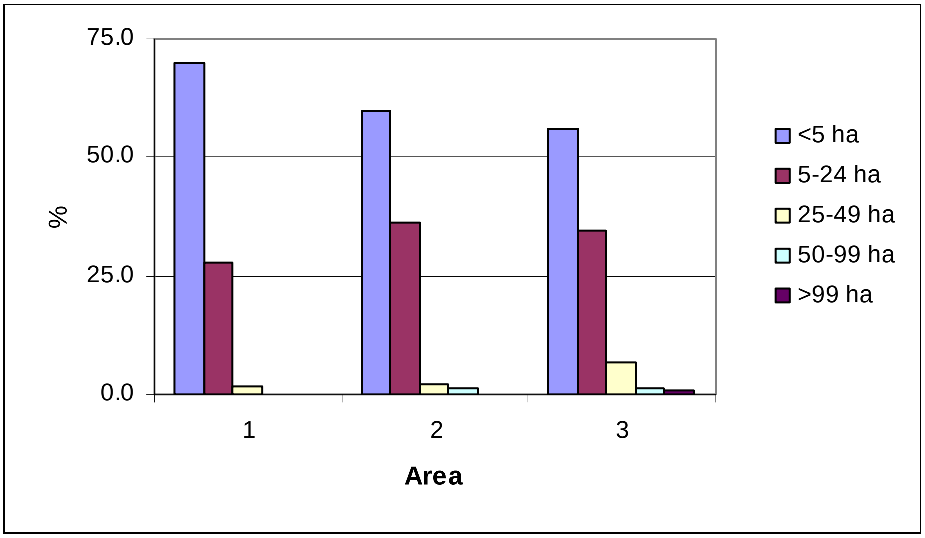
	1		**2**		**3**		**NAESI**	
Area	**Size (ha)**	**Area (%)**	**Size (ha)**	**Area (%)**	**Size (ha)**	**Area (%)**	**Size (ha)**	**Area (%)**
Forest type								
Deciduous	3,656	18.3	1739	8.7	738	3.7	26,488	8.0
Mixed	498	2.5	614	3.1	271	1.4	4234	1.3
Other land	15,846	79.2	17,647	88.2	18,991	94.9	298,820	90.7
	20,000	**100.0**	**20,000**	**100.0**	**20,000**	**100.0**	**329,542**	**100.0**
Habitat								
Edge		21.9		28.0		28.8		26.7
Core		78.1		72.0		71.2		73.3
		100.0		100.0		100.0		100.0
Age								
< 21 yrs		10.2		6.5		9.8		10.5
21 - 40 yrs		3.2		5.0		3.7		7.4
41- 60 yrs		26.3		31.3		30.8		35.5
> 60 yrs		60.3		57.3		55.7		46.6
		100.0		100.0		100.0		100.0

Table 14: Spatial landscape indices, habitat suitability and carrying capacity for study area 1, 2 and 3.

	Area 1	**Area 2**	**Area 3**
# of forest patches	114	217	284
# of suitable population patches*	37	87	128
Average patch size (>5 ha) (ha)	10.2	13.5	19.2
Total area of suitable population patches (km^2)	3.7	11.7	24.6
Amount of deciduous and mixed forest in landscape (%)	5.1	11.8	20.8
Amount of suitable forest habitat in landscape (%)*	1.8	5.8	12.3
Average HSI value for suitable population patches	0.90	0.88	0.93
Total carrying capacity (females)	339	1065	2325

**patch size >5 ha; average HSI value per patch>0.51*

Figure 27: Patch size distribution for case study area 1, 2 and 3 in the NAESI pilot project area



3.3.3. *Results from the spatial PVA*

The results from the spatial population viability analysis indicate that all three metapopulations have a high risk of extinction and thus strongly negative population trends. Figures 28, 29, and 30 show the average population trajectory, metapopulation occupancy and the time to extinction for case study area 1, 2 and 3. The simulated metapopulation in area 1 (low density) with a carrying capacity of 339 females went extinct in 475 out of 500 replicate runs (Table 15). Even the higher density area 3 (highest average deciduous and mixed forest cover in the NAESI pilot project area) exhibited an extinction risk of 69% after 50 years of simulation time.

