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**THE EFFECTS OF AMOUNT OF AVAILABLE HABITAT IN THE LANDSCAPE ON
RELATIONS BETWEEN ABUNDANCE AND DISTRIBUTION OF BOREAL
FOREST SONGBIRDS**

Lisa A. Venier, B.Sc., B.Ed., M.Sc.

**Thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of**

Doctor of Philosophy

**Department of Biology
Carleton University
Ottawa, Ontario
September 1996**

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**"The Effects of Amount of Habitat in the Landscape,
Scale, and Ecological Specialization on Relations Between
Abundance and Distribution of Boreal Forest Songbirds"**

submitted by
Lisa A. Venier, B.Sc., B.Ed., M.Sc.

in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

Chair, Department of Biology

Thesis Supervisor

External Examiner

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ABSTRACT

It has been clearly demonstrated that abundance and distribution of species are positively related. I hypothesized that, on a patchy landscape, more available breeding habitat would result in both higher abundance and wider distribution because of an increased number of successful dispersers. Therefore a positive distribution-abundance relationship is expected for a group of species if individual species have differences in habitat use and therefore different amounts of habitat are available to them on the same landscape. Using a spatially-explicit, stochastic, individual-based simulation model I varied the amount of breeding habitat in a simulated landscape and found a positive correlation between (1) mean abundance of individuals in occupied cells and the number of breeding habitat cells (2) distribution (proportion of cells occupied by individuals) and the number of breeding habitat cells and, (3) abundance and distribution. Therefore, differences in amount of available habitat could account for a positive relationship between abundance and distribution.

The explanation above predicts that there will be a significant positive abundance-distribution relationship for a single species, with abundance and distribution measured in many different landscapes. I tested this hypothesis for twenty species of boreal forest songbirds using meta-analysis techniques and I found an overall significant positive correlation ($P < 0.05$) between abundance and distribution.

I also estimated the amount of habitat for each of 8 species on the landscape and examined directly the relationship between local abundance and amount of habitat in the landscape for each species. There was a generally positive influence of amount of habitat

in the landscape on local abundance and distribution (measured as presence of individuals).

The influence of the amount of habitat on both abundance and distribution should be limited by the dispersal distance of the species in question. I examined the relationship between local abundance and amount of habitat in landscapes of different scales. Results indicated that the amount of habitat in the landscape does not influence local abundance at a distance greater than 10 km for the eight species examined. In a highly conservative test, results for two species confirmed that in at least some species the influence of amount of habitat is at a small scale relative to the vagility of these species.

Lastly I examined the interspecific relationship (33 songbird species) between (1) abundance and distribution, (2) niche width and both local abundance and distribution and (3) average amount of habitat within 200 m of samples and both local abundance and distribution. I found a positive relationship in all cases and I conclude that both variation in niche width and variation in amount of available habitat can generate a positive abundance-distribution relationship.

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GENERAL INTRODUCTION

A positive relationship between local abundance and distribution among species in an assemblage has been thoroughly demonstrated at many scales for many groups of taxa (Appendix 1). There are only a few examples where either no relationship or a negative relationship has been found in contrast to an overwhelming number of cases where positive relationships have been found (Gaston and Lawton 1990b). These studies indicate that more widespread species are more abundant locally whereas narrowly distributed species are locally more rare. Patterns of the abundance and distribution of species are one of the central issues in the study of ecology (Andrewartha and Birch 1954) and the relationship between them could be one of the few general rules of ecology (Hanski 1982b) that are widely applicable to many situations and species.

The operational definitions of both abundance and distribution vary greatly among the studies listed in Appendix 1. The most common definition of abundance used in abundance-distribution studies is the mean abundance at occupied sites but the size and nature of a site varies among studies and could be important in the subsequent interpretation of the results. However, differences in the size and nature of the site do not appear to affect the qualitative relationship between distribution and abundance in most cases with one noted exception (Gaston and Lawton 1990b). Gaston and Lawton (1990b) provided evidence that when the site or sites at which local abundance is measured are different than most of the area throughout which distribution is measured then a positive abundance-distribution relationship is not necessarily expected. Results from Ford (1990)

were also consistent with this view.

Hanski *et al.* (1993) defined three scales of distribution. Geographical distribution is the species' geographical range: the smallest area with a reasonably smooth outline that includes all observations of the presence of the species. Range maps are the best known representation of distribution measured at this scale. They are necessarily created from incomplete knowledge of where the species is present and where the species is absent. Empirical studies on the distribution-abundance relationship are limited to a fairly narrow group of taxa largely because of the lack of information on the geographic distributions of most taxa (Udvardy 1969, Gaston 1990).

Regional distribution as defined by Hanski *et al.* (1993) is a function of the area used by the species at a scale smaller than its geographical range but larger than the local population. It is usually measured as the fraction of samples that are occupied within the region. Regional and local scales have no absolute definition in the literature, rather they are defined relative to one another. As with different scales of abundance, different scales of distribution appear to have no qualitative effect on the abundance-distribution relationship (Appendix 1).

The ubiquity of the relationship, its existence at many scales of both abundance and distribution, suggests that more than one mechanism may be operating to generate the positive abundance-distribution relationship and many hypotheses have been suggested. Four such hypotheses are cited frequently in the literature. For the purposes of this discussion the four hypotheses will be called (1) the null hypothesis (Wright 1991), (2) the sampling hypothesis (Bock and Ricklefs 1983), (3) the ecological specialization hypothesis

(Brown 1984), and (4) the metapopulation hypothesis (Gyllenberg and Hanski 1992).

The null hypothesis for a relationship between abundance, measured as the mean abundance in occupied sites, and distribution, measured as the fraction of sites occupied, is a positive relationship (Wright 1991). If some species are more abundant than other species and individuals within a species are randomly (Poisson) distributed then the relationship between abundance and distribution will be positive. A relationship that results from a random distribution of individuals requires no biological explanation; however, most species are not distributed randomly (Taylor *et al.* 1978, Wright 1991). The most common distribution is the negative binomial distribution which is defined in part by a clumping parameter. A Poisson distribution is a limiting case of the negative binomial distribution where the clumping parameter is zero. Wright (1991) also demonstrated that a positive abundance-distribution relationship is expected when individuals within species are distributed as a negative binomial but this cannot be considered a null hypothesis because the clumped distribution requires explanation.

A positive relationship between abundance and distribution has also been suggested to be the result of a sampling artifact. Ricklefs (1972) argued that if the abundance of any species is distributed such that abundance is greatest at the centre of its range and least at the periphery of the range (Grinnell 1922, Hengeveld and Haeck 1982, Brown 1984) and the study area is an arbitrarily defined geographic area, then species only peripherally found in the study area would also be scarce locally compared to species whose centres of abundance were included in the study area. This sampling artifact probably contributes to the positive relationship found in some studies but the abundance-

distribution relationship persists when the artifact is controlled for. Bock and Ricklefs (1983) examined the abundance and distribution of a group of birds within the entire continental United States plus some of southern Canada. Large proportions of the ranges of all species were included so there were no peripheral species. Bock (1984) used a similar technique whereby at least 75% of the ranges of all species were within the study area. The positive abundance-distribution correlation persisted in both cases and Bock and Ricklefs (1983) concluded that a positive correlation between geographical range and local abundance may be an inherent property of most groups of species.

Brown (1984) proposed his hypothesis of ecological specialization within the framework of his general theory on the distribution of abundance of species. He proposed that interspecific differences in ecological specialization may explain the positive relationship between distribution and abundance. This theory was developed based on three assumptions. First, the dimensions of a species' multidimensional niche (Hutchinson 1957) are defined by many physical and biotic variables that determine the abundance and distribution of each species. Second, some sets of environmental variables are distributed independently of each other and the variation in these variables is autocorrelated such that the probability of sites having similar combinations of environmental variables is an inverse function of the distance between them. Third, ecologically similar species vary in only a small number of niche dimensions. Population density should be bivariate normally distributed over the species' range if many different niche dimensions, acting additively to influence population density, are distributed independently of each other in space. Species with wide tolerances should be able to achieve high densities at the centre of their

range where conditions are optimal and they should be able to occupy more places because more places will fall within their range of tolerances. Conversely, species with narrow tolerances are expected to be less abundant locally and are expected to be able to occupy few places. This hypothesis implies that specialized species are unable to use resources efficiently and as a result are found at low abundances locally. Kouki and Häyrinen (1991) argue that this view is contrary to the more common view that specialists are efficient in using local resources and thus become locally abundant, but are not widespread.

The direct evidence for the ecological specialization hypothesis is equivocal. The hypothesis states that generalized species are widely distributed and locally common and that specialized species are narrowly distributed and locally rare. Kouki and Häyrinen (1991) found that species of birds in mires in Finland that were able to inhabit several mire types had large geographical ranges, but were not locally abundant. In a sample of British butterflies, generalists had a wider distribution than specialists but not a greater average abundance (Hanski *et al.* 1993). Gaston and Lawton (1990) reviewed 15 independent tests of the relationship between species abundance and niche breadth for taxa including plants, insects, mammals, birds, molluscs and amphibia. Seven studies showed positive relationships, 2 showed negative relationships and the remaining 6 showed no relationship. Also, many of the studies of abundance and distribution demonstrate an asymmetrical relationship whereby species that are narrowly distributed are locally rare but some species that are widely distributed are also locally rare (Gaston 1988, Gaston and Lawton 1988a, 1988b). It is not clear if Brown (1984) would argue that these species should be

generalists or specialists. Hanski *et al.* (1993) examined the relationship between the degree of ecological specialization and both distribution and abundance in data sets from seven groups of taxa. To support the ecological specialization hypothesis, the degree of ecological specialization must be negatively correlated (niche width must be positively correlated) with both abundance and distribution. None of the seven groups of taxa supported the hypothesis.

Rabinowitz *et al.* (1986) also provides evidence contrary to Brown's (1984) hypothesis. In previous work Rabinowitz (1981) identified a classification for rarity of species based on three traits that all species possess including geographic range (wide or narrow), local population size (somewhere large or everywhere small) and habitat specificity (broad or restricted). A common species was identified as one that was widespread, somewhere abundant with broad habitat specificity. In a survey of flora in the British Isles, Rabinowitz *et al.* (1986) found that of the rare types, species with wide geographic distribution, restricted habitat but high local population size are the most numerous category of plants (71 of 128 species). The second most numerous form of rarity (14 species) is the classic restricted endemic: habitat specialist, small range, but common when found. The combination of wide geographic distribution, restricted habitat and high local abundance should not be a common one according to the mechanism proposed by the ecological specialization hypothesis.

Brown's (1984) proposed mechanism is predicted to operate at a large scale and reflects a macro ecological emphasis (Brown 1995). Macro ecological studies are based on the assumption that some of the general processes that regulate the abundance,

distribution, and diversity of organisms are reflected in emergent patterns in the statistical distributions of individuals, populations, and species (Brown 1995). Two of his assumptions reflect this large scale (biogeographic) perspective. First, he suggests that environmental variables are autocorrelated, such that sites that are closer together are more likely to be similar than sites that are far apart with respect to these environmental variables. This autocorrelation occurs at the continental scale due to gradients in variables such as temperature and precipitation over the entire continent. But environments can be autocorrelated at smaller scales which results in strongly multi-modal distributions. At a smaller scale, environmental variables are dictated by topography. Topography influences the terrain (slope, aspect, etc.), hydrology and soil among other things at a small scale; therefore vegetation types are patchily distributed (Mackey 1994). I expect species to respond locally to habitat type which, at the scale dictated by topography, will necessarily create a multi-modal distribution of abundance. Brown (1984) acknowledged this effect of scale but he dismissed it by suggesting that if the sites were averaged over a large enough area the pattern of abundance would cease to be multi modal. However, many of the studies that have demonstrated a positive relationship between distribution and abundance have done so at scales where a multi-modal pattern of abundance is in fact expected and where the local habitat type is expected to influence the local abundance and probability of occurrence (Appendix 1). At the within-habitat scale, it is not clear that a generalist would be expected to be more abundant than a specialist.

The metapopulation hypothesis (Gyllenberg and Hanski 1992) predicts a positive relationship between local abundance in occupied habitat patches and the fraction of

patches occupied, as a result of metapopulation dynamics. It has been suggested that populations of most species are made up of a number of local populations (Andrewartha and Birch 1954, Levins 1969, Gilpin and Hanski 1991) which are loosely termed a metapopulation (Levins 1969). The strictest definition of a metapopulation implies that species exist in a balance between extinction and colonization of these local populations. However, this has not been found to be the structure and dynamic of most populations of species (Harrison 1994), where identification of local populations is often subjective. The metapopulation paradigm emphasizes the role of immigration and emigration in population dynamics. It is this aspect of spatial population structure that is relevant to the metapopulation hypothesis (Gyllenberg and Hanski 1992) regardless of whether the classic metapopulation definition fits the population in question or not.

Gyllenberg and Hanski (1992) formulated a general metapopulation model which included a model of local dynamics along with balance equations for dispersing individuals. A positive relationship between abundance in occupied patches and the distribution (fraction of patches occupied) is predicted given an assemblage of species in which the species differ from each other in only one of the following parameter combinations (1.) dispersal rate in relation to intrinsic growth rate (2.) local extinction probability in relation to dispersal rate and colonization rate or (3.) the probability that a disperser finds a patch before dying. The model presented by Gyllenberg and Hanski (1992) emphasizes the potential role of dispersal (immigration and emigration) in the dynamics of existing local populations. Local population sizes must be influenced by effects of emigration and immigration for an abundance-distribution relationship to be

expected.

There is much empirical evidence that local populations are influenced by emigration and immigration. Increasing patch isolation has been shown to decrease colonization rate (van Dorp and Opdam 1987, Smith 1970, 1980, Pokki 1981, Hanski 1986) and reduce immigration (Faeth and Simberloff 1981). Also, density of orb spiders on small islands increased with decreasing isolation (Toft and Schoener 1983). Immigration has been shown to increase the size of small local populations (Smith 1974, Holliday 1977, Gottfried 1979, Rey 1981, Rey and Strong 1983, Connor *et al.* 1983, Fahrig and Merriam 1985), and Greenbank (1973) demonstrated that dispersal from outbreak foci of spruce budworm contributed to the growth of other populations.

Distribution-abundance relationships cannot be used to test the metapopulation model or any other model but the metapopulation model does make specific predictions about which kinds of species have certain combinations of abundance and distribution and these predictions can be tested (Hanski *et al.* 1993). According to the metapopulation model, for a given average abundance, a more dispersive species should have a wider distribution than a less dispersive species. This prediction is supported by the data for British butterflies, but not in four other taxa examined (carabids, gastropods, fen plants, Dytiscids) (Hanski *et al.* 1993). In all four cases Hanski *et al.* (1993) argued that dispersal measures were probably inadequate for the task. Some positive evidence in support of the metapopulation hypothesis was found in an examination of bryophyte species which showed a positive abundance-distribution relationship. Three species that had large local populations and low distributions also had high local growth rates but low

dispersal rates. This combination of traits supports the metapopulation hypothesis (Söderström 1989).

Variation in the probability of successful dispersal is the underlying mechanism of the metapopulation hypothesis. However, Gyllenberg and Hanski (1992) did not propose a landscape driven phenomenon. The metapopulation hypothesis was developed by varying combinations of species-specific parameters in deterministic models which resulted in a positive abundance-distribution relationship for an assemblage of generic species. Variation in some of these parameter combinations generated variation in dispersal success among species. Landscape structure also affects dispersal success (Dunning *et al.* 1992, Taylor *et al.* 1993, Fahrig and Merriam 1994), and amount of habitat on the landscape is a fundamental component of landscape structure.

The objective of this thesis is to examine the potential influence of amount of habitat in the landscape on the relationship between distribution and abundance. For the purposes of this thesis a landscape is just an area of land that may or may not have relevance to a local population. It is the scale of the landscape that determines its relevance. In Chapter 1, I use individual based, stochastic simulation modelling to examine the relationship between the amount of breeding habitat on the landscape and both the abundance and distribution of organisms. More breeding habitat on a landscape results in more successful dispersal. Within a species assemblage on any one landscape, variation among species in the amount of habitat is expected because of differences in habitat preferences. For the amount of habitat on the landscape to generate a positive abundance-distribution relationship it must have a positive influence on both ' 1

abundance (mean abundance in occupied sites) and distribution (fraction of sites occupied). Simulation results indicate that both of these relationships are expected.

Chapters 2-5 involve empirical examinations of the potential influence of amount of habitat in the landscape on the abundance-distribution relationship using data on the distribution and abundance of boreal forest songbirds. A list of species used in these analyses can be found in Appendix 2 including a selection of information on life history traits. Species examined in this thesis all belong to the order Passeriformes which are all land birds. The majority of species included here are migratory. In fact, more than 80% of all bird species breeding in or to the north of the boreal region winter further to the south (Erskine 1977). Most migrant species spend only from 3 months (obligate insect eaters) to five months (insectivores which also eat seeds and fruit) in the boreal region (Erskine 1977). All species examined have altricial development such that young are immobile and downless and must be fed (Ehrlich *et al.* 1988). All species are also active during the day. Most species are insectivorous but some are granivorous or omnivorous (DeGraff *et al.* 1985). Return rates to the breeding grounds for migratory species in northern Ontario are recorded from April 20 to May 26 depending on the species (Denis 1961). Average clutch sizes range from 3 to 6 eggs (Peck and James 1983). All estimates of abundance and distribution were made for the breeding season of all species before the fledging of young.