Figure 28: Average population trajectory, (A) metapopulation occupancy (B) and time to extinction (C) for 500 simulation runs for study area 1 (low density) for Study Area 1 (low density). Simulation time is 50 years.

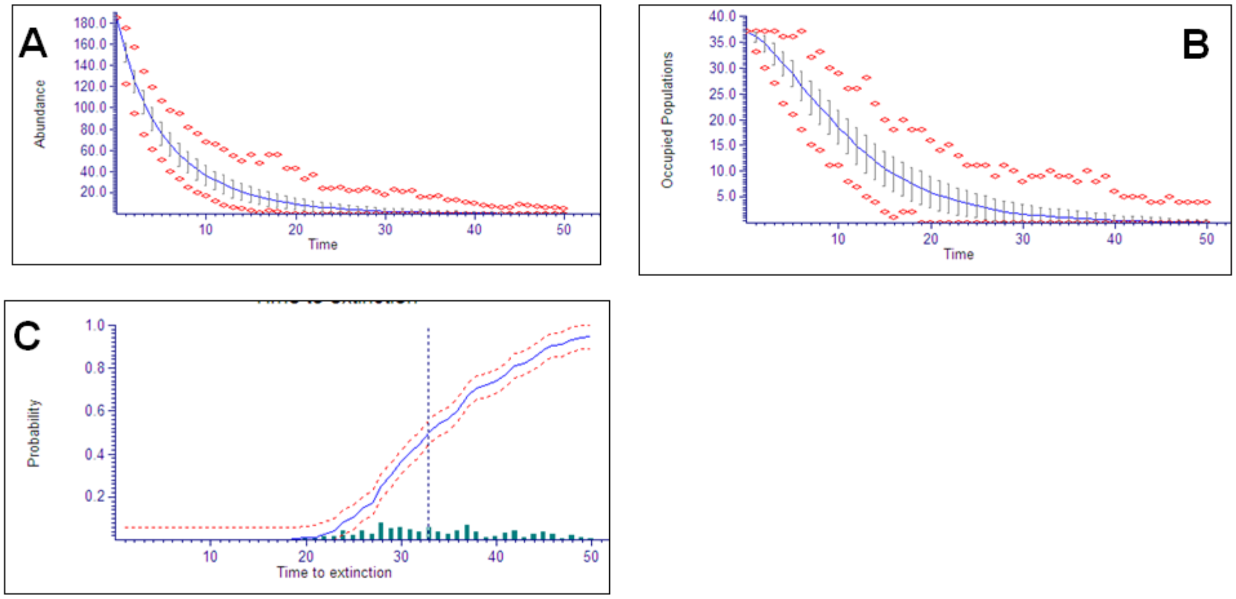


Figure 29: Average population trajectory, (A) metapopulation occupancy (B) and time to extinction (C) for 500 simulation runs for study area 2 (medium density). Simulation time is 50 years