In Chapter 2, I test the prediction of a positive relationship between abundance and distribution for a single species where abundance and distribution are measured in many different landscapes. If variation in amount of habitat can generate a positive

distribution-abundance relationship, then a positive abundance-distribution relationship is expected in the absence of species differences as long as landscape variation is present. In Chapter 2, I test this prediction using data on abundance and distribution of 20 boreal forest songbirds in northwestern Ontario. I employ the technique of meta-analysis (Hunter and Schmidt 1990) to assess the generality of the relationship across the species examined.

In Chapter 3, I test another prediction of Chapter 1: that there should be a positive relationship between the amount of habitat in the landscape and both the local abundance and distribution. Vegetation was characterized into types of a vegetation classification system (Sims *et al.* 1989). Habitat in the landscape was classified as being of better quality than the local sample or of worse quality. I defined amount of habitat as being a function of area and quality. Better quality habitat (more habitat) in the landscape than at the local site was predicted to have a positive influence on local abundance. Worse quality habitat (less habitat) in the landscape than at the local site was predicted to have a negative influence on local abundance. The relationships are examined within boreal forest songbird species on northwestern Ontario landscapes of approximately 1 km² which is likely to be within the natal and breeding dispersal distance of philopatric songbirds (Greenwood and Harvey 1982, Villard 1991). Chapters 1-3 have been submitted to journals for publication and are included in this thesis in their submitted form. Therefore there is some redundancy in content. Chapter heading pages indicate co-authors of these manuscripts.

Dispersal-mediated ecological processes are not expected to operate at all scales.

Scales of influence will be defined by dispersal distance. In Chapter 4, I examine the influence of scale of the landscape on the relationship between amount of habitat in the landscape and the local abundance for a group of boreal forest songbirds. This is an exploratory analysis since very little is known about the dispersal distance of songbirds (Villard *et al.* 1995) and therefore no explicit predictions can be made about the expected scale beyond which influence of amount of habitat is not expected to affect local abundance. Different opinions exist in the literature on the probable dispersal distances of passerines. Discussions of dispersal have suggested that songbirds are sufficiently mobile that any species from a regional avifauna may visit a given site (Lincoln 1939, Ambuel and Temple 1983, Blake 1991). Alternatively, evidence that juvenile birds choose future breeding sites during a post-fledging dispersal phase (Berndt and Winkel 1980, Nice 1964, Catchpole 1972, Adams and Brewer 1981), suggests that natal dispersal may be more limited than migration distance might suggest.

Natal dispersal (movement from the site of birth to the site of first breeding) is generally more common and extensive than breeding dispersal (movement from one breeding site to another) (Greenwood and Harvey 1982). Therefore it is likely to be natal dispersal that dictates the scale of influence of the landscape. Greenwood and Harvey (1982) suggested that passerines were generally philopatric with a median value of dispersal of less than 10 territories from the natal area but their conclusions were based on very few species. For passerines, most studies on natal philopatry have been done on nonmigratory species, and relatively little is known about natal philopatry of migratory species (Pärt 1990, 1991, Weatherhead and Boak 1986). Weatherhead and Forbes (1993)

compared return rates in migratory and nonmigratory species based on published and unpublished data. They concluded that a higher proportion of young passerines breed near their natal area in resident than in migratory populations. Although some migratory populations had high natal philopatry, in nearly all cases these populations were isolated. These results suggest that current estimates of dispersal distance for passerines are biased towards low dispersal distance but there is no information on the possible degree of this bias.

There is some evidence of long-distance dispersal in passerines. Robinson (1992) suggested that populations in small woodlots in central Illinois might be maintained by immigrants from source populations over 200 km away. In contrast, isolation effects have been observed in other studies of forest birds (Lynch and Whigham 1994, Robbins *et al.* 1989a, Askins *et al.* 1987, Askins and Philbrick 1987) which suggests that long-distance dispersal is not the norm.

The objectives of chapter 5 are (1) to examine the interspecific relationship between abundance and distribution in boreal forest songbirds (2) to test the ecological specialization hypothesis which predicts that habitat generalists will be more widely distributed and more locally abundant than habitat specialists and (3) to test the hypothesis that amount of habitat in the landscape can account for the positive abundance-distribution relationship among species.

Until now, explanations for the abundance-distribution relationship have ignored habitat heterogeneity at the scale at which individuals choose habitat. The ecological specialization hypothesis deals with this heterogeneity by assuming that it is averaged over

large areas (Brown 1984). However, many studies that demonstrate a positive abundance-distribution relationship have measured abundance and distribution within habitat (Appendix 1). The metapopulation hypothesis assumes that all species in an assemblage see the habitat as equally suitable (Hanski 1982) which is unlikely ever to be the case. In this thesis, I show that this habitat heterogeneity and the differences among species in their response to habitat types generates the positive abundance-distribution relationship.

GENERAL METHODS

Study Area and Site Selection

The empirical data used in this thesis for Chapters 2 to 5 were collected as part of an ongoing research program at the Canadian Wildlife Service - Ontario Region, Environment Canada. The study area is located in northwestern Ontario in an area approximately 300 km x 100 km. The sampled forest stands ranged from 48.18 N, 89.49 W to 50.28 N, 88.87 W (south to north) and 48.91 N, 91.83 W to 49.81 N, 86.62 W (west to east) (Figure 1). Forest stands were selected initially using Forest Resource Inventory Maps, a system of forest (timber) inventory carried out by the Ontario Ministry of Natural Resources and based mainly on aerial photograph interpretation and some ground truthing (Gillis and Leckie 1993). Forest stands were selected to obtain samples of all vegetation types. Selection was limited by accessibility of forest landscapes and rarity of some types. Five sample sites were located in each forest stand and were on average 300 m apart, at least 200 m apart and at least 100 m from the road. There was a total of 171 forest stands making up 855 sampling sites. One hundred and forty forest sites were selected and sampled for forest songbirds and vegetation in 1989 and 32 new sites were selected and sampled in 1991.

The largest proportion of the area sampled was in the boreal forest region where plant species diversity and productivity is relatively low (Baldwin 1991). The boreal region is characterized by extensive stands of black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) as well as mixed stands of conifer and

Figure 1: Map of study area in northwestern Ontario, Canada. Solid dots represent 171 sampled forest stands.

broadleaved species such as trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*) and balsam poplar (*Populus balsamifera*). Catastrophic disturbances such as extensive and repetitive forest fires and cyclical insect infestations contribute to the dynamics of the boreal forest. The climate is characterized by short, moderately warm, moist summers and long, extremely cold and dry winters (Bonan and Shugart 1989). Some of the northwestern region is made up of Great Lakes - St. Lawrence forest region which is characterized by a diversity of conifer and hardwood species, including white pine (*Pinus strobus*), red pine (*Pinus resinosa*), red maple (*Acer rubrum*), and ash (*Fraxinus nigra*) (Rowe 1972). This area is generally more productive than the boreal forest region (Baldwin 1991).

Bird Counts

Bird counts were conducted at all 855 sites. An unlimited-distance point count method was used based generally on an approach described by Blondel *et al.* (1970) and more specifically described by Welsh (1995). Observers record all birds seen or heard during a 10 minute period. All records are mapped to keep track of movements and to record simultaneous observations. Mapping minimizes the recording of single individuals more than once (Welsh 1995). Each site was visited twice by the same observer, once in early to mid June and once in mid to late June within 4 hours of sunrise. Surveys were conducted only in calm to light winds (<15 km/hr) and not in the rain. Counts began 10-30 seconds after observers arrive at the station.

The status of the bird observed is recorded (singing male, pair, female, nest, calling

bird). The status is used as a measure of breeding evidence; some levels assume a pair, others only a single bird. A singing male, observed pair, occupied nest, and a family group are all considered to be a pair. All other birds seen or heard calling are counted as singles.

Local Vegetation (Forest Ecosystem Classification of Northwestern Ontario)

At each census site the vegetation type, based on the Forest Ecosystem Classification (FEC) for Northwestern Ontario, was identified at the centre of the site and at 50 meters from the centre directly north, south, east and west. The FEC is a classification system that recognizes 38 mature forest types in northwestern Ontario (Appendix 3). The FEC was developed by the Ontario Ministry of Natural Resources (OMNR), and Forestry Canada, Ontario Region (FCOR) (Sims *et al.* 1989). It is based on data collected from mature forests over 50 years of age sampled across a range of landform features, slope positions, soil texture, moisture conditions and geographical location throughout northwestern Ontario (Figure 1). The FEC is based on an ordination analysis of the abundance information for all vegetation species for 2100 field plots (10 m x 10 m). Thirty-eight vegetation types or modes were identified. This number of vegetation types appears sufficient to characterize the wide range of conditions that prevails in the area (Sims *et al.* 1989). Vegetation types are the modal description of the group of similar plots.

The FEC system has been designed as a field tool. Vegetation types are identified on the basis of overstory tree species composition with some consideration of the dominant understory, ground layer and moss cover. The basic sampling unit for assigning

a vegetation type is a 10 m x 10 m plot which is easily and quickly assessed in the field, however, a standard point census count samples birds in a circular area with a radius of approximately 50 to 100 metres. A single FEC assessment would be insufficient to estimate the vegetation type for the same area. Therefore 5 FEC were conducted for each point count, as described above.

Local Vegetation (Overstory cover types)

Local vegetation was also characterized more coarsely by estimating the percentage cover for all canopy trees at the site in a radius of approximately 50 m around the site. Sites were then classified as conifer (>80% conifer cover), conifer dominant mixedwood (51-80% conifer), deciduous dominant mixedwood (51-80% deciduous), or deciduous (>80% deciduous cover). Sites that were classified as type 38 based on the FEC system were classified as wetland. Only one hundred and thirty-one forest stands (655 sites) of the original 171 stands were sampled for overstory vegetation due to time constraints.

Landscape Vegetation

Vegetation at the landscape level was identified using classified Landsat Thematic Mapper data provided by the Ontario Ministry of Natural Resources (OMNR 1992). This spatial data base of forest cover types has been developed as part of an ongoing research program. The database was developed using a supervised classification to produce 16 map categories of which 10 are forest types. A complete description of the methods for

the development of this database can be found in OMNR (1992). I condensed the original classification into the 5 vegetation categories listed above (conifer, conifer dominant mixedwood, deciduous dominant mixedwood, deciduous, wetland). The digital data of the classified Landsat image are the property of OMNR and are not freely available. I was provided with cover estimates of all vegetation categories for circular areas defined by radii of 200 m, 500 m, 1,000 m, 2,000 m, 5,000 m, 10,000 m, 15,000 m, 25,000 m, 50,000 m.

Geographic Position

Accurate latitudes and longitudes were measured for 131 of the 171 forest stands using a Garmin Survey II Global Positioning System with differential processing (accuracy of 1-3m). The remaining 40 stands were not sampled due to time constraints.

CHAPTER 1. HABITAT AVAILABILITY CAN CAUSE THE SPECIES ABUNDANCE-DISTRIBUTION RELATIONSHIP

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ABSTRACT

The objective of this study was to examine the effect of different amounts of available habitat on the relationship between the distribution and abundance of species using a spatially-explicit, stochastic, individual-based simulation model. We define abundance as the mean abundance of a species in occupied breeding habitat sites and distribution as the proportion of breeding habitat sites that are occupied by that species. We hypothesized that on a patchy landscape, more available breeding habitat will result in both higher abundance and wider distribution because of an increased number of successful dispersers. Therefore, a positive relationship between distribution and abundance is expected for a group of species in a landscape if individual species have differences in habitat use and therefore different amounts of habitat are available to them on the same landscape. In the simulation experiment the amount of breeding habitat was varied to examine the effects on abundance and distribution. We found a positive correlation between (1) abundance and the number of breeding habitat cells on the simulation landscape (2) distribution and the number of breeding habitat cells on the landscape and, (3) abundance and distribution. These results suggest that differences in amount of available habitat could account for a positive relationship between abundance and distribution.

INTRODUCTION

A positive relationship between local abundance of individuals and their distribution has been demonstrated in numerous groups of taxa and at many different scales (see Gaston and Lawton 1990b for review). This relationship has been attributed to artifacts of sampling (Wright 1991), patterns of resource use (Brown 1984), and differences among species in movement patterns within metapopulations (Gyllenberg and Hanski 1992); and has been reviewed recently in the context of these three hypotheses (Hanski *et al.* 1993, Gaston 1994).

The purpose of this study was to examine the effect of different amounts of available habitat on the relationship between abundance and distribution using a spatially explicit simulation model.

Distribution has been defined as both the range of a species (Gaston 1990) and as the amount (or percent) of area within a region that a species uses (Hanski 1982a). In this paper we use the latter definition and we measure the amount of area used by calculating the proportion of sites occupied, where a site is defined as potential breeding habitat. We define abundance as the mean abundance in occupied sites.

The sampling hypothesis as argued by Wright (1991), suggested that if individuals of a species were distributed randomly (Poisson distribution) at sites, and some species were more abundant than others, then the expected relationship between distribution and abundance would be positive, and therefore no explanation would be necessary. However, he also acknowledges that in most species, individuals are not distributed randomly, but as a negative binomial, which also generates the positive relationship

between abundance and distribution. The definition of the negative binomial distribution requires a clumping parameter and is therefore not suitable as a null model. Since there is no *a priori* null distribution for individuals of a species, and one can imagine a set of distributions for a group of species in which the relationship between distribution and abundance is not positive, it seems appropriate to examine other possible hypotheses for the relationship.

Brown's (1984) hypothesis suggests that the relationship exists because of differences among species in their abilities to use resources. Species that are able to use many different kinds of resources (generalists) would have a wider distribution than specialists because their resources are more likely to be found over a greater range or in more places. Therefore, using either range size or amount of area used, this hypothesis predicts that generalists should have wider distributions than specialists. In addition, Brown (1984) argued that generalists would be more abundant locally because they would have more resources available to them at any one place. The empirical evidence for Brown's hypothesis is equivocal. Seagle and McCracken (1986) found no correlation between abundance and niche breadth for 4 separate taxa including small mammals, slugs, salamanders, and wintering bird assemblages. Other negative evidence exists for plants (Adams and Anderson 1982) and birds (Ricklefs 1972). There are also studies that support the hypothesis for insects (Mullenberg *et al.* 1977, Hanski and Koskela 1978) and plants (Parrish and Bazzaz 1976, Johnson 1977). Intuitively, the first half of Brown's argument is easier to accept than the second. That species that can use more habitat types will occupy more area or be found in more places seems plausible, the exception being

species that specialize on a single very common habitat type. At a local site however, more resources are not necessarily available to a generalist than a specialist especially if generalists use resources less efficiently than specialists.

A third hypothesis, the metapopulation hypothesis (Hanski *et al.* 1993), also predicts a positive relationship between the local abundance at occupied sites and the fraction of occupied sites (distribution), given an assemblage of species with variation in one or more of (1) dispersal rate in relation to intrinsic growth rate, (2) probability that a disperser finds a patch before dying or (3) extinction rate in relation to rate of successful colonization. These predictions are based on a structured metapopulation model (Hanski 1991) in which local population size is affected by dispersal between patches as well as by dynamics within patches. The underlying mechanism of the metapopulation hypothesis is variation in the rate of successful dispersal.

Landscape structure affects dispersal success (Dunning *et al.* 1992, Taylor *et al.* 1993, Fahrig and Merriam 1994), and amount of habitat on a landscape is a fundamental component of landscape structure. Species within the assemblages that have been used to demonstrate the empirical abundance - distribution relationship are usually taxonomically related but show substantial differences in the kinds of habitat they use. Therefore any given landscape will offer a different amount of habitat to each species within a group of such organisms. We hypothesized that these differences in habitat availability will have a strong effect on the success rate of dispersers. This will lead to a positive relationship between distribution and abundance through the mechanism proposed by Gyllenberg and Hanski (1992).

If the abundance-distribution relationship relies on differences in amount of available habitat then on average, generalists will be more widely distributed and more abundant than specialists because they will, on average, have more habitat available to them. Whereas Brown's (1984) hypothesis argued that species that could use more types of resources would have a wider distribution, we have generalized this to suggest that species that have more resources available to them will have a wider distribution. Thus, specialists that specialize on a common habitat type should have high abundance and wide distribution.

We used a spatially-explicit, stochastic and individual-based model to examine the influence of habitat amount on distribution and abundance. The amount of breeding habitat on the simulation grid was varied and related to the abundance and distribution of individuals on the grid. The simulations demonstrate that availability of habitat on a landscape can generate a positive relationship between distribution as measured by the proportion of occupied sites and the mean abundance in occupied sites. This relationship arises in the absence of variation in resource specialization or dispersal ability.

METHODS

Model Overview

In the simulation model, space is represented by a two-dimensional rectangular landscape of 900 "cells" (30 by 30). There are two kinds of landscape cells: breeding habitat and non-breeding habitat. Individuals may die, reproduce, and/or move within each time step; the order of these events is randomized for each individual in each time step. Parameters

in the model can be divided into three general categories: (1) parameters determining the spatial structure of the landscape, (2) demographic parameters determining reproduction and mortality, and (3) movement parameters (See Table 1.1 for a list of all parameters and their values).