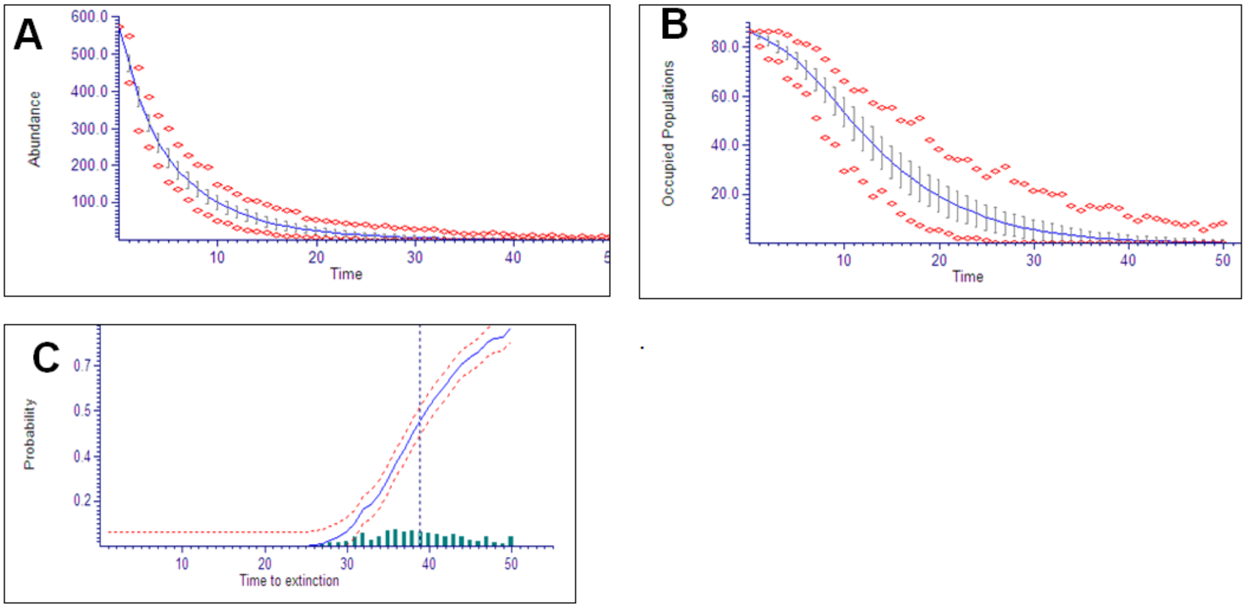


Figure 30: Average population trajectory, (A) metapopulation occupancy (B) and time to extinction (C) for 500 simulation runs for study area 3 (high density). Simulation time is 50 years.

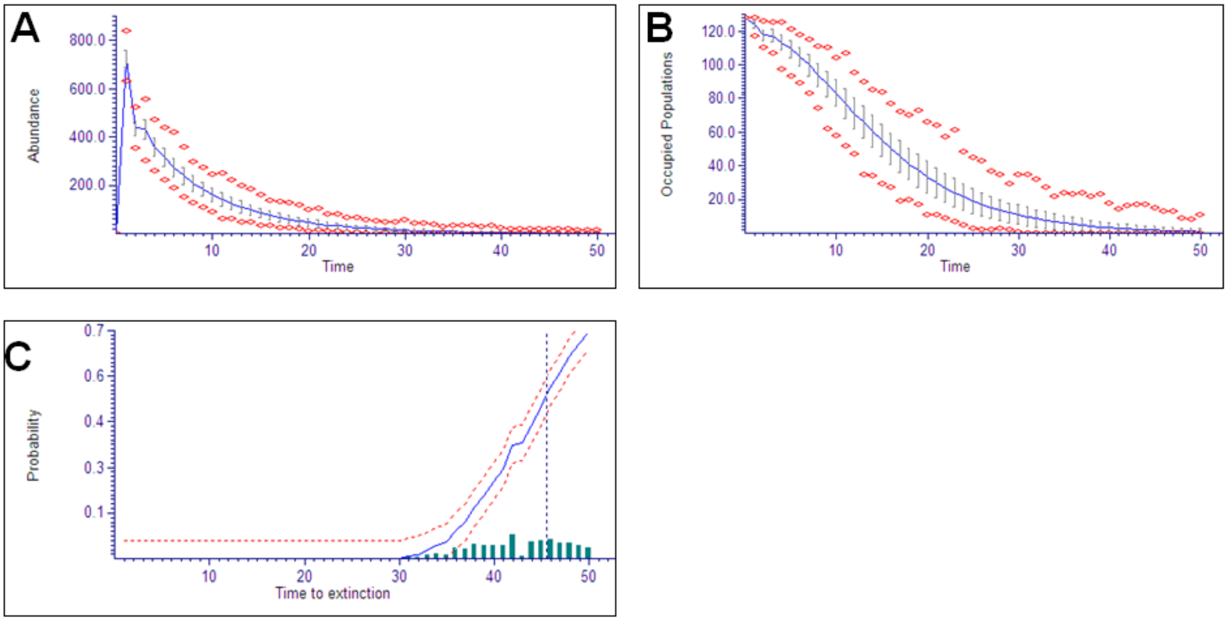


Table 15: Summary of population viability measures for study area 1, 2 and 3 (500 replicate simulation runs).