Landscape

The parameter of interest for this examination is COVER, the proportion of landscape in breeding habitat. COVER was varied randomly between 0 and 1 between simulation runs. The spatial pattern of the breeding habitat on the landscape is specified by a clumping parameter which determines the degree of spatial contagion in the distribution of breeding habitat cells. The algorithm for setting up the spatial pattern of breeding habitat on the landscape is essentially the same as correlated or interacting percolation models (Anderson and Family 1988, reviewed by Plotnik and Gardner 1993). The clumping parameter was set at 0.05 for all simulation runs, which results in moderate clumping. The pattern of breeding habitat is fixed for each simulation run.

Demographics and Movement

Reproduction occurs only in breeding habitat and is determined by the probability of reproduction per time step per individual and the number of offspring per reproduction event. The probability of reproduction is density-independent. However the within cell population is not permitted to exceed the maximum cell occupancy. The probability of mortality is specified separately for breeding and non-breeding habitat (see Table 1.1 for

Table 1.1: Parameter values used in the simulation experiment.

1. Spatial structure of the landscape		
Landscape size	(# of cells)	900
Proportion of grid in breeding habitat (COVER)		Varied (0-1)
Breeding habitat clumping parameter		0.05
2. Demographic parameters determining reproduction and mortality		
Starting number of individuals		500
Maximum cell occupancy		10
Reproduction probability		0.5
Offspring per reproduction		1
Mortality probability in breeding habitat		0.3
Mortality probability in non-breeding habitat		0.5
3. Movement Parameters		
Maximum movement distance		10
Movement probability in breeding habitat		0.05
Movement probability in non-breeding habitat		1.0

values).

Movement direction of individuals is random. Movement distance is also random, but is limited to a maximum distance. From the point of view of moving individuals, the landscape is "wrapped"; an individual that crosses the edge of the landscape continues in the same direction on the opposite edge (Haefner *et al.* 1991).

Simulations

The proportion of the landscape in breeding habitat (COVER) was selected randomly for each simulation run. We conducted 100 simulation runs. Each simulation began with 500 individuals distributed randomly over the landscape and was conducted for 500 time steps. The output variables were the number of individuals in breeding habitat cells and the number of occupied breeding habitat cells at each time step. The two response variables were (1) mean abundance of occupied breeding habitat cells (abundance) and (2) the proportion of breeding habitat cells that were occupied (distribution).

The combination of a large maximum movement distance (10), a high probability of movement of individuals in non-breeding habitat (1), and a high probability of mortality in non-breeding habitat (0.5) ensured that most individuals on the landscape were found in breeding habitat. Values for the fixed parameters in the model were selected based on sensitivity analysis conducted by Fahrig (unpublished manuscript).

RESULTS

We examined the relationship between the amount of breeding habitat on the simulation landscape (COVER) and both the mean abundance in occupied cells and the distribution (proportion of breeding cells that are occupied). Populations in landscapes with less than 5% COVER were extinct within 500 time steps ($n=3$). In general, landscapes with less breeding habitat took more time steps to stabilize but there were no visible trends in either mean abundance or distribution after approximately 250 time steps. (see Figure 1.1 and Figure 1.2 for examples of simulation runs with 86% COVER and 24% COVER). After populations had stabilized there was a positive relationship between COVER and the mean abundance in occupied habitat (Figure 1.3; Spearman Rank Correlation; $\rho = 0.81$, $p=0.0001$, $n=97$, calculated at time step 500). There was also a positive relationship between the amount of breeding habitat and the distribution after populations were stabilized (Figure 1.4; Spearman Rank Correlation, $\rho=0.95$, $p=0.0001$, $n=100$). Mean abundance and distribution are therefore strongly correlated (Figure 1.5; Spearman Rank Correlation, $\rho=0.86$, $p=0.0001$, $n=97$). In addition, mean abundance and distribution are not correlated when COVER is controlled for using partial correlation (Partial Spearman Rank Correlation, $\rho=-0.01$, $p=0.92$, $n=97$), indicating that the correlation between abundance and distribution is due to the effect of COVER on each.

The simulation results also indicate that there is more variation in the mean abundance at lower levels of distribution (Figure 1.5). All points below a distribution of 0.7 had less than 15% breeding habitat (COVER), and a wide range of mean abundances (5.2 to 8.7; Figure 1.5).

Figure 1.1 : Mean abundance per occupied breeding habitat cell plotted against time at intervals of 10 time steps for two sample landscapes with 86% COVER and 24% COVER.

Figure 1.2 : Distribution plotted against time at intervals of 10 time steps for two sample landscapes with 86% COVER and 24% COVER.

Figure 1.3 : Mean abundance per occupied breeding cell plotted against COVER
(proportion of the total landscape area in breeding habitat) for 100 simulation runs. Data are from the 500th time step for each run. Spearman rank correlation; $\rho = 0.81$, $p = 0.0001$, $n = 97$.

Figure 1.4 : Distribution (measured as the proportion of breeding habitat cells that are occupied) plotted against COVER (proportion of the total landscape area in breeding habitat) for 100 simulation runs. Data are from the 500th time step for each run. Spearman rank correlation; $\rho=0.95$, $p=0.0001$, $n=100$.

Figure 1.5 : Distribution plotted agaist mean abundance at the 500th time step, for 100 simulation runs. Spearman Rank correlation; $\rho=0.86$, $p=0.0001$, $n=97$.

DISCUSSION

The results from our simulations suggest that differences in amount of available breeding habitat for species, all other things being equal, can account for a positive relationship between distribution and abundance of species. Landscapes with more breeding habitat reached a higher mean abundance level and a greater distribution and did so more quickly than landscapes with less breeding habitat, resulting in a positive relationship between abundance and distribution.

On a single landscape, each species of an assemblage will perceive the habitat composition differently to a lesser or greater degree, depending on habitat preferences, and therefore different amounts of habitat will be available to each species. Most landscapes consist of many types of habitat in different amounts. Those species that use a higher percentage of the landscape by using more common habitat types or more habitat types (generalists), are expected to be both more abundant and more widely distributed.

Success rate of dispersers, as defined by the probability of finding a patch before dying, is the mechanism through which amount of available habitat influences abundance and distribution. Dispersal is more likely to be successful when there is more habitat available to disperse to. Several empirical studies indicate that immigration can increase the size of small populations (Connor *et al.* 1983, Rey and Strong 1983, Fahrig and Merriam 1985). Askins *et al.* (1987) indicate that for forest-interior birds, density is higher in forest patches that occur in regions of abundant forest and they suggest that dispersal from other forests may be contributing to maintaining the local population. This result supports the suggestion of Ambuel and Temple (1983) that forest-interior bird

populations are regional in that population levels are dependent on the regional forest content.

The metapopulation hypothesis (Hanski *et al.* 1993) suggests that in many natural assemblages, species differ from one another in several respects. Variation in one or more of (1) dispersal rate in relation to intrinsic growth rate, (2) probability that a disperser finds a patch before dying or (3) extinction rate in relation to rate of successful colonization results in a positive relationship between distribution and abundance (Gyllenberg and Hanski 1992). The metapopulation hypothesis was formulated using modelling studies in which the amount of available habitat was fixed and the population parameters were varied. In contrast, we varied habitat availability while holding population parameters constant. We are proposing that the factor controlling the success of dispersers is likely to be the amount of available habitat. This is not explicitly dealt with in the formulation or discussion of the metapopulation hypothesis (Gyllenberg and Hanski 1992). Differences in disperser success can account for the abundance - distribution relationship as argued by Hanski *et al.* (1993). However we hypothesize that differences in disperser success are consistently expected both between and within species because of differences in habitat availability.

Many empirical studies of the relationship between distribution and abundance are conducted on assemblages of taxonomically related species, but these species do not necessarily have the same habitat usages. Several studies, for example, rely on wintering bird data for a large variety of species in North America (Bock and Ricklefs 1983, Bock 1984). We argue that under conditions where the abundance-distribution relationship

exists and species are likely to have different habitat usages, differences in habitat availability is the simplest and most likely cause for the relationship. The relationship need not rely on differences in demographic characteristics between species.

If the abundance-distribution relationship results from variation in habitat availability then we predict a positive relationship between abundance and distribution for single species, where distribution and abundance are measured in a variety of regions that vary in habitat composition. In this case, differences in niche breadth among populations within the species are not likely to account for the relationship. Therefore the resource-use hypothesis (Brown 1984) would not apply, and species differences in parameters such as dispersal rate or dispersal distance would not be relevant. Positive intra-specific relationships between mean abundance and distribution have been examined at very fine scales to develop efficient sampling schemes for pest insects (Yamamura 1990, Hergstrom and Niall 1990, Ward *et al.* 1986, Wilson and Room 1983). There is some work at coarser scales (Bart and Klosiewski 1989, Robbins *et al.* 1989b) which assesses the usefulness of presence-absence measures to detect changes in bird population density over time. It reveals a positive relationship between mean abundance and distribution. These studies lend support to the idea that the positive distribution-abundance relationship is not dependent on interspecific differences. However in most of the above mentioned studies mean abundance is calculated from all sites not just occupied sites, which confounds the result.

Our model has some simplifying assumptions including density independent reproduction and dispersal. The rate of mortality is somewhat density dependent in that

there is a ceiling on the number of individuals within each cell. In any case, we do not anticipate that density dependent reproduction or mortality would qualitatively influence the expected relationship between distribution and abundance. The overall cell densities are expected to be lower but the effects of disperser success on both abundance and distribution are the same. Density dependent dispersal, with an increased rate of dispersal with increasing cell density, will reduce the density of the highest cells relative to lower density cells but overall there will be more dispersal and therefore likely more successful dispersal when average abundance is higher. Therefore the form of the relationship is not expected to change.

The relationship between abundance and distribution appears to hold less well at low levels of breeding habitat than when breeding habitat is abundant (Figure 1.5). Some cells can reach high abundance in the absence of successful dispersal due to stochastic reproduction and mortality. At low levels of breeding habitat these cells will have a large impact on the mean abundance. However, whether a cell is occupied or not depends almost entirely on the amount of successful dispersal which will be low at low levels of breeding habitat. Therefore we expect and find more variation in mean abundance than in distribution at low levels of breeding habitat (see Figures 1.3 and 1.4).

The relationship between regional habitat availability and both distribution and local abundance is significant to problems of conservation. For example, the relationship between population size and the amount of available habitat is not linear if the mean local abundance decreases with decreasing amount of habitat regionally. Therefore, it is necessary to understand the form and magnitude of this relationship to make estimates of

the impact of habitat removal on population size and viability.

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**CHAPTER 2. INTRA-SPECIFIC ABUNDANCE-DISTRIBUTION
RELATIONSHIPS: EVIDENCE FOR THE INFLUENCE OF AMOUNT OF
HABITAT IN THE LANDSCAPE**

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ABSTRACT

Mechanisms that have been proposed to explain the relationship between abundance (mean abundance at occupied sites) and distribution (proportion of occupied sites) have been based on (1) differences among species that affect either their ability to exploit resources or their ability to move through the landscape or (2) the influence of amount of habitat in the landscape on the successful dispersal of individuals. Existence of an intra-specific relationship where species differences cannot be a factor, would provide evidence that amount of landscape habitat contributes to the inter-specific abundance-distribution relationship. We examined the intra-specific relationship between abundance and distribution for twenty species of boreal forest songbirds. Abundance and distribution were calculated for each species in 52 to 119 locations over an area of 300 km x 100 km of northwestern Ontario. Based on separate regressions, sixteen of the species demonstrated significant positive relationships between abundance and distribution at $\alpha=.05$. The weighted mean partial correlation for all species combined was greater than zero ($P<.05$). Meta-analysis indicated that there is no significant variation in the abundance-distribution correlation between species. This study provides evidence that amount of landscape habitat contributes to a positive intra-specific abundance-distribution relationship and therefore suggests that this factor could also contribute to the positive abundance-distribution relationship that is commonly found within species assemblages.

INTRODUCTION

A positive relationship between abundance and distribution of species within a taxonomically related species assemblage has been well documented in the literature (see Brown 1984, Gaston and Lawton 1990b, Hanski *et al.* 1993, Gaston 1994 for review) but for a few exceptions (Gaston and Lawton 1990b). Mechanisms that have been proposed to explain the relationship between abundance (mean abundance at occupied sites) and distribution (proportion of occupied sites) have been based on (1) differences among species that affect either their ability to exploit resources or their ability to move through the landscape (Brown 1984, Gyllenberg and Hanski 1992) or (2) the influence of amount of habitat in the landscape on the successful dispersal of individuals (Gyllenberg and Hanski 1992, Venier and Fahrig in press).

The two most commonly cited hypotheses to explain the positive distribution-abundance relationship are the ecological specialization hypothesis (Brown 1984) and the metapopulation hypothesis (Gyllenberg and Hanski 1992). It has also been noted that when individuals of species are distributed randomly (Poisson) at sites, and some species are more abundant than others, then the expected relationship between distribution and abundance is positive (Wright 1991). Brown (1984) argues that if niches are multidimensional and if spatial variation in the environment tends to be autocorrelated then species that can exploit a large number of different resources (generalists) locally will have high local densities. A species is expected to be more abundant locally when there are more resources available to it locally. These species will also be able to survive in many places and therefore over large areas. Conversely, those species that can exploit

only a few resources (specialists) will be neither locally abundant nor widely distributed (Brown 1984). Therefore, given a species assemblage where there is variation in the level of ecological specialization, a positive relationship between distribution and abundance is expected.

The metapopulation hypothesis (Gyllenberg and Hanski 1992) is an alternative but not mutually exclusive explanation for the abundance-distribution relationship. It predicts a positive relationship between the local abundance at occupied sites and the fraction of occupied sites (distribution), given an assemblage of species with variation in one or more of (1) dispersal rate in relation to intrinsic growth rate, (2) probability of a disperser finding a patch before dying or (3) extinction rate in relation to rate of successful colonization. These predictions are based on a structured metapopulation model in which local population size is affected by dispersal between patches as well as by dynamics within patches. The metapopulation hypothesis argues that any characteristics that vary among species and can create differences in the rate of successful dispersal will generate a positive abundance-distribution relationship.

Venier and Fahrig (in press) argue that the most likely characteristic to generate differences in disperser success is the area of habitat in the landscape. On a single landscape, each species of an assemblage perceives the habitat composition differently depending on habitat preferences. Therefore different amounts of habitat are available to the different species. Most landscapes consist of many types of habitat in different amounts. Those species that use a higher percentage of the landscape by using more common habitat types or more habitat types, are expected to be both more abundant and

more widely distributed because of an increased rate of successful dispersal. Dispersal is more likely to be successful when there is more habitat available to disperse to.

The influence of amount of habitat in the landscape on the abundance and distribution relies on the same mechanism, that of dispersal success, as the metapopulation hypothesis, however the attribute responsible for variation in dispersal success is explicitly suggested to be amount of habitat on the landscape. In Brown's (1984) hypothesis, the local abundance of individuals is dependent on the local abundance of resources. Generalists should have more local resources available to them and will therefore produce more young or survive longer. Venier and Fahrig (in press) however are proposing that the area of habitat on the landscape will positively influence the local abundance due to an increased dispersal success.

These hypotheses were all proposed to explain a positive relationship between distribution and abundance for an assemblage of species. Mechanisms that rely on variation in amount of habitat in the landscape also predict a positive intra-specific abundance-distribution relationship where abundance and distribution of a single species are measured in different landscapes containing different amounts of habitat. This is not true of the ecological specialization hypothesis which relies on variation between species in the degree of ecological specialization. For a single species there is little or no variation in specialization. Therefore this hypothesis cannot address the intra-specific relationship. The metapopulation hypothesis addresses this relationship indirectly. A positive intra-specific relationship cannot be accounted for through differences between species in their movement abilities, but as we have argued, variation in amount of habitat on the landscape

can generate variation in dispersal success. A single species in different regions will experience variation in landscape composition and configuration. If metapopulation dynamics are operating through variation in amount of habitat on the landscape then we predict a positive intra-specific relationship.

We tested the prediction of a positive intra-specific relationship between abundance and distribution for each of twenty species of boreal forest songbirds in northwestern Ontario, Canada. A positive intra-specific relationship would support the idea that variation in amount of habitat on the landscape influences the metapopulation dynamics of species to generate a positive relationship over a number of different landscapes. This landscape variation could also account for a positive inter-specific abundance-distribution relationship on a single landscape for the reasons outlined above and in Venier and Fahrig (in press - Chapter 1).

METHODS

Study Area and Site Selection

As part of an ongoing research program at the Canadian Wildlife Service, Environment Canada, bird census, vegetation and global positioning data were collected in 131 landscapes in an area of approximately 300 km x 100 km throughout northwestern Ontario in 1989 and 1991. The sampling points ranged from 48.18 N, 89.49 W to 50.28 N, 88.87W (south to north) and 48.91N, 91.83 W to 49.81 N, 86.62 W (west to east) (Figure 2.1). Five sample points (sites) were located in each landscape and were on average approximately 300 m apart and at least 100 m from the road. The sites of a

Figure 2.1: Map of study area in northwestern Ontario with location of 131 forest stands sampled for this study.

landscape were in a circle or a line. Landscapes were selected to obtain samples of all vegetation types. Selection was limited by accessibility of forest landscapes and rarity of some types. Initial selection of the landscapes was conducted using Forest Resource Inventory Maps, a system of forest (timber) inventory carried out by the Ontario Ministry of Natural Resources and based mainly on aerial photograph interpretation and some ground truthing (Gillis and Leckie 1993).