	Area 1	**Area 2**	**Area 3**
Extinction risk (100 yrs)	100%	100%	100%
Extinction risk (50 yrs)	95%	87%	69%
Estimated minimum abundance (EMA)	0.1	0.2	0.6
Population trend (effective growth rate t_{50}/t_1)	<0.001	<0.001	0.001

With respect to the sensitivity of parameters of the spatial model we found that pairing success resulted in the highest change in the model ouput (Table 16). Changes in the relationship between patch size and pairing success have a high effect on population viability, because the pairing success rate alters the fecundity rate in each patch. Generally, a pairing success rate below 72% (i.e., a patch size of ~ 100 ha) will result in an ovenbird population being a sink. Note that this conclusion may be altered if the maximum patch size to allow 100% pairing success is changed and/or should the fledging rate deviate from the assumed 1.4 female/adult female. During the sensitivity analysis we also found that changes in the carrying capacity did not result in significant changes of the model output. This is largely due to the fact that the temporal dynamics of the majority of populations are usually far below the carrying capacity, i.e. in most cases populations do not reach the population ceiling imposed by the model. Finally, we found that an increase in the dispersal distance/rate did not increase population persistence. In general, we found no dispersal-limitation as ovenbirds are primarily limited by the size of suitable forest patches.

Table 16: Summary of parameter sensitivity for additional model parameters in the spatial ovenbird HSM and PVA.

HS/population model parameter	Effect on model output	Comment
Pairing success	high	Changes in the patch size – pairing success relationship have a high effect on population viability; a pairing success below 72% will result in a patch being a population sink ($\lambda<1.0$); an increase in the assumed maximum patch size required for 100% pairing success (250 ha) will reduce metapopulation viability
Carrying capacity	low	Changes in the HSI - carrying capacity relationship have a low effect on population viability; an increase in the carrying capacity does not decrease extinction risk as the majority of (small) populations are population sinks and do not reach the population ceiling imposed by the model
Dispersal rate/distance	low	No dispersal limitation; in fragmented areas (where dispersal barriers often limit population growth) ovenbirds are primarily limited by the size of suitable forest patches; therefore, increase in the assumed dispersal distance/rate does not increase population persistence

Based on the model assumptions and the projections we therefore conclude that the current amount of forest cover and the small patch sizes of deciduous and mixed forests in the NAESI area do not support persistent ovenbird populations. We suggest that the entire NAESI area may be a population sink and is only maintained if sufficient numbers of birds immigrate from other areas. Donovan et al. (1995) came to a similar conclusion for ovenbird habitat in Wisconsin and Minnesota: when similar demographic values were used in population growth models, ovenbird populations in fragments declined to near extinction within 20 years without immigration.

Notably, between, 1966 and 2003 ovenbirds showed a slightly positive population trend in the NAESI area (Figure 19). This contradiction is explained by two facts. Firstly, during the past decades agricultural lands in the NAESI pilot study area have been abandoned and forest cover has generally increased. Secondly, recent findings in dispersal ecology of song birds which showed that median natal dispersal distances for many North American songbird species are more than an order of magnitude larger than previously reported (Tittler et al., 2006). Therefore source sink population dynamics occur over large spatial scales and may result in apparently positive trends in agriculture-dominated and fragmented areas with otherwise low persistence.

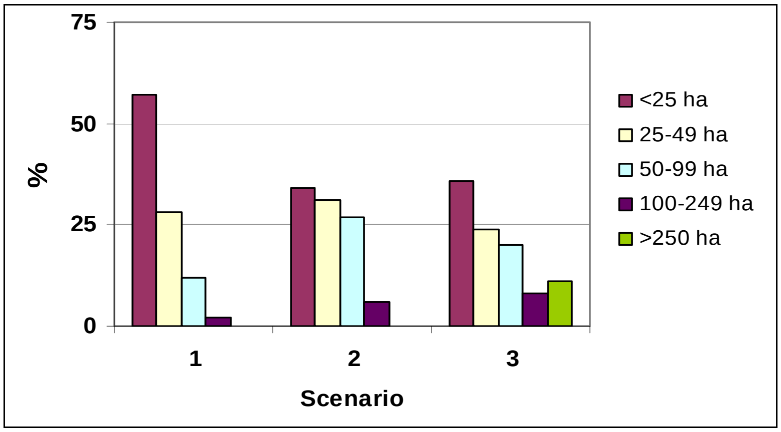
Due to the apparent high extinction risk of ovenbirds in the NAESI pilot project study area we aimed at finding a threshold scenario which could indicate suitable landscape conditions for longer term ovenbird persistence without immigration from outside. We generated three metapopulation scenarios where 101, 91 and 69 populations were randomly placed on a 200 km^2 ha landscape. Each population patch was assigned a patch size and a HS value between 0.85 – 0.95 (average range for NAESI case study areas) and fecundity and carrying capacity were re-calculated for each patch. The summary statistics show that average patch size was 36.1, 54.9 and

91.8 for scenario 1, 2 and 3, respectively (Table 17). This is equivalent to 18.2%, 24.9% and 31.7% of suitable forest land cover, respectively. Patch size distributions for scenario 1, 2 and 3 indicate an increase in the proportion of larger patch sizes with up to 8 patches of more than 250 ha in scenario 3 (Figure 31).

Table 17: Landscape indices and total carrying capacity of scenario 1, 2 and 3.

	Scenario 1	Scenario 2	Scenario 3
# of suitable population patches	101	91	69
Average patch size (ha)	36.1	54.9	91.8
Amount of suitable forest habitat in landscape (%)	18.2	24.9	31.7
Total carrying capacity (females)	3578	4916	7550

Figure 31: Patch size distribution of scenario 1, 2 and 3.

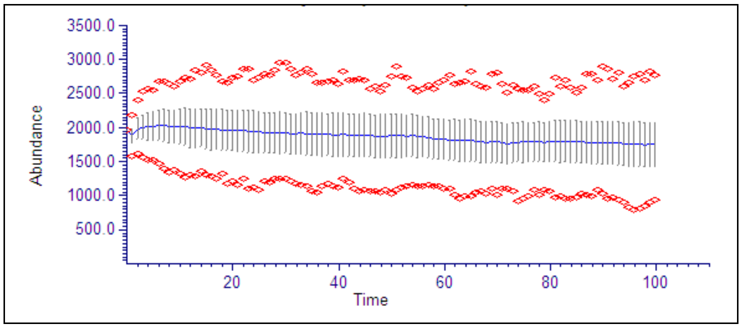


The only scenario that generated a persistent metapopulation with 5% confidence over a time frame of 100 years was scenario 3 with more than 30% of suitable forest cover and a 19% proportion of source patches larger than 100 ha (i.e., λ>1.0) (Table 18). Even though extinction risk was 0% the population trend was clearly negative with a population decline to 63% of the initial abundance. This was due to the fact that the majority of smaller forest patches act as population sinks (with low fecundity) and become unoccupied during the course of a simulation. Thus, in order to achieve stable population trends the proportion of larger source patches must be significantly higher. For example, for a scenario of 25 suitable forest patches each 250 ha in size (i.e., 100% pairing success) and 25 patches of 50 ha, totaling ~37.5% suitable forest cover (i.e., 50% of the metapopulation being source patches) the population trend over 100 years increased to an effective growth rate of 0.89 (Figure 32). When these patches were 100 ha and 50 ha, respectively, totaling to the same habitat amount of 37.5% (i.e., 50*100 ha and 50*50 ha patches), extinction risk was 42% and the population trend strongly negative. This led us to the conclusion that the proportion of sink vs. source population patches and the respective size distribution of the source patches may be a strong predictor of ovenbird viability. Interestingly the threshold range that we found (30-40% suitable forest cover) corresponds well with findings from a recent study on thresholds in songbird occurrence in relation to landscape structure (Betts et al., in press). This study reports a significant threshold in ovenbird occurrence at ~28% forest cover on a slightly smaller spatial scale.

Table 18: Summary of population viability measures for scenario 1, 2 and 3 (500 replicate simulation runs).