Bird Counts

Bird census data were collected using a point count method (Welsh 1995). Each site was visited twice by the same observer, once in early to mid June and once in mid to late June between sunrise and 10 am. Observers conducted 10 minute counts at each site for each visit. All birds seen or heard were recorded. The larger of the counts from the two visits was used as the estimate of abundance for each site and singing males were recorded as 2 individuals (Welsh 1995). Abundance for a landscape was calculated as the mean abundance in occupied sites of the landscape. Distribution was measured as the maximum number of sites occupied in the landscape.

Vegetation

The vegetation type of each site was described according to the Forest Ecosystem Classification (FEC) of Northwestern Ontario (Sims *et al.* 1989). The FEC is a classification of the common, mature (over 50 years of age) vegetation associations of northwestern Ontario which describes 38 separate vegetation types. A classification key is

used to identify the vegetation type of a 10 m x 10 m plot. Five of these plots were keyed out at each site for vegetation type, one at the centre of the site and one at each plot 50 metres from the centre of the site directly north, south, east and west. The mode of the vegetation types for the 25 plots (5 stations) was used to characterize the vegetation type of the landscape.

The geographic position (latitude and longitude) was determined at most sites within all landscapes using a Garmin Survey II Global Positioning System with differential processing (accuracy of 1-3m). The position of the most central site of the landscape where data were available was used as the position of the landscape.

Statistical Analyses

Twenty species of forest songbirds that occurred on at least 50 landscapes were examined for an intra-specific relationship between abundance and distribution at landscapes. We examined the distribution of individuals at sites within each of the species by calculating the index of dispersion (I) (Pielou 1974) and computing the statistic

$$\sqrt{[2I]} - \sqrt{[2n-1]}.$$

This test statistic falls between -1.96 and +1.96 95% of the time when individuals are randomly distributed. Species with distributions that were not distinguishable from random should be removed from the analysis because a positive abundance-distribution relationship is expected when the distribution is random (Wright 1991).

A multiple regression (SAS Institute 1988) was performed with log transformed

mean abundance (at occupied sites) as the response variable and with vegetation type, latitude, longitude, second order latitude, second order longitude and distribution as explanatory variables.

Vegetation type was entered as a class variable to control for a potentially spurious positive relationship. Both abundance and distribution will be similarly affected by vegetation type. A station that is composed of good habitat is more likely to be occupied and to have higher abundance. If there are good quality landscapes which should on average have high distribution and high abundance and bad quality landscapes with low distribution and low abundance then there will be a positive relationship between distribution and abundance due to the differences in habitat quality between landscapes and the fact that habitat tends to be of the same quality within landscapes. Vegetation type was included to remove this possible effect.

Populations at the edge of a species' range typically have low abundance and distribution (See Brown 1984 for examples), while those at the centre of the range have high abundance and distribution. To control for this possible effect, we included the geographic position of the site in the statistical models relating abundance to distribution. In this way, any variation in abundance that is due to the geographic position is removed before examining the remaining relationship with distribution. By including both latitude and longitude in the model we can fully describe the 2 dimensional space that is the range of the species. By including the second order terms we can model the change in abundance of the species over its range regardless of where the centre of the range is.

We examined the Type III Mean Square of distribution to determine if there was a

relationship between distribution and abundance after controlling for the effects of vegetation type and geographic location. We conducted a separate regression for each species. The sample size for each species was dependent on the number of landscapes where the species was found and ranged from 52 to 119.

We combined the results of the 20 analyses into a single meta-analysis (Hunter and Schmidt 1990), using the partial r_i value for the distribution variable as the effect size for each species i . The objective of the meta-analysis is to determine the amount of variance in the estimates of the effect size. If the variance is not different from zero then the overall weighted r value for all species combined ($\sum [N_i r_i] / \sum N_i$) (Hunter and Schmidt 1990; p. 100) can be used as the population correlation coefficient, where N_i is the number of observations for species i . The meta-analysis assumes that the variance of the population correlations can be calculated as the variance of observed correlations minus the sampling error. The variance of the observed correlations is estimated as

$$s_r^2 = \frac{\sum [N_i (r_i - \bar{r})^2]}{\sum N_i}$$

And the sampling error is calculated as

$$\sigma_e^2 = (1 - \bar{r}^2)^2 / (N - 1)$$

The r_i values were calculated as the square root of the Type III regression sums of squares for distribution over the total sums of squares for the model. We considered sampling

error as the only artifact. We calculated a 95% confidence interval around the weighted r value based on the overall sample size to determine if the overall correlation was different from zero (Zar 1984).

RESULTS

For all 20 species we rejected the null hypothesis of a Poisson distribution (Table 2.1), therefore all species were included in the analysis. Sixteen species showed a significant positive relationship between distribution and abundance at the $\alpha = .05$ level (Table 2.2). The remaining four species did not show a significant relationship. All slope estimates were positive (Table 2.2). The residuals from all models were examined and fit the assumptions of linear regression.

The meta-analysis using the partial r_i for distribution as the effect size (Table 2.2) indicated that the weighted average r was $+.261$. The total sample size was 1651 and the average sample size was 82.6. The sample (observed) variance was .00933 and the sampling error variance was .0107 therefore the population correlation variance was $-.001$ which strongly indicates that there was no demonstrable difference in the effect size (r_i) among species (Hunter and Schmidt 1990: p.109). A negative correlation variance is not unexpected in a meta-analysis because the correlation is calculated as the difference between the variance of observed correlations (which is a sample estimate) and the statistically given sampling error variance. There will be some error in the sample estimate and therefore when the correlation variance is zero the error will cause the estimate to be negative about half the time (Hunter and Schmidt 1990). The lower limit of the 95%

Table 2.1: Index of Dispersion and the normally distributed dispersion statistic for each of 20 species. The null hypothesis is a Poisson distribution of abundance at sites. The null hypothesis is rejected in all species.

Species Common Name	Latin Name	N	I	$\sqrt{(2I)} - \sqrt{(2n-1)}$
American Robin	<u>Turdus migratorius</u>	335	555	7.44
Blackburnian Warbler	<u>Dendroica fusca</u>	350	620	8.78
Black-throated Green Warbler	<u>Dendroica virens</u>	315	556	8.25
Chipping Sparrow	<u>Spizella passerina</u>	355	718	11.28
Dark-eyed Junco	<u>Junco hyemalis</u>	260	516	9.35
Golden-crowned Kinglet	<u>Regulus satrapa</u>	500	839	9.36
Hermit Thrush	<u>Catharus guttatus</u>	420	899	13.43
Least Flycatcher	<u>Empidonax minimus</u>	395	1221	21.38
Magnolia Warbler	<u>Dendroica magnolia</u>	395	740	10.38
Nashville Warbler	<u>Vermivora ruficapilla</u>	560	1391	19.29
Ovenbird	<u>Seiurus aurocapillus</u>	505	840	9.23

Table 2.1 continued

Red-breasted Nuthatch	<u>Sitta canadensis</u>	355	529	5.91
Red-eyed Vireo	<u>Vireo olivaceus</u>	330	612	9.33
Ruby-crowned Kinglet	<u>Regulus calendula</u>	450	780	9.50
Swainson's Thrush	<u>Catharus ustulatus</u>	510	1010	13.02
Tennessee Warbler	<u>Vermivora peregrina</u>	350	979	17.81
White-throated Sparrow	<u>Zonotrichia albicollis</u>	595	1277	16.05
Winter Wren	<u>Troglodytes troglodytes</u>	515	841	8.93
Yellow-bellied Flycatcher	<u>Empidonax flaviventris</u>	295	505	7.51
Yellow-rumped Warbler	<u>Dendroica coronata</u>	550	816	7.26

Table 2.2: Sample sizes and statistics from multiple regression models for each of 20 species of forest songbirds. The response variable for all models is Log (Abundance+1). The independent variables are Distribution, Latitude, Longitude, Latitude², Longitude² and Vegetation Type. Partial r_i values are for the Distribution variable. N is the number of observations for each species.

Species Name	N	Dist. MS Type III	Dist. F	Dist. P	Partial r_i	Slope Est.
American Robin	67	.286	9.44	.004	.33	+.35
Blackburnian Warbler	70	.205	4.59	.038	.27	+.28
Black-throated Green Warbler	63	.297	6.42	.016	.30	+.33
Chipping Sparrow	71	.518	16.44	.000	.42	+.48
Dark-eyed Junco	52	.311	11.95	.001	.38	+.48
Golden-crowned Kinglet	100	.147	6.90	.011	.23	+.22
Hermit Thrush	84	.304	7.25	.010	.24	+.34
Least Flycatcher	79	1.023	12.55	.001	.34	+.42
Magnolia Warbler	62	.001	.06	.811	.03	+.02
Nashville Warbler	112	1.028	31.30	.000	.35	+.44
Ovenbird	101	.357	9.76	.003	.18	+.39
Red-breasted Nuthatch	71	.022	2.46	.125	.18	+.10
Red-eyed Vireo	90	.856	21.56	.000	.33	+.59
Ruby-crowned Kinglet	66	.303	10.16	.003	.29	+.42
Swainson's Thrush	102	.766	15.50	.000	.31	+.45
Tennessee Warbler	70	.312	4.33	.044	.18	+.47

Table 2.2 continued

White-throated Sparrow	119	1.110	19.51	.000	.38	+.41
Winter Wren	103	.139	4.35	.041	.20	+.18
Yellow-bellied Flycatcher	59	.017	.98	.330	.09	+.11
Yellow-rumped Warbler	110	.088	2.81	.098	.14	+.14

confidence limit on p was 0.2156 and the upper limit was .3050 suggesting that there is an overall positive relationship between abundance and distribution.

DISCUSSION

The results of the current analysis are consistent with idea that of the amount of habitat on the landscape influences the positive inter-specific abundance-distribution relationship. By examining the within-species relationship we have effectively controlled for any variation in species traits. The only attributes that vary from sample to sample are landscape related ones because each sample is taken in a different landscape. We have argued previously that for a species assemblage in a single location there is also variation between species in the amount of habitat on the landscape (Venier and Fahrig in press). Each species perceives the landscape differently depending on its own specific habitat usage.

Results from simulation experiments (Venier and Fahrig in press) indicate that differences in amount of breeding habitat for species within a landscape, all other things being equal, can account for a positive relationship between distribution and abundance of species. Populations in simulated landscapes with more breeding habitat reach a higher mean abundance level and a greater distribution and do so more quickly than populations in landscapes with less breeding habitat. The amount of habitat has been used in previous studies as a measure of landscape structure (Askins *et al.* 1987, van Dorp and Opdam 1987, Lehmkuhl *et al.* 1991). The proportion of habitat on simulated landscapes has been demonstrated to be related to many indices of patch spatial pattern (Gustafson and

Parker 1992).

More breeding habitat makes successful dispersal much more likely. Successful dispersal has been shown to increase the size of small populations in several empirical studies (Connor *et al.* 1983, Rey and Strong 1983, Fahrig and Merriam 1985). Similarly, successful dispersal to unoccupied patches will increase the distribution of the species. Therefore we expect a positive abundance-distribution relationship when there is variation in amount of habitat.

In the intra-specific case, variation in the amount of habitat on the landscape comes from sampling different landscapes. In the inter-specific case, a single landscape is likely to offer different amounts of habitat to different species because each species has different habitat usages. In effect, the same landscape is different for every species. Therefore the influence of amount of available habitat can also explain the inter-specific abundance-distribution relationships. The presence of the intra-specific relationship suggests that variation in habitat amount on the landscape could function to generate a positive distribution-abundance relationship. This indirectly provides support for the influence of amount of available habitat on the inter-specific abundance distribution relationship. Hypotheses that rely directly on differences between species (Gyllenberg and Hanski 1992), such as dispersal ability or differences in ecological specialization (Brown 1984) would not predict a positive intra-specific relationship.

The two most commonly cited hypotheses to explain the positive inter-specific distribution-abundance relationship use either the variation in the level of ecological specialization (Brown 1984) or movement within metapopulations (Gyllenberg and Hanski

1992). The ecological specialization hypothesis (Brown 1984) relies on between-species variation in ecological specialization of which there is none in the intra-specific case. Therefore the existence of an intra-specific relationship between distribution and abundance cannot be predicted from Brown's hypothesis. This does not suggest that the ecological specialization mechanism is not operating but it does suggest that other mechanisms are operating.

The metapopulation hypothesis (Gyllenberg and Hanski 1992) argues that variation in (1) dispersal rate in relation to intrinsic growth rate, (2) probability of a disperser finding a patch before dying or (3) extinction rate in relation to rate of successful colonization, can generate a positive relationship between abundance and distribution. The current study provides is consistent with the second and third parts of this hypothesis. Variation in these two can be due to variation in amount of habitat on the landscape. The first part of this hypothesis could still be operating but would not predict the intra-specific abundance-distribution relationship. In addition, differences between species that caused variation between species in disperser success would not generate a prediction of an intra-specific relationship.

Wright (1991) suggested that when species were randomly distributed a positive abundance-distribution relationship was expected. None of the species examined here were randomly distributed. However a more common distribution for organisms is a negative binomial distribution which describes a clumped distribution (Taylor *et al.* 1978). Species distributed as a negative binomial also show a positive abundance-distribution relationship (Wright 1991). The question then becomes what causes the clumping.

Wright (1991) suggested that many different unrelated ecological factors can produce clumping and therefore contribute to the distribution-abundance relationship. These factors include spatial variation in habitat, social behaviour, localized reproduction and stochastic immigration-extinction processes. In the context of this study the spatial variation in habitat quality has been controlled and juveniles do not remain at the same site therefore localized reproduction is not expected to be a factor in generating a clumped distribution. For boreal forest songbirds, the dominant intra-specific interaction during the breeding season is territoriality which seems unlikely to generate aggregation at the smallest scales. Stochastic immigration-extinction is essentially the mechanism proposed in this paper. Other factors may cause clumping and we have made no attempt to eliminate all hypotheses. We present the positive intra-specific relationship as a result consistent with our hypothesis and not related to species-specific differences. More direct tests are required to say more.

To our knowledge, this is the first study that tests for an intra-specific relationship between independent measures of distribution and abundance. The intra-specific relationship between abundance and distribution has been examined in the past but always in the context of using distribution (proportion of sites occupied) to estimate abundance (Bart and Klosiewski 1989, Gerrard and Chiang 1970, Hergstrom and Niall 1990, Robbins *et al.* 1989b, Wilson and Room 1983, Ward *et al.* 1986). Positive relationships have always been found but the results are confounded because the abundance that is relevant to these studies is the abundance in all sites including the empty ones. Abundance measured in this way is necessarily related to distribution because both measures are

influenced the same way by empty sites.

The size of the landscape on which a study is conducted is important in determining the potential influence of amount of habitat on abundance and distribution. The mean abundance of occupied sites is measured at the scale of an individual site. The amount of habitat around that site (the landscape) is expected to influence the abundance at that site. Distribution however is measured at the scale of the landscape. The size of the landscape on which abundance and distribution are measured is an arbitrarily defined area, but the area that potentially influences abundance and distribution is not. For the mechanism of dispersal success to influence both abundance and distribution through amount of habitat, the sampled landscape must be similar in scale to the dispersal distance of the organisms. Habitat outside the dispersal distance of an organism will have much less influence over the abundance and distribution than habitat within the dispersal distance.

The existence of a positive intra-specific abundance-distribution relationship is consistent with the idea that variation in amount of habitat on the landscape can generate a positive abundance-distribution relationship but it is not a direct test of the idea. A direct test would require an examination of the relationship between the amount of habitat on the landscape and both the abundance and distribution. Habitat can be of different qualities depending on its ability to supply the necessary resources for reproduction and survival, so the area of habitat on the landscape would have to be weighted by its quality. This weighting would be different for each species in the inter-specific case.

Given the ubiquity of the relationship between abundance and distribution, it is

likely that different mechanisms are responsible for the relationship under different conditions. However, the positive intra-specific relationship that we found overall argues strongly for the influence of amount of habitat on the landscape on the relationship. This would also be true for different species in the same landscape since the realized habitat of the landscape depends on the species' interaction with it.

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CHAPTER 3: THE INFLUENCE OF THE AMOUNT OF HABITAT IN THE LANDSCAPE ON THE DISTRIBUTION-ABUNDANCE RELATIONSHIP

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ABSTRACT

The objective of this study was to examine empirically the relationship between the amount of habitat in the landscape and both the local abundance and distribution of individuals for each of ten species of songbirds of the boreal forest of northwestern Ontario, Canada. We predicted that the amount of habitat in the landscape would be positively related to both the local abundance and the distribution because dispersal success would be more likely in landscapes with more habitat. Therefore variation in amount of habitat in the landscape could account for the positive distribution-abundance relationship. We found a generally positive influence of habitat in the landscape when habitat in the landscape was of better quality than local habitat. Conversely, we found a negative influence when habitat in the landscape was of poorer quality. Based on logistic regressions, the amount of habitat in the landscape was positively related to the presence of individuals in all 8 species examined and explained a significant amount of variance in 5 of 8 species examined. The results of this study matched our predictions. Both local abundance and distribution were positively related to the amount of habitat in the landscape.

INTRODUCTION

A positive relationship between distribution and abundance has been found in many groups of taxa (Brown 1984, Gaston and Lawton 1990) but for a few exceptions (Gaston and Lawton 1990). This relationship has been attributed by some to the operation of metapopulation dynamics (Gyllenberg and Hanski 1992, Hanski *et al.* 1993, Venier and Fahrig in press). The modelling studies conducted by Gyllenberg and Hanski (1992) have demonstrated that a species assemblage with variation among species in demographic and movement parameters, such as probability of a disperser finding a patch before dying, will have a positive relationship between abundance and distribution. Venier and Fahrig (in press) have argued that the most likely attribute to generate differences in disperser success among species is the amount of available habitat in the landscape. Results from simulation modelling suggest that the amount of available breeding habitat in a landscape positively influences both distribution and abundance (Venier and Fahrig in press). Therefore, variation in the amount of breeding habitat on landscapes can generate a positive relationship between abundance and distribution (Venier and Fahrig in press) through the mechanism of variation in dispersal success. More available breeding habitat makes successful dispersal more likely. Successful dispersal has been shown to increase the size of small populations in several empirical studies (Connor *et al.* 1983, Rey and Strong 1983, Fahrig and Merriam 1985). Successful dispersal to unoccupied patches will also increase the distribution of the species.

Our objective in this study is to provide a direct test of the influence of amount of available habitat on the landscape on the relationship between abundance and distribution.

We examined the relationship between amount of habitat in the landscape on abundance and on distribution for each of ten boreal songbird species in northwestern Ontario, Canada. We predict that the influence will be positive for both abundance and distribution. If both relationships are positive we can infer that the abundance-distribution relationship is mediated, at least in part, by habitat amount at the landscape scale. This test requires that we can measure the amount of habitat in an area surrounding a local measure of abundance and occupancy. The amount of habitat in the landscape is a function of area and quality of habitat. The local habitat also contributes to the variation in abundance so it must be controlled for before examining the influence of amount of habitat in the landscape.

The abundance-distribution relationship is primarily discussed in the context of a species assemblage. Variation in amount of available habitat on a landscape is expected within an assemblage of species because there will be differences in habitat preferences of species. Each species in a group will therefore perceive that same landscape in very different ways. Landscape structure will differ among species because of the different habitat types that they can use. Many aspects of species specific landscape composition and structure are influenced by habitat usage but the amount of habitat on the landscape can be viewed as a general measure of landscape structure as it influences dispersal dynamics. Gustafson and Parker (1992) have demonstrated that the proportion of habitat on simulated landscapes is related to many indices of patch spatial pattern. Several empirical studies have also used amount of habitat as a measure of landscape structure (Askins *et al.* 1987, van Dorp and Opdam 1987, Lehmkuhl *et al.* 1991). Landscape level

studies have also shown the negative influence of isolation (as measured inversely by amount of regional habitat) on the density of forest birds (Askins *et al.* 1987). Any species assemblage that has variation in amount of habitat on the landscape among species and therefore variation in disperser success should have a positive relationship between distribution and abundance.

The influence of the amount of habitat in the landscape on the abundance-distribution relationship for an assemblage of species (Venier and Fahrig in press) is consistent with the prediction that there will be a positive relationship between abundance and distribution for a single species in a number of different landscapes. Each landscape provides a different amount of habitat to the species. The influence of this habitat is positive for both abundance and distribution.

Attributes that can influence the metapopulation dynamics of a species can be divided into two types. The first type are those belonging to the species that dictate its ability to move through the landscape such as dispersal ability and dispersal rate. An explanation of the abundance-distribution relationship that relies on this type of attribute cannot explain an intra-specific relationship. The second type are attributes belonging to the landscape that dictate its structure including its composition, configuration and connectivity. The amount of habitat on the landscape belongs to this second type. Explanations relying on this second type of attribute do predict a positive intra-specific relationship. In the within species case any possible differences among species are controlled for leaving only those explanations that rely on landscape attributes.

Venier and Fahrig (unpublished data) have demonstrated a positive intra-specific

relationship for a group of boreal forest songbirds. They examined the distribution and abundance in a number of landscapes for each of twenty species, where abundance was measured as the mean abundance in occupied sites and distribution was measured as the proportion of sites occupied. Wright (1991) argued that a random distribution of abundance would result in a positive relationship between distribution and abundance. However all species had non-random distributions. The existence of a positive abundance-distribution relationship for a species in different landscapes suggests that some mechanisms are operating to generate this relationship that do not rely on species differences.

Some previous studies have examined this intra-specific relationship between distribution and abundance (Bart and Klosiewski 1989, Gerrard and Chiang 1970, Hergstrom and Niall 1990, Robbins *et al.* 1989b, Wilson and Room 1983, Ward *et al.* 1986). The objective of these studies was to examine the accuracy of using distribution (the proportion of occupied sites) as an index of abundance. Positive relationships have always been found but the results are confounded because the abundance that is relevant to these studies is the abundance in all sites including the empty ones. Abundance measured in this way is necessarily related to distribution because both measures are influenced in the same way by empty sites.

A positive intra-specific relationship between abundance and distribution is indirect evidence for the influence of the amount of habitat in the landscape on the relationship. In this study we examine directly the relationship between the amount of habitat in the landscape and both the abundance at occupied sites and the distribution measured as the

probability of a site being occupied. A positive relationship for both abundance and distribution is predicted and will confirm the influence of amount of habitat in the landscape on a positive abundance-distribution relationship.

METHODS

Overview

The objectives of these methods are to examine: (1) the relationship between local abundance and amount of habitat available in the landscape and, (2) the relationship between distribution and amount of habitat available in the landscape. Amount of habitat is a function of both the area of habitat and quality of the habitat. Within the given data set quality must be estimated using abundance. As a result, methods had to be designed to avoid circularity.

Study Area and Site Selection

As part of an ongoing research program at the Canadian Wildlife Service, Environment Canada, bird census, and vegetation data were collected in 171 landscapes in an area of approximately 300 km x 100 km throughout northwestern Ontario in 1989 and 1991 (Figure 1 - General Methods). Samples were not collected specifically for this study. We use the term landscape here to include an area of approximately 1 km² although this value is somewhat variable. Five sample points (sites) were located in each landscape and were on average approximately 300 m apart and at least 100 m from the road. The sites were located within the landscapes in a variety of configurations such that

they met the above criteria of distance apart and distance from the road. Landscapes were selected to obtain samples of all vegetation types. Selection was limited by accessibility of forest landscapes and rarity of some types. Initial selection of the landscapes was conducted using Forest Resource Inventory Maps, a system of forest (timber) inventory carried out by the Ontario Ministry of Natural Resources and based mainly on aerial photograph interpretation and some ground truthing (Gillis and Leckie 1993).

Bird Counts

Bird census data were collected using a point count method (Welsh 1995). Each site was visited twice by the same observer, once in early to mid June and once in mid to late June between sunrise and 10 am. Observers conducted 10 minute counts at each site for each visit. All birds seen or heard were recorded. The larger of the counts from the two visits was used as the estimate of abundance for each site and territorial singing males were recorded as a breeding pair (Welsh 1995). Abundance for a landscape was calculated as the mean abundance in occupied sites of the landscape. Distribution was measured as the maximum number of sites occupied in the landscape.

Vegetation

The vegetation type of each site was described according to the Forest Ecosystem Classification (FEC) of Northwestern Ontario (Sims *et al.* 1989). The FEC is a classification of the common, mature (over 50 years of age) vegetation associations of northwestern Ontario which describes 38 separate vegetation types and is based on an

ordination of 2100 plots. A classification key is used to identify the vegetation type of a standard 10 m x 10 m plot. Vegetation types were keyed out at five plots at each bird census site, one at the centre of the station and one at each plot 50 metres from the centre of the station directly north, south, east and west. The mode of the vegetation types for the 25 plots (5 sites) was used to characterize the vegetation type of the landscape. Local scale, for the purposes of this study, includes the area sampled by a bird point count which is an area approximately described by a circle with radius 100m (3.14 ha). The local vegetation measure (5 vegetation plots) samples this area. The landscape scale includes an area around the census site that is sampled by all sites of the landscape. Landscapes were chosen as forest stands (Gillis and Leckie 1993) from Forest Resource Inventory Maps. These stands are areas within which the forest type is judged to be similar based on aerial photographs. The area of the stands selected for this study range from 20 - 586 ha. All sites within the stand were on average 300 m apart. The landscape area sampled is within 800 m of the local site. We discuss the implications of the scale of sampling in the Discussion.

Local Abundance and Landscape Habitat

We tested for an effect of amount of habitat in the landscape on local abundance. Each landscape contained 5 sampling sites. Since local and landscape habitat was likely correlated we needed to separate the effects of landscape habitat from local habitat. We did this as follows. We used a single site to measure the local bird abundance and local habitat type and the remaining 4 sites to measure the amount of habitat on the landscape.

We selected the single site with the lowest quality for the first analysis and the single site with the highest quality for the second analysis. Habitat for the site (local) was described by the vegetation type for the site. The site having the worst habitat was defined as the site with the vegetation type expected to have the lowest abundance; converse for the best. The expected value of the site was calculated as the mean abundance for all sites with that vegetation type based on all data (855 sites). If all vegetation types for the landscape were the same then the landscape was discarded. We then calculated the observed value minus the expected value for each selected site i.e. the worst or the best site. We hypothesized that the amount of habitat in the vicinity of a site will positively influence the abundance at a site. We predicted therefore that for a site surrounded by better habitat (worst site), the better habitat would raise the value of the local abundance beyond what was expected just based on the local habitat type. The observed value minus the expected value was therefore predicted to be positive. Conversely we predicted that for a site surrounded by worse habitat (best site), the worse habitat would lower the value of the local abundance below what was expected just based on the local habitat type for the best site. For the best site the observed value minus the expected value was therefore predicted to be negative. We conducted a t-test for each case (worst and best) on the difference between observed and expected abundance to test this prediction against the null hypothesis that the difference is not positive (worst) or not negative (best).

We conducted both of these tests with two sets of data for each of the ten most abundant species. The first data set contained all available sites including those that had no individuals in them. The second approach was to use only those sites where the species

occurred and to calculate the expected value for occupied sites.

Distribution and Landscape Habitat

The goal of the previous analyses was to examine the relationship between local abundance and the amount of habitat in the landscape. The goal of the analyses described in this section is to examine the relationship between amount of habitat in the landscape and the distribution, with distribution measured as the probability of occurrence at a site. If both abundance and distribution are positively influenced by the amount of habitat in the landscape then variation in the amount of habitat in the landscape can generate a positive abundance-distribution relationship. Distribution has been defined in some studies as the area within a defined area that a species uses (Hanski 1982, Gaston 1990). This attribute has traditionally been measured as the proportion of locations that are occupied by a species (Hanski 1982, Hanski *et al.* 1993). We have used the probability that a site is occupied as a measure of distribution.

To examine the relationship between the distribution and the amount of habitat in the landscape we conducted a logistic regression for each of the ten boreal songbird species. The response variable is the presence or absence (distribution) of the species at one site within a landscape. The explanatory variable of interest is the amount of habitat in that landscape. We selected the site within the landscape with the most unique vegetation type within each landscape to generate the greatest possible difference between the expected influence of the local vegetation and the landscape level amount of available habitat in the landscape. The most unique vegetation type was defined as the one that was

farthest from other vegetation types of the site in the vegetation ordination space of a vegetation classification conducted by Sims *et al.* (1989). If all of the vegetation types for a site were the same then the site was discarded.

The amount of habitat available in the landscape (LANDSCAPE) was derived from the 20 vegetation plots at the other 4 sites within the landscape. The frequency of each of the vegetation types for the landscape was calculated based on these 20 plots. The quality of each vegetation type for each species was estimated as the mean abundance per site of the species for the vegetation type based on all of the data except for the landscape for which the estimate was being made. The frequency of each vegetation type in a landscape was multiplied by the estimated quality of that vegetation type. The amount of available habitat in the landscape where the site was located was then estimated by summing over all vegetation types in the 4 sites. In this way, the area of habitat on the landscape was weighted by the quality of that habitat.

We conducted logistic regressions with presence/absence as the response variable. Local vegetation type (VEGETATION), measured as the mode of 5 vegetation plots for the site, was included first in the model as a class variable to control for its effects on the probability of occurrence and then the amount of habitat on the landscape was added. There were insufficient data to model presence within 38 vegetation types so we grouped the vegetation types according to similar vegetation composition into 11 groups. Vegetation types are class variables and therefore dummy variables were used to represent the separate levels of the class variable. Some of the vegetation types were still poorly represented which caused an incomplete separation of the sample points and which

prevented the model from running (SAS Inc. 1988). We removed sites that represented the less common vegetation types until the model would run. We conducted three logistic regressions for each of ten species. The first model included just the local vegetation dummy variables (VEGETATION). The second model included just the amount of habitat on the landscape (LANDSCAPE). The third model (COMBINED) included both VEGETATION and LANDSCAPE.

Estimates of amount of habitat for the landscape were based in part on the assumption that the vegetation types as described by the FEC reflect habitat types that species select according to their own habitat preferences. A significant relationship between the probability of occurrence and vegetation types supports this assumption. Species for which the VEGETATION model was not significant were discarded.

RESULTS

Forty-four of the original 171 landscapes were homogeneous with respect to vegetation types sampled and were therefore removed from the analysis leaving 127 landscapes.

Abundance and Landscape Habitat

The mean difference between observed abundance at the worst site of a landscape and the expected value at the site based on the local habitat was positive for all 10 species as predicted. These differences were significantly different from zero for 5 species ($\alpha=0.05$) (Table 3.1). Conversely, the mean difference between observed abundance

2

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PRECISIONSM RESOLUTION TARGETS

Table 3.1: Paired comparisons of observed abundance minus expected abundance at worst and best local habitat of a landscape.

Species Common Name	Latin Name	N	Worst Local Habitat			Best Local Habitat		
			X Difference	T	P	X Difference	T	P
Hermit Thrush	<u>Catharus guttatus</u>	126	.203	1.95	.054	-.425	-3.67	.000
Nashville Warbler	<u>Vermivora ruficapilla</u>	127	.230	1.26	.211	-.342	-1.70	.090
Ovenbird	<u>Seiurus aurocapillus</u>	127	.575	3.21	.002	-.548	-3.04	.003
Red-eyed Vireo	<u>Vireo olivaceus</u>	127	.358	2.46	.015	-.640	-3.67	.000
Ruby-crowned Kinglet	<u>Regulus calendula</u>	125	.165	1.77	.079	-.291	-2.45	.016
Swainson's Thrush	<u>Catharus ustulatus</u>	127	.396	2.51	.013	-.297	-1.51	.134
Tennessee Warbler	<u>Vermivora peregrina</u>	122	.708	3.94	.000	-.765	-3.99	.000
White-throated Sparrow	<u>Zonotrichia albicollis</u>	127	.115	.70	.484	-.467	-3.02	.003
Winter Wren	<u>Troglodytes troglodytes</u>	127	.142	1.16	.249	-.235	-1.62	.109
Yellow-rumped Warbler	<u>Dendroica coronata</u>	127	.177	1.41	.161	-.098	-.676	.501

at the best site of the landscape and the expected value at the site based on the local habitat was negative for all 10 species as predicted and significantly so for 7 species (Table 3.1).

Abundance at occupied stations only was also examined. The mean difference between observed abundance at the worst occupied site and the expected value based on the local habitat was positive in 8 of 10 species and significant in 2 of these 8 species. Conversely, the mean difference between observed abundance at best occupied site and the expected value based on the local habitat was positive for 9 of 10 species and significant in 2 of these 8. Generally, the mean differences were associated with low P values when the sign was in the direction predicted (Table 3.2). The highest P values were those associated with estimates with a sign in the direction not predicted (Table 3.2).

Distribution and Landscape Habitat

Of the ten species, two had non-significant VEGETATION models (White-throated Sparrow (Deviance=140.5, $P=.68$, $N=105$) and Winter Wren (Deviance=142.3, $P=.41$, $N=105$)); and therefore no LANDSCAPE or COMBINED models were calculated for these species. The LANDSCAPE variable in the COMBINED model was positively related to the presence of each of the 8 remaining species and significantly so in 5 at $\alpha=.05$ (Table 3.3) based on Type 3 sums of squares. The addition of LANDSCAPE to the COMBINED model results in an increase in percentage of concordant pairs by an

Table 3.2: Paired comparisons of observed abundance minus expected abundance at worst and best local habitat of a landscape. Only landscapes where species is present are included in the analysis.