	Scenario 1	**Scenario 2**	**Scenario 3**
Simulation time 50 yrs			
Extinction risk	23%	0%	0%
Estimated minimum abundance (EMA)	6.8	82.8	374.2
Population trend (effective growth rate t_{50}/t_1)	0.03	0.12	0.77
Simulation time 100 yrs			
Extinction risk	91%	17%	0%
Estimated minimum abundance (EMA)	0.3	18.8	267.4
Population trend (effective growth rate t_{100}/t_1)	<0.001	0.03	0.63

Figure 32: Average population trajectory (500 replicate runs) for a scenario with a 50% proportion of source patches (250 ha; fecundity = 1.4) and 50% sink patches (50 ha; fecundity = 0.82). Effective growth rate (t_{100}/t_1) is 0.89.



3.4 Conclusions

Based on the demographic model shown in the previous section we found a MVP size of 89 adult female ovenbirds to be viable with 95% confidence over a time frame of 100 years. For eastern Ontario in the vicinity of the NAESI pilot project study area average densities for occupied forest patches are reported at 0.12 ind/ha. Based on these estimates we calculated a minimum viable patch size of ~742 ha for an ovenbird population to be persistent over 100 years with a confidence of 95%.

For the spatial version of the ovenbird model we developed a habitat suitability index (HSI) model that describes the relationship between habitat features and ovenbird habitat suitability and demography. As opposed to the binary suitability in the marsh wren model, land cover availability and knowledge on habitat requirements allowed a continuous suitability index for each spatial unit on the landscape. The HSI value for each cell in the spatial ovenbird model was determined by multiplying the HSI value of forest type by forest age and reducing this value by 50% if a habitat cell was located at an edge to an open or near-open habitat. The suitability values that were calculated for the habitat suitability map were then used to determine the carrying capacity K for each ovenbird population patch. Pairing success in the model is a function of the size of a patch, i.e. fecundity increases with patch size and reached 100% for patches larger than 250 ha. Forest patches smaller than 5 ha were considered to be unsuitable.

Due to the large extent of the NAESI pilot project study area we selected three case study areas, approximately 200 km^2 in size, and created a HS map for each of these areas. All areas have a high proportion of smaller forest patches and only a few larger than 100 ha. The total amount of suitable forest cover was 8%, 5.8% and 12.3%, respectively. The results from the spatial population viability analysis indicate that all three metapopulations have a high risk of extinction and thus strongly negative population trends. Based on the model assumptions and projections we therefore conclude that the current amount of forest cover and the small patch sizes of deciduous and mixed forests in the NAESI area do not support persistent ovenbird populations. We propose that the entire NAESI area may act as a population sink and is only maintained if a sufficient number of birds immigrate from outside.

To find a habitat threshold for ovenbirds we then generated three hypothetical landscape scenarios (~200 km^2 in size) with higher suitable forest cover and larger patch sizes. We found that the proportion of sink vs. source populations patches and the respective size distribution of source patches was a strong predictor of ovenbird viability. Habitat-based standards related to dispersal (such as maximum tolerable distance between two nearest patches) were found to be less important due to the area-sensitivity of ovenbirds. For the ovenbird we propose the following habitat-based standards that need to be fulfilled in order to achieve longer term persistence and near stable population trends for fragmented agricultural areas in eastern Ontario (assuming no immigration from outside):

1. a minimum viable patch size of ~742 ha assuming that all individuals reside in one patch/population,
2. a minimum metapopulation patch size that allows a minimum intrinsic growth rate of 1.0 (~100 ha in this study),
3. a minimum of 30-40% suitable forest cover on a 200 km2 landscape scale (depending on the patch size distribution), and
4. for near stable population trends a minimum proportion of ~50% source patches with a minimum source patch size that facilitates 100% pairing success (250 ha in this study).

Note, that this latter ‘threshold’ of 50% may be lower if patches are significantly larger than 250 ha or it may be higher if the majority of source patches are near an intrinsic growth rate of 1.0 (~100 ha patch size assumed in this model). In addition these ‘standards’ may vary if fecundity and survival rates differ from the parameterization used in this model. Moreover, it is important to denote that the amount of suitable forest cover may be significantly lower than the actual amount of forest cover in a landscape (for example, up to ~8% for area 3) since patches smaller than 5 ha and coniferous forests were assumed to be unsuitable. In general, habitat-based standards related to dispersal (such as maximum tolerable distance between two nearest patches) were found to be less important due to the area-sensitivity of ovenbirds.

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