Species Common Name	Latin Name	N	Worst Local Habitat			Best Local Habitat		
			X Difference	T	P	X Difference	T	P
Hermit Thrush	<u>Catharus guttatus</u>	41	.359	2.30	.027	-.394	-1.97	.056
Nashville Warbler	<u>Vermivora ruficapilla</u>	69	.495	2.12	.038	-.164	-.68	.497
Ovenbird	<u>Seiurus aurocapillus</u>	100	.313	1.75	.084	-.481	-2.53	.013
Red-eyed Vireo	<u>Vireo olivaceus</u>	67	.403	1.85	.069	-.371	-1.59	.118
Ruby-crowned Kinglet	<u>Regulus calendula</u>	37	-.001	-.01	.999	-.112	-.45	.658
Swainson's Thrush	<u>Catharus ustulatus</u>	79	.203	1.30	.196	-.110	-.56	.579
Tennessee Warbler	<u>Vermivora peregrina</u>	50	.263	1.01	.319	-.293	-.86	.396
White-throated Sparrow	<u>Zonotrichia albicollis</u>	78	-.008	-.05	.958	-.499	-3.15	.002
Winter Wren	<u>Troglodytes troglodytes</u>	67	.063	.59	.556	.027	.18	.857
Yellow-rumped Warbler	<u>Dendroica coronata</u>	81	.073	.68	.501	-.158	-1.02	.309

Table 3.3: Logistic regression results for VEGETATION, LANDSCAPE and COMBINED models for 8 species of birds that had significant relationships between presence of the species and the local vegetation types. All regressions are based on 105 observations.

Species Common Name	Deviance of VEGETATION model	Deviance of COMBINED model	LANDSCAPE P value in COMBINED model	LANDSCAPE Parameter Estimate	VEGETATION Concordant Pairs (%)	COMBINED Concordant Pairs (%)
Hermit Thrush	97.9	95.4	.246	.038	66	72
Nashville Warbler	130.2	128.8	.050	.021	62	73
Ovenbird	88.7	71.5	.000	.038	75	87
Red-eyed Vireo	106.2	86.1	.000	.060	75	88
Ruby-crowned Kinglet	96.0	89.6	.672	.050	68	74
Swainson's Thrush	127.6	123.4	.124	.044	70	80
Tennessee Warbler	92.6	68.4	.000	.062	65	84
Yellow-rumped Warbler	120.0	119.8	.000	.012	65	88

average of 11.3.

DISCUSSION

The results of the comparisons between observed abundance at local sites and their expected abundance based on local conditions alone, strongly suggests that some part of the local abundance is explained by the landscape level habitat composition. The analyses that were based on all sites including empty ones indicated a stronger relationship between abundance and the amount of habitat in the landscape than those that used only occupied sites. This result is expected if both occupancy and abundance where occupied are similarly affected by the amount of habitat in the landscape. Abundance measured at all sites including empty ones is necessarily related to the distribution measured as occupancy. The logistic regressions also clearly demonstrate a positive relationship between the probability of a site being occupied and the amount of habitat in the landscape independent of the type of local habitat. These tests are conservative because we can only attribute to the landscape that variance in distribution and abundance that is not attributable to the local habitat type. Since local habitat type and the amount of habitat in the landscape are often correlated there is a great deal of overlapping variance explained.

This study demonstrates that both distribution and abundance are positively correlated with the amount of habitat in the surrounding area beyond the local habitat. Therefore even in the absence of any other effects, variation in the amount of habitat in the landscape will cause a positive relationship between distribution and abundance. This is true both for single species among landscapes and for multiple species within a single

landscape.

The objective of this study is to demonstrate that differences in amount of landscape habitat can result in a positive relationship between distribution and abundance. A positive intra-specific relationship between distribution and abundance has been demonstrated for these and several other species in a previous study (Venier and Fahrig, unpublished data) using the same sampling scheme. A positive intra-specific relationship is indirect evidence of the influence of landscape habitat on the abundance-distribution relationship since any between species differences are controlled for leaving only variation between landscapes (Venier and Fahrig in press). The current study demonstrates the influence of landscape habitat amount on the relationship; however it does not attempt to eliminate other hypotheses or suggest that only one mechanism is operating. Variation in the amount of habitat available to a species on a landscape is a sufficient condition to generate a positive relationship between distribution and abundance.

Venier and Fahrig (in press) have argued that for any species assemblage of taxonomically related organisms such as forest songbirds, each species will perceive the landscape differently and will therefore have different amounts of habitat available to it on the same landscape. Such a species assemblage, with variation in amount of available habitat, should have a positive relationship between distribution and abundance. This relationship was predicted from simulation experiments that varied the amount of available breeding habitat on the landscape and measured the abundance at occupied sites and distribution (proportion of occupied sites) (Venier and Fahrig, in press). In the case of the simulation experiments, the mechanism controlling the abundance -distribution relationship

is the likelihood of successful dispersal. More available habitat on a landscape results in higher probability of successful dispersal. This is the same mechanism proposed by Gyllenberg and Hanski (1992); however they discussed the mechanism in terms of differences between species that might generate differences in disperser success and not in terms of habitat amount.

This study was limited because the landscapes were chosen as forest stands which were delimited on aerial photographs as areas of homogenous forest cover type. To separate the effects of local and landscape habitat, sampling would be best where local habitat was different from landscape habitat (Pearson 1993). It is difficult to statistically separate the variance in abundance or occupancy that is explained by local versus landscape habitat when the two are highly correlated in the samples. Although it is clear that there is unique variance explained by landscape habitat it is not clear how important these factors might be relative to local factors.

The landscape level sampling for this study was conducted at a single scale. It appears that the amount of habitat within approximately one kilometre of a local site influences the local abundance and the probability of occupancy at that site. We propose that dispersal success increases with increasing amount of habitat in the landscape. Therefore the area of the landscape that will influence a local site depends on the dispersal behaviour of organisms. The relationship between influence and distance from a point would be interesting to elucidate but impossible in the context of this single scale study. The area within which the amount of habitat on the landscape and therefore the dispersal success is expected to influence local abundance and distribution could be termed an

ecological neighbourhood. (Antonovics and Levin 1980, Addicott *et al.* 1987). Addicott *et al.* (1987) suggest that for mobile organisms the area of the neighbourhood will be defined by the movement behaviour of the organism. It is the dispersal behaviour of forest songbirds that will dictate the scale of the interaction between the amount of available habitat, success of dispersers and the abundance and distribution. Not a great deal is known about the dispersal behaviour of most forest songbirds. Ambuel and Temple (1983) assume that the distribution of forest birds is not limited by their ability to locate and colonize habitat because of their high vagility. Villard *et al.* (1995) however, suggest that a positive correlation between vagility and dispersal ability has not been demonstrated in passerine birds. Greenwood and Harvey (1982) reviewed the dispersal literature and concluded that most passerines were philopatric meaning that they had high breeding site fidelity of adults and a median natal dispersal of both sexes usually less than ten territories from the birth site. The validity of this summary has been questioned however (Villard *et al.* 1995), mostly based on the difficulty in assessing dispersal distance with low recapture rates. Villard (1991) reviewed the dispersal literature and suggested that the natal dispersal recovery rates were generally low (<10%) with a median dispersal distance of 1 km or less. The breeders were recovered more often and had a shorter median dispersal distance of <500 m. Villard *et al.* (1995) conclude that the actual fate of most juveniles fledged in a given area and surviving until their first breeding attempt is unknown. So it is difficult to assess the appropriate scale to look for an effect of amount of habitat on the landscape on local abundance and distribution on forest songbirds, although whenever the dispersal distance is greater than the scale of the study

landscape then the relationship is expected . Processes that rely on dispersal should be examined at several scales to provide insight into the size of the ecological neighbourhood for species. This neighbourhood size would provide some insight into appropriate scales for management.

The amount of available habitat is expected to influence dispersal success in a number of ways. First, more available habitat means that a disperser is more likely to find suitable habitat. Also, amount of habitat is related to many indices of landscape structure such as isolation and connectivity. Gustafson and Parker (1992) used simulated random pixel landscapes and random clumped landscapes to relate amount of habitat on the landscape to many indices of landscape structure such as mean patch size and nearest neighbour distance. The landscape structure will influence an organism's ability to disperse through the landscape. Several studies on the influence of landscape structure on species abundance and richness have used amount of regional habitat as an inverse measure of isolation (Askins *et al.* 1987, van Dorp and Opdam 1987, Lehmkuhl *et al.* 1991). The influence of amount of habitat in the landscape on local species abundance and richness has been documented in several empirical studies (Askins *et al.* 1987, Pearson 1993, McGarigal and McComb 1995). McGarigal and McComb (1995) found that in 5 of 15 species there was a strong effect of habitat area on local abundance and in another 5 species there was a moderate effect. Pearson (1993) examined 8 species or groups of species and found that landscape variables explained significant amounts of variance in local abundance in 4 species. The amount of deciduous and pine forest in the landscape was the variable that explained the most variance with partial r^2 of .19 to .65.

To conclude, this study demonstrated directly that both abundance and distribution are positively related to the amount of habitat on the landscape. Variation in the amount of habitat in the landscape could therefore account for the positive intra-specific relationship between distribution and abundance as suggested by the simulation studies of Venier and Fahrig (in press). We can extrapolate these results to say that variation among species in the amount of habitat in a landscape could also generate a positive inter-specific relationship between distribution and abundance.

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CHAPTER 4. THE INFLUENCE OF SCALE ON THE RELATIONSHIP BETWEEN LOCAL ABUNDANCE AND AMOUNT OF HABITAT IN THE LANDSCAPE

ABSTRACT

I examined the relationship between scale and the influence of amount of habitat in the landscape on the local abundance of eight species of boreal forest songbirds. Amount of habitat in the landscape is expected to positively influence the probability of successful dispersal and therefore positively influence local abundance of species. This mechanism is only expected to operate within the scale dictated by dispersal distance. Results indicated that the amount of habitat in the landscape does not influence local abundance at a distance of greater than 10 km, and generally for the eight species examined here the distance of potential influence is much less than 10 km. There appeared to be variation among species in the scale at which they responded to the landscape which implies that there is variation in the dispersal distances among species. In a highly conservative test, with local habitat controlled for, two species showed significant best fits of regression models of $\ln$ (local abundance) versus amount of habitat in circular areas defined by 2,000 m radius (Swainson's Thrush) and 5,000 m radius (Ruby-crowned Kinglet). This result confirmed that in at least some species the surrounding landscape explained() variance in local abundance beyond what is attributable to local habitat choice, and that this influence is at a small scale relative to the vagility of these species.

INTRODUCTION

A positive relationship between distribution and local abundance has been demonstrated for many groups of taxa (see Hanski 1982b, Brown 1984, Gaston and Lawton 1990b for examples). This relationship is sufficiently ubiquitous that Hanski (1982) proposed it as a general ecological law. Many hypotheses have been proposed to explain this relationship (Hanski *et al.* 1993) and it is likely that more than one mechanism contributes to it. Venier and Fahrig (in press - Chapter 1) used individual-based simulation modelling experiments to demonstrate that variation in the amount of habitat in the landscape could generate a positive relationship between distribution and abundance, through the mechanism of dispersal success. The likelihood of successful dispersal is positively related to the amount of habitat in the landscape, and more successful dispersal results in higher local abundance and a higher proportion of occupied sites (distribution). Variation in the probability of successful dispersal is also the underlying mechanism of the metapopulation hypothesis that was proposed by Gyllenberg and Hanski (1992) to explain the positive abundance-distribution relationship; however they did not propose a landscape driven phenomenon. They varied species-specific parameters in deterministic models to generate variation in dispersal success among species. The result of this variation was a positive distribution-abundance relationship for an assemblage of generic species.

Some direct and indirect empirical evidence exists that variation in amount of habitat in the landscape can generate a positive abundance-distribution relationship. Venier *et al.* (unpublished manuscript - Chapter 3) demonstrated that the habitat in the landscape was positively correlated with the local abundance and the probability of

occupancy for some boreal forest songbirds. Local sites surrounded by more habitat had more individuals than expected based on local habitat type alone whereas local sites surrounded by less habitat had lower abundance than predicted by local habitat type alone.

Variation in the amount of habitat in the landscape is predicted to generate a positive abundance-distribution relationship both among species on a single landscape and within species on several landscapes. Therefore a positive intra-specific relationship is consistent with the hypothesis that the amount of habitat in the landscape influences the abundance-distribution relationship. Such a positive relationship has been demonstrated generally for a group of boreal forest songbirds (Venier and Fahrig, unpublished manuscript - Chapter 2) as predicted. Positive intra-specific abundance-distribution relationships have been demonstrated in several other studies (Bart and Klosiewski 1989, Gerrard and Chiang 1970, Hergstrom and Niall 1990, Robbins *et al.* 1989b, Wilson and Room 1983, Ward *et al.* 1986) but always in the context of using distribution (proportion of occupied sites) to estimate abundance (mean abundance in all sites). In these studies the result is confounded by the lack of independence among measures of abundance and distribution.

There is empirical evidence that immigration may significantly increase the growth rate of small populations (Smith 1974, Holliday 1977, Gottfried 1979, Rey 1981, Rey and Strong 1983, Connor *et al.* 1983, Fahrig and Merriam 1985), a necessary condition if amount of habitat in the landscape is to influence the abundance-distribution relationship. This is essentially the rescue effect (Brown and Kodric-Brown 1977), a modification of the McArthur and Wilson (1963) model whereby extinction probability is considered to be

a function of immigration as well as size of the patch.

Patterns of distribution and abundance that rely on dispersal dynamics are not expected to exist at all scales. The dispersal distance of the species will limit the scale of influence that landscape composition and configuration will have on local populations. The objective of this study is to examine the relationship between local abundance and the amount of habitat in the landscape at a variety of scales for each of eight species of forest songbirds (passerines) in areas of essentially continuous boreal forest. Previous work on these bird species has demonstrated that amount of habitat in the landscape does influence the local abundance where the individual landscapes measured were approximately 1 km² (Venier *et al.* unpublished manuscript - Chapter 3). As long as the scale of the landscape considered is at or below the dispersal distance, then I predict that dispersal can operate as a mechanism to influence local abundance. At scales larger than the dominant dispersal distance the influence of habitat in the landscape should be greatly reduced.

Unfortunately, the dispersal behaviour and dominant dispersal distances of species of songbirds are not well known (Villard *et al.* 1995). Passerines are generally philopatric and Greenwood and Harvey (1982) suggested that an appropriate definition of philopatry would be if the median value of dispersal is less than 10 territories from the natal area. As an example, for a 6 ha territory, 10 territories represents a distance of approximately 2500 m. Natal dispersal (movement from the site of birth to the site of first breeding) is generally more common and extensive than breeding dispersal (movement from one breeding site to another) (Greenwood and Harvey 1982). Therefore it is likely to be natal dispersal that dictates the scale of influence of the landscape. Recapture rates of

passerines are very low; therefore estimates of dispersal distance are not likely to be very accurate (Villard *et al.* 1995). Because dispersal distances of boreal songbirds are not well known, the predictions of this study cannot be explicit. However, I do predict that the amount of variation explained by the amount of habitat in the landscape will be highest in areas around the sample site and will decline at some distance from the sample point. The distance at which the influence starts to decline should reflect the dominant dispersal distance of the species but would have to be confirmed with independent data of dispersal distance.

METHODS

Overview

I examined the relationship between the local abundance at forest stands of each of eight species of songbirds and the amount of habitat available to these species at a number of different scales. The scales ranged from approximately 13 ha to 600,000 ha. I examined the influence of scale on the relationship between local abundance and amount of habitat in the landscape in two ways. First, I examined the regression coefficients between local abundance and the amount of habitat in a series of ring areas around each site. I predicted that the amount of habitat in ring areas close to the site should explain more variance in local abundance than those far from the site. This first analysis indicates the distance beyond which an influence of amount of habitat is **not** found. However, for those smaller distances where I found a relationship it is potentially confounded. The problem is that in all cases the amount of habitat within the smallest area measured (200

m) is correlated with the amount of habitat in the most immediate larger areas. In some cases, measures of amount of habitat are positively correlated at all scales. The smallest area probably reflects the local habitat type that individuals are choosing directly.

However, I am interested in the effect of habitat as it influences dispersers and as a result local populations, not in the direct effect of local habitat. Therefore, in the context of this analysis, when outer rings explain variance in local abundance it may be because of the correlation in amount of habitat between outer and inner rings. When outer rings do not explain variance in local abundance I can conclude that amount of habitat at that scale is not influencing local abundance.

In the second approach, I examined the regression coefficients between local abundance and the cumulative amount of habitat in ring areas around each site while controlling for the effect of local habitat. I predicted that the cumulative amount of habitat in rings beyond the local area would explain a significant amount of variance. Which ring should explain the most variance cannot be predicted in the absence of information on dispersal distance. This is a conservative test since all of the variance explained by local vegetation and any overlapping variance explained by local and landscape vegetation are removed first leaving only variance in abundance that is uniquely explained by amount of habitat in the landscape.

The data for this study consisted of estimates of local bird abundance at each site, classification of the vegetation at the local scale using two different classification schemes (Forest Ecosystem Classification (FEC) and a Landsat Classification (LC)), and estimates of the amount of each vegetation type (LC) in circular areas around a set of 5 sites (a

stand) using a classified Landsat image (see Table 4.1 for size and location of areas).

Amount of habitat available was estimated as the sum of the area of each vegetation type weighted by the quality of that type for the species in question.

Study Area and Site Selection

As part of an ongoing research program at the Canadian Wildlife Service-Ontario Region, Environment Canada bird census and vegetation data were collected in 171 forest stands in an area of approximately 300 km x 100 km throughout northwestern Ontario in 1989 and 1991 (Figure 1 - General Methods). Samples were not collected specifically for this study. See General Methods for more a more detailed description of the site selection.

Bird Counts

Bird census data were collected using an unlimited distance point count method (Welsh 1995) at 5 sites in each stand. Details are in the General Methods. For the purposes of this study, local scale includes the area sampled by the 5 point counts in the stand. Note that this is the landscape scale in Chapter 3. The area of the stands selected for this study range from 20 to 586 ha; however the area sampled by the 5 sites in the stand is similar in all stands.

Table 4.1 : Ring sizes and locations for first and second analyses. Rings were defined by an inner and outer radius.

For First Set of Regression Analyses				For Second Set of Regression Analyses			
Ring Number	Ring	Inner Radius (m)	Outer Radius (m)	Area (km ²)	Ring Number	Ring	Area (km ²)
1A	0	200		.1256	1B	200	.6594
2A	200	500		.6594	2B	200	3.0144
3A	500	1,000		2.355	3B	200	12.4344
4A	1,000	2,000		9.42	4B	200	78.3744
5A	2,000	5,000		65.94	5B	200	313.8744
6A	5,000	10,000		235.5	6B	200	706.3744
7A	10,000	15,000		392.5	7B	200	1962.374
8A	15,000	25,000		1256	8B	200	7849.874
9A	25,000	50,000		5887.5	----	-----	-----

Local Vegetation

To model the relationship between local abundance and local vegetation type the vegetation type of each site was described according to the FEC of Northwestern Ontario (Sims *et al.* 1989). See the General Methods for a description of the FEC. Also, the proportion of cover of each overstory tree species was estimated for an area of radius 50 m around each site.

Landscape Vegetation

Vegetation at the landscape level was identified using classified Landsat Thematic Mapper data provided by the Ontario Ministry of Natural Resources (OMNR 1992). Vegetation types from the Landsat classification were conifer, conifer dominant mixedwood, deciduous dominant mixedwood, deciduous and wetland. The total area of each vegetation type was identified in circular areas (defined by radii listed in Table 4.1) around the most central site in each stand.

To estimate of the amount of habitat available to each species in a landscape, I needed to weight the Landsat estimates of area of each vegetation type by the quality of that vegetation type to the species in question. To estimate habitat quality for weighting, local vegetation was sampled by estimating the percentage cover for all canopy trees at the site in a radius of approximately 50 m around the site. Sites were then classified as conifer (>80% conifer cover), conifer dominant mixedwood (51-80% conifer), deciduous dominant mixedwood (51-80% deciduous), deciduous (>80% deciduous cover). Sites

that were classified as type 38 based on the FEC system were then reclassified as wetland. Canopy cover data were available for 655 sites.

To limit the amount of dependence between estimates of amount of habitat in the landscape I selected 31 stands from the original 171 stands so that stands were at least 10 km apart (Figure 4.1). Sites that were closer together would have large amounts of overlap in the areas sampled for the amount of habitat in the landscape.

Statistical Analyses

To determine the distance at which the amount of habitat does not influence the local abundance I ran a simple linear regression with local abundance in the stand (the sum of 5 sites) as the response variable and the amount of habitat in ring areas around the stand as the explanatory variable for 31 stands. Local (stand) abundance is expected to be influenced by the amount of habitat available to the species in the area due to the influence of dispersal. Ring areas beyond dispersal distance are not expected to explain variance in local abundance. There were 9 ring areas (1A-9A see Table 4.1) and therefore I conducted 9 regressions for each bird species. I examined the residuals of all models and where necessary I log transformed abundance to improve the distribution of residuals. For each species I plotted the regression coefficient against ring number with 95% confidence intervals. Confidence intervals were calculated using the method described by Zar (1984).

To examine the correlation structure of the landscape rings for each species I ran correlations between all combinations of amount of habitat in all rings.

The smallest ring in the analysis is defined by a radius of 200 m around the most

Figure 4.1: Location of thirty-one forest stands selected from 171 in northwestern Ontario, Canada to be at least 10 km apart.

central site in the stand. This ring probably reflects the local habitat that individual birds are choosing directly. This reflects a direct effect on local abundance rather than an effect due to successful dispersal. I wanted to examine the relationship between local abundance and amount of available habitat in the landscape while controlling for the influence of local habitat type. To remove this effect of local habitat I modeled the local abundance (site) as a function of FEC vegetation type using ANOVA (855 sites). This model was at the site (not stand) scale. The residuals from this model represent a site measure of abundance with the effect of local habitat removed. Measures of amount of habitat on the landscape are associated with stands not sites. Therefore I summed the residuals of all sites in a stand to get an index of abundance at the stand scale (RESSUM).

I conducted simple linear regressions with RESSUM as the response variable and the cumulative ring area (1B-8B, Table 4.1) as the explanatory variable. A separate regression was conducted for each ring and species. The 200 m ring area was excluded from the analysis because it reflects the local habitat, the effect of which has already been removed. Notice that in this analysis the ring areas are cumulative such that ring 2B includes the area of ring 1B, ring 3B includes the area of 2B etc. Each model contains only one explanatory variable; therefore this design allowed me to compare the r^2 values of the models directly to identify the ring that explained the most variance.

RESULTS

For each species the amount of habitat among rings is highly correlated (Figure 4.2). Rings that are close together are more likely to be correlated than rings that are

Figure 4.2 : Correlation structure of the amount of habitat in rings 1A-9A (see Table 4.1).

A black square (■) indicates a positive correlation. An open square (□) indicates no correlation. Ring number 1A is found in the top left corner of each box. Ring number 9A is found in the bottom right of each box.

Hermit Thrush

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Ruby-crowned Kinglet

Nashville Warbler

Swainson's Thrush

Ovenbird

Tennessee Warbler

Red-eyed Vireo

Yellow-rumped Warbler

farther apart (Figure 4.2). The 200 m (1A) ring is positively correlated with rings 2A-5A in all species (Figure 4.2). For this reason, the regressions of local abundance in the stand versus amount of habitat in rings around the local stand show the scale at which the amount of habitat in the landscape does not influence the local abundance but do not provide the scale at which amount of habitat in the landscape does influence local abundance. For the eight species examined here, more distant landscapes appeared to be less likely to influence local abundance than closer landscapes although there appeared to be some variation among species in this response (Figures 4.3-4.10). Very few rings at ring 6A (5-10km) or beyond explained a significant amount of variance in local abundance. In all but one species (Swainson's Thrush), the first ring (200 m) explained a significant amount of variance. For those rings where the relationship was positive it is difficult to say if it is due to the influence of the amount of habitat in the landscape or if it is due to the correlation between the amount of habitat in the rings and the amount of local habitat.

The results of the ANOVAs for local abundance versus local vegetation type show that in all 8 species, local vegetation type as described by the FEC explains a significant part of the variance in abundance (Table 4.2). After controlling for the influence of local vegetation type (by using RESSUM as the response variable) I examined the relationship between local abundance and amount of habitat in the landscape at different scales. Two species showed a significant positive relationship between local abundance and amount of habitat in the landscape. The ring area that explained the most variance in local abundance of Ruby-crowned Kinglet was 4B (200 m-5,000 m) (Figure 4.11; $r^2=0.21$, $P=0.01$). The

Figure 4.3 : Regression coefficients (●) of relationship between local abundance of Nashville Warbler at the stand level and amount of habitat in the ring plotted against ring number. Ring locations and sizes are described in Table 4.1. Open triangles indicate upper and lower 95% confidence intervals.

Figure 4.4 : Regression coefficients (●) of relationship between local abundance of Ovenbird at the stand level and amount of habitat in the ring plotted against ring number. Ring locations and sizes are described in Table 4.1. Open triangles indicate upper and lower 95% confidence intervals.

Figure 4.5 : Regression coefficients (●) of relationship between local abundance of Red-eyed Vireo at the stand level and amount of habitat in the ring plotted against ring number. Ring locations and sizes are described in Table 4.1. Open triangles indicate upper and lower 95% confidence intervals.

Figure 4.6 : Regression coefficients (●) of relationship between local abundance of Ruby-crowned Kinglet at the stand level and amount of habitat in the ring plotted against ring number. Ring locations and sizes are described in Table 4.1. Open triangles indicate upper and lower 95% confidence intervals.

Figure 4.7 : Regression coefficients (●) of relationship between local abundance of Swainson's Thrush at the stand level and amount of habitat in the ring plotted against ring number. Ring locations and sizes are described in Table 4.1. Open triangles indicate upper and lower 95% confidence intervals.

Figure 4.8 : Regression coefficients (●) of relationship between local abundance of Tennessee Warbler at the stand level and amount of habitat in the ring plotted against ring number. Ring locations and sizes are described in Table 4.1. Open triangles indicate upper and lower 95% confidence intervals.

Figure 4.9 : Regression coefficients (●) of relationship between local abundance of Yellow-rumped Warbler at the stand level and amount of habitat in the ring plotted against ring number. Ring locations and sizes are described in Table 4.1. Open triangles indicate upper and lower 95% confidence intervals.

Figure 4.10 : Regression coefficients (●) of relationship between local abundance of Hermit Thrush at the stand level and amount of habitat in the ring plotted against ring number. Ring locations and sizes are described in Table 4.1. Open triangles indicate upper and lower 95% confidence intervals.

Table 4.2 : An ANOVA was conducted on each species with abundance at the site as the response variable and vegetation type as the explanatory variable. The thirty-eight vegetation types were entered as class variables. Each model was based on 855 observations.

Species	R ²	P
Hermit Thrush	.54	.0001
Nashville Warbler	.51	.0001
Ovenbird	.44	.0001
Ruby-crowned Kinglet	.39	.0001
Red-eyed Vireo	.23	.0001
Tennessee Warbler	.28	.0001
Swainson's Thrush	.21	.0001
Yellow-rumped Warbler	.21	.0001

Figure 4.11 : Regression coefficient (●) of local abundance index for Ruby-crowned Kinglet (with effect of local habitat type statistically removed) versus amount of habitat in rings 1B-8B (see Table 4.1 for location and size of rings) plotted against ring number. Open triangles indicate upper and lower 95% confidence intervals.

Figure 4.12 : Regression coefficient (●) of local abundance index for Swainson's Thrush (with effect of local habitat type statistically removed) versus amount of habitat in rings 1B-8B (see Table 4.1 for location and size of rings) plotted against ring number. Open triangles indicate upper and lower 95% confidence intervals.

best model for Swainson's Thrush was ring 3B (200 m-2,000 m) (Figure 4.12; $r^2=0.25$, $P=0.00$). Two other species (Hermit Thrush and Nashville Warbler) had almost significant positive 1B rings (both with $r^2=0.10$, $P=0.08$). One species (Yellow-rumped Warbler) had a barely significant negative relationship between RESSUM and amount of habitat in the ring ($r^2=0.12$, $P=0.05$) while one species (Tennessee Warbler) had an almost significant negative effect in ring 3B ($r^2=0.11$, $P=0.06$). The remaining 2 species (Ovenbird and Red-eyed Vireo) had no significant relationships between RESSUM and amount of habitat in the landscape.

DISCUSSION

The objective of this study was to examine the influence of scale on the relationship between local abundance and the amount of habitat in the landscape. I predicted that the influence of the amount of habitat in the landscape should decrease with distance from the local population. The ecological neighbourhood concept (Addicott *et al.* 1987) would predict that dispersal distance of the species should dictate the distance at which the decrease in influence of amount of habitat in the landscape is most significant. However, very little is known about the dispersal distances of forest songbirds (Greenwood and Harvey 1982, Villiard *et al.* 1995). This makes any kind of explicit prediction impossible, but I have examined the data for the general expected pattern.

The results indicate that the amount of habitat in the landscape does not influence local abundance at a distance greater than 10 km, and generally for species examined here the distance of potential influence is much less than 10 km. The first analysis indicates the

distance beyond which an influence of amount of habitat is not found. However, for those distances where I found a relationship it is potentially confounded for reasons discussed in the Methods. Therefore, based on this analysis, I cannot conclude anything about the influence of amount of habitat in rings that showed a significant effect except that there is potential for landscapes at this scale to explain variance in local abundance.

In the second analysis, with the influence of local habitat type controlled for, results from two species demonstrate clearly that the amount of habitat in the landscape positively related to the local abundance. The best models in these cases were for habitat up to 2,000 and 5,000 m from the local population. This result confirms that in at least some species, the surrounding landscape explains variance in local abundance beyond what is attributable to local habitat choice and that this influence is at a small scale relative to the vagility of these species (their ability to move as evidenced by migration distance). Both Ruby-crowned Kinglet and Swainson's Thrush are migrants which travel thousands of kilometers seasonally. However, the dispersal distances indicated by these results are not inconsistent with estimated dispersal distances of passerines. Villard (1991) reviewed dispersal studies on passerines and summarized estimated median dispersal distances where information was available. I averaged the dispersal distances for all estimates of all passerine species reviewed to obtain a mean median dispersal distance of approximately 1200 m. Median dispersal distances of species reviewed ranged from 250 m to 6,000 m. None of the species included in this study have been examined for dispersal distance and the validity of previous studies on dispersal distance have been questioned (Villard 1991) due to the very low recapture rates that most results are based on.

In previous chapters of this thesis (Chapters 1-3) I have proposed that amount of habitat in the landscape can generate a positive abundance-distribution relationship. This variation in amount of habitat can occur for a single species over a variety of landscapes or for an assemblage of species on a single landscape. Habitat is only available when it is within the dispersal distance of individuals within the local population in question. Therefore this mechanism is not expected to operate at all scales. Results here suggest that it would be inappropriate to apply this mechanism to explain a positive distribution-abundance relationship that is found at biogeographic scales. For dispersal success to function to generate the relationship, each measure of distribution and abundance must be taken where the landscape is expected to influence both measures in the same way. Each pair of distribution and abundance measures must be taken over an area where amount of habitat is definable as a single measure, applicable to both abundance and distribution.

The area of influence for ecological (or genetic) processes has been termed an ecological neighbourhood (Southwood 1977, Antonovics and Levin 1980, Addicott *et al.* 1987 and others). For mobile organisms the dispersal distance will usually define the neighbourhood for most ecological processes (Cunningham 1986, Ford and Krumme 1979, Jumars 1976, Koepl *et al.* 1978, Southwood 1977). Certainly the dispersal distance should define the neighbourhood size for the influence of amount of habitat on abundance and distribution. The ecological neighbourhood size must be defined separately for a specific ecological process, an appropriate time period and for a specific organism. Definitions of ecological neighbourhoods are critical in the context of land management because impacts of management options are expected to be felt anywhere

within the ecological neighbourhood of the management action. Results from this study indicate that there is variation in the size of the neighbourhood for dispersal mediated processes among boreal forest songbirds. Generally, for the group of species examined, the size of the neighbourhood is defined by a radius of less than 10 km and for most species less than 2 km. Dispersal distances are difficult to estimate for a variety of reasons (Villard 1991). The examination of the effect of scale on a process such as the influence of amount of habitat in the landscape on local abundance, which depends on dispersal, could provide much needed insight into dispersal distances. Conversely, when examining such a dispersal mediated process, the scale of the examination must be tailored to suit the approximate size of the ecological neighbourhood of the species. If studies are conducted at scales larger than dispersers can effectively influence dynamics then results may be ambiguous.

CHAPTER 5. THE EFFECTS OF THE AMOUNT OF HABITAT IN THE LANDSCAPE AND ECOLOGICAL SPECIALIZATION ON THE ABUNDANCE-DISTRIBUTION RELATIONSHIP

ABSTRACT

The objective of this chapter was to test the prediction of the ecological specialization hypothesis that niche width will be positively related to both local abundance and distribution and to test the prediction that amount of habitat in the landscape will be positively related to both local abundance and distribution for a group of 33 boreal forest songbirds. I used only the sites of the most preferred vegetation type for each species so that values of abundance and distribution are comparable between species. I found a positive relationship between abundance (mean abundance in occupied sites) and distribution (proportion of sites occupied). I tested and rejected the hypothesis that the positive abundance-distribution relationship was a function of a Poisson distribution of individuals. I found positive relationships between (1) niche width and both local abundance and distribution and (2) average amount of habitat within 200 m of local samples and both local abundance and distribution. I concluded that both variation in niche width and variation in amount of available habitat can generate a positive abundance-distribution relationship and are not mutually exclusive hypotheses.

INTRODUCTION

The objective of this chapter is to examine the interspecific relationships between abundance, distribution, degree of habitat specialization and amount of habitat in the landscape for a group of 33 boreal forest songbirds. A positive relationship between abundance (mean abundance at occupied sites) and distribution (proportion of sites occupied) has been demonstrated empirically for numerous groups of taxa at a diversity of scales (Appendix 1). Several hypotheses have been proposed and commonly cited to explain the relationship including the ecological specialization hypothesis (Brown 1984) and the metapopulation hypothesis (Gyllenberg and Hanski 1992). The ecological specialization hypothesis proposes that those species that can use a wide range of resources (broad niche) are expected to be more widely distributed and more locally abundant than species that are more restricted in their habitat use (narrow niche) (See General Introduction for more details). Therefore variation in the degree of ecological specialization (or niche width) among species is predicted to generate a positive relationship between distribution and abundance.

The metapopulation hypothesis argues that variation in metapopulation dynamic parameters can generate a positive relationship between distribution and abundance, particularly variation in parameters that influence dispersal success (See General Introduction for more details). It has also been suggested that the amount of habitat in the landscape can generate variation in disperser success and therefore a positive abundance-distribution relationship (Venier and Fahrig in press - Chapter 1). Venier *et al.* (unpublished manuscript - Chapter 3) have demonstrated a positive intra-specific

relationship between (1) local abundance and amount of habitat in the landscape and (2) distribution and amount of habitat in the landscape.

In this chapter I examine interspecific relationships. I used data of abundance, distribution, niche width and amount of habitat in the landscape for a group of 33 boreal forest songbirds to examine the influence of variation in both ecological specialization and amount of habitat in the landscape. First, if variation in niche width (the ecological specialization hypothesis) generates the positive abundance-distribution relationship then I predict a positive relationship between (1) niche width of bird species and their local abundance and (2) niche width and distribution (proportion of sites occupied). Second, if variation in amount of habitat in the landscape generates the positive distribution-abundance relationship then I predict a positive relationship between (1) amount of available habitat in the landscape and local abundance of bird species and (2) amount of available habitat and distribution.

METHODS

The study area was in northwestern Ontario (Figure 1 - General Methods). There were 171 sampling locations as described in the General Methods. At each site the abundance of 74 boreal forest songbirds was measured (See General Methods for point count methods). Of these species, 33 were selected that are found predominantly in mature forest and for which northwestern Ontario is not at the periphery of their ranges (Table 5.1). Local vegetation type was assessed for each site using the Forest Ecosystem

Table 5.1 : Thirty-three species of boreal forest songbirds selected for analysis. Species were selected that are found predominantly in mature forest and for which northwestern Ontario is not at the periphery of their range.

Species Common Name	Latin Name
Bay-breasted Warbler	<i>Dendroica castanea</i>
Black-capped Chickadee	<i>Parus atricapillus</i>
Blackburnian Warbler	<i>Dendroica fusca</i>
Boreal Chickadee	<i>Parus hudsonicus</i>
Brown Creeper	<i>Certhia americana</i>
Black-throated Green Warbler	<i>Dendroica virens</i>
Black-and-White Warbler	<i>Mniotilta varia</i>
Canada Warbler	<i>Wilsonia canadensis</i>
Cape May Warbler	<i>Dendroica tigrina</i>
Connecticut Warbler	<i>Oporornis agilis</i>
Dark-eyed Junco	<i>Junco hyemalis</i>
Eastern Wood-Pewee	<i>Contopus virens</i>
Golden-crowned Kinglet	<i>Regulus satrapa</i>
Hermit Thrush	<i>Catharus guttatus</i>
Least Flycatcher	<i>Epidonax minimus</i>
Magnolia Warbler	<i>Dendroica magnolia</i>
Nashville Warbler	<i>Vermivora ruficapilla</i>
Orange-crowned Warbler	<i>Vermivora celata</i>
Olive-sided Flycatcher	<i>Contopus borealis</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Pine Siskin	<i>Carduelis pinus</i>
Purple Finch	<i>Carpodacus purpureus</i>
Red-breasted Nuthatch	<i>Sitta canadensis</i>

Table 5.1 (continued)

Species Common Name	Latin Name
Ruby-crowned Kinglet	<i>Regulus calendula</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>
Solitary Vireo	<i>Vireo solitarius</i>
Swainson's Thrush	<i>Catharus ustulatus</i>
Tennessee Warbler	<i>Vermivora peregrina</i>
Veery	<i>Catharus fuscenscens</i>
Winter Wren	<i>Troglodytes troglodytes</i>
White-throated Sparrow	<i>Zonotrichia albicollis</i>
Yellow-bellied Flycatcher	<i>Epidonax flaviventris</i>
Yellow-rumped Warbler	<i>Dendroica coronata</i>

Classification (FEC) for Northwestern Ontario (Sims *et al.* 1989 - See General Methods for more detail), and using a more coarse classification based on overstory tree composition (Landsat Classification, see Chapter 4 for more details).

Sampling for this study has been conducted at a small scale in many different types of vegetation. The 33 species selected for this study prefer different habitat types which will strongly influence their abundance in these samples. To compare the abundance of these species while controlling for the effects that differences in local habitat and differences that habitat selection will have on local abundance, I selected only those sites for each species that are the most preferred vegetation type for each species. I identified the most preferred vegetation type by calculating the mean abundance for each species in each FEC vegetation type. For each species, I considered the vegetation type with the highest mean abundance to be the most preferred vegetation type. I calculated the local abundance (MAX) as the mean abundance in occupied sites for only those sites that are of the preferred vegetation type for that species. This abundance value is comparable between species even though these species prefer different habitat types. I calculated distribution (DIST) as the fraction of the preferred sites for a species that are occupied.

I calculated niche width in two ways. I measured niche width as the number of different FEC vegetation types used by a species (VEGSUM). However, this measure does not take into account the evenness with which the vegetation types are used. To examine the importance of evenness to the measure of niche width I calculated niche width (NICHE) using an information statistic, the Shannon index which was calculated as

$$NICHE = \sum -p_i \ln(p_i)$$

(McNaughton and Wolf 1970, Magguran 1988), where p_i is the proportion of individuals of a species that use vegetation type i when all vegetation types are sampled equally. In this study, all vegetation types are not sampled equally so I calculated the mean number of individuals per site x_i for each vegetation type i and then I calculated p_i as

$$p_i = \frac{x_i}{\sum x_i}$$

so that all vegetation types were equally represented in the calculation of niche width. This index is independent of the abundance of a species. A species that uses the same proportion of all vegetation types will have a niche width index of 1 irrespective of its abundance whereas a species that uses only one type will have a niche width index of 0 regardless of its abundance in that type. I compared these two measures of niche width (NICHE and VEGSUM) and found a strong positive correlation between them ($r=0.96$, $P=0.0001$, $N=33$). Therefore for the remaining analyses I used VEGSUM as the measure of niche width because it is simpler and easier to interpret.

I estimated the amount of habitat in the landscape available to a species by: (1) measuring the amount of each vegetation type from the classified Landsat image (conifer, conifer-dominant mixedwood, deciduous dominant mixedwood, deciduous and wetland), (2) weighting each vegetation type by a standardized estimate of quality for the species in question and (3) adding up the weighted area estimates for all vegetation types. The

quality of each vegetation type i was measured as the mean abundance (x_i) of the species in stands of that vegetation type.

I weighted each vegetation type by the quality standardized so that the total weighting for the vegetation types for the species was equal to 1 for each species

$$w_i = \frac{x_i}{\sum x_i}$$

where x_i is the mean abundance in each vegetation type i and w_i is the weighting factor for each Landsat vegetation type and

$$\sum w_i = 1$$

The above measure of amount of habitat is independent of the abundance of the species but also does not entirely capture the meaning of amount of available habitat which should be the number of available spaces for the species to safely go. However, there is no way to measure the number of available spaces for the species to safely go that is independent of abundance. For the purposes of this study, where I am interested in the relationship between amount of habitat and abundance, it is a necessary compromise to use an estimate of amount of habitat that is computationally independent of abundance.

I calculated the amount of habitat available to each species on 2 scales (1) the entire sampling area (HABITAT) and (2) a circular area defined by a radius of 200 m (HABSMALL) around the samples of preferred habitat for each species. Based on the results from Chapter 4, the scale of the entire sampling area is probably too large to

influence the local abundance and distribution of these stands in a similar way unless the amount of habitat in the entire landscape is correlated with the amount of habitat in much smaller areas. The amount of habitat at the smaller scale (200 m) has been shown to influence local abundance for individual species (Chapter 4).

I conducted a simple linear regression of $\ln(\text{MAX})$ versus DIST (Distribution measured as the proportion of stands occupied of the preferred type). I tested whether or not this set of species conforms to the Poisson null model by plotting the natural logarithm of the frequency of absences ($\ln(1-p)$) against the mean abundance omitting any cases with no absences from the analysis (Wright 1991). Under the Poisson null hypothesis, this regression should have a slope of -1. I tested the significance of the deviation of the observed slope from -1 using a t-test (Zar 1984, pp. 271-272).

I also conducted the following series of simple linear regressions to examine the relationship between both abundance and distribution versus niche width and habitat amount; (1) $\ln(\text{MAX})$ vs VEGSUM, (2) DIST vs VEGSUM, (3) $\ln(\text{MAX})$ vs HABITAT, (4) DIST vs HABITAT, (5) $\ln(\text{MAX})$ vs HABSMALL, (6) DIST vs HABSMALL. I anticipated that species with wider niche width would have, on average, more habitat available to them so I also conducted a multiple regression with $\ln(\text{MAX})$ as the response variable and HABSMALL and VEGSUM as explanatory variables to examine (1) the influence of habitat amount on abundance with niche width controlled for and (2) the influence of niche width with the amount of habitat in the landscape controlled for.

RESULTS

I found a significant positive relationship between the mean abundance (in occupied sites) for the preferred site type of each species ($\ln(\text{MAX})$) and the distribution in those sites of the preferred type (DIST) (Figure 5.1). I conducted an analysis suggested by Wright (1991) to discover if the relationship could be most simply attributed to a Poisson distribution of individuals. Three of the thirty-three species occupied all sites and so were omitted from the analysis. The observed slope of $\ln(1-p)$ versus mean abundance was -0.4998 with a Standard Error of the estimate of 0.065. This regression coefficient was significantly different from -1 ($t=7.695$, $t_{0.05(2), 30} = 2.042$). Therefore the frequency distribution of individuals did not reflect a random distribution and other explanations for the abundance-distribution relationship were examined.

There was a significant positive relationship between $\ln(\text{MAX})$ and VEGSUM (Figure 5.2) and between DIST and VEGSUM (Figure 5.3). HABITAT did not explain a significant amount of variance in $\ln(\text{MAX})$ ($r^2 = 0.016$; $b=0.00$; $F=0.51$; $N=33$; $P=0.48$) or in DIST ($r^2 = 0.002$; $b=0.00$; $F=0.06$; $N=33$; $P=0.82$). There was a non-significant positive trend between HABSMALL and $\ln(\text{MAX})$ (Figure 5.4). HABSMALL and DIST were positively related (Figure 5.5). With VEGSUM already in the model HABSMALL was almost significant in explaining variance in $\ln(\text{MAX})$ (Figure 5.6) and with HABSMALL in the model VEGSUM became more significant in explaining variance in $\ln(\text{MAX})$ than it had been when in the model as the only explanatory variable (partial $r^2 = 0.18$; $t=0.01$; $F=7.05$ of VEGSUM; $N=33$; $P=0.013$ of VEGSUM). The relationship between DIST and HABSMALL became more significant with VEGSUM in the model

Figure 5.1: Relationship between the natural log of mean abundance in occupied sites of the preferred vegetation type for each species and distribution measured as the proportion of sites of the preferred vegetation type for each species occupied for 33 species of boreal forest songbirds. Each dot in this figure represents one species. Line of best fit based on a simple linear regression is plotted.

Figure 5.2: Relationship between the natural log of mean abundance in occupied sites of the preferred vegetation type for each species and the niche width measured as the number of vegetation types used for 33 species of boreal forest songbirds. Each dot in this figure represents one species. Line of best fit based on a simple linear regression is plotted.

Figure 5.3: Relationship between distribution measured as the proportion of sites (of the preferred vegetation type for each species) occupied and niche width measured as the number of vegetation types used for 33 species of boreal forest songbirds. Each dot in this figure represents one species. Line of best fit based on a simple linear regression is plotted.

Figure 5.4: Relationship between the natural log of mean abundance in occupied sites of the preferred vegetation type for each species and the amount of habitat available to each species within 200 m of the sample point for 33 species of boreal forest songbirds. Each dot in this figure represents one species. Line of best fit based on a simple linear regression is plotted.

Figure 5.5: Relationship between distribution measured as the proportion of sites occupied (of the preferred vegetation type for each species) and the amount of habitat available to each species within 200 m of the sample point for 33 species of boreal forest songbirds. Each dot in this figure represents one species. Line of best fit based on a simple linear regression is plotted.

Figure 5.6: Relationship between the residuals from a simple linear regression of local abundance versus niche width (see Figure 5.2) and the average amount of habitat within 200 m of each sampling site for each species for 33 species of boreal forest songbirds. Each dot in this figure represents one species. Line of best fit based on a simple linear regression is plotted.

(partial $r^2 = 0.14$; $b=34.5$; $F=8.00$ of HABSMALL; $N=33$; $P=0.0083$ of HABSMALL).

The relationship between DIST and VEGSUM also became more significant with HABSMALL in the model (partial $r^2 = 0.35$; $b=0.018$; $F=19.81$ of VEGSUM; $N=33$; $P=0.0001$ of VEGSUM). There was no significant relationship between VEGSUM and HABSMALL ($r^2=0.004$; $b=-198$; $F=0.13$; $N=33$; $P=0.717$).

DISCUSSION

Consistent with most studies of this nature (Brown 1984, Gaston and Lawton 1990b, Hanski *et al.* 1993), I found a significant positive relationship between local abundance and distribution of a group of 33 species of boreal forest songbirds. Tests suggested by Wright (1991) confirmed that this result was not just a function of a Poisson distribution of individuals.

The positive distribution-abundance relationship is sufficiently common that several hypotheses have been developed to explain it. The ecological specialization hypothesis predicts that species with broader niches will be more locally abundant and will occupy more of the available sites than species that have narrower niches. My tests confirmed that there is a significant positive relationship between niche width and both local abundance and distribution. Previous tests of this prediction have produced equivocal evidence for this hypothesis. So Δ studies have found positive relationships between abundance, distribution and niche width and others have found no such relationship (Rabinowitz *et al.* 1986, Gaston and Lawton 1990b, Kouki and Häyrinen 1991, Hanski *et al.* 1993). I have reviewed these studies in detail in the General

Introduction of this thesis.

There is a difficulty in testing the prediction of a positive relationship between distribution, abundance and niche width where sampling is conducted randomly so that the frequency distribution of habitat types is in proportion to their occurrence on the landscape or if samples are stratified so that each habitat type is sampled equally. In both of these cases there is an *a priori* reason to expect a positive relationship between abundance, distribution and niche width. Generalists (those species that use more habitat types or have a wider niche) are more likely to be sampled in more suitable habitat than specialists so they are likely to have higher local abundance in occupied sites in the sample and are more likely to occupy sites that are sampled. This relationship between niche width and abundance (and distribution) is a function of sampling and not the mechanism that Brown's (1984) ecological specialization hypothesis suggests. The ecological specialization hypothesis suggests that generalists would be more efficient at using resources and as a result would become more abundant locally. This assumption has been questioned in the literature (Kouki and Häyrinen 1991) but I do find some support for it here. If generalists are in fact more efficient at using resources than specialists then generalists in preferred habitat should be able to achieve higher abundance than specialists in preferred habitat. I calculated local abundance in only the preferred habitat of each species. Species that used more vegetation types were more abundant in their preferred vegetation type than species that used fewer vegetation types.

The metapopulation hypothesis predicts that more dispersive species will be more locally abundant and more widespread than less dispersive species. Therefore variation in

ability to disperse will generate a positive relationship between distribution and abundance. Hanski *et al.* (1993) tested this prediction on a number of groups of taxa. The prediction was supported by the data for British butterflies but in the four other taxa examined (carabid beetles, gastropods, fen plants, dytiscid beetles) the predictions were not supported. Hanski *et al.* (1993) suggested that the dispersal data for the four taxa were probably inadequate for the task. Data do not exist on the relative dispersal abilities of the species used in this study so I was not able to test this prediction.

Venier and Fahrig (in press - Chapter 1) argued that variation in the amount of habitat available to species in the landscape could also generate variation in dispersal success. More habitat would result in higher disperser success. Species that have more habitat available to them in the landscape should be more locally abundant and more widely distributed due to this higher disperser success than species with less habitat available to them. In this study I found that when amount of habitat was measured at the scale of the entire study area it did not explain a significant amount of variance in the local abundance or distribution. Based on the results from Chapter 4, I expected this to be the case. It is unlikely that the amount of habitat in the entire study area influences the average disperser success of all sites in this study. The amount of habitat available to influence disperser success at each site must be measured within the dispersal distance of each site. The average amount of habitat within 200 m of each stand did explain significant variance in both abundance and distribution.

I anticipated that species that used more habitat types would on average have more habitat available to them. This was not the case at the 200 m scale. When I controlled for

the amount of habitat in the 200 m landscape before examining the relationship between abundance and niche width or distribution and niche width, the niche width variable explained more variance than it had previously without amount of habitat in the model. The same was true when I included niche width first in the model and then added amount of habitat. The amount of habitat explained more variance in local abundance (or distribution) with niche width in the model. Therefore niche width and amount of habitat explain different variance in abundance and distribution. Since both niche width and amount of habitat explain significant amounts of variance in abundance and distribution both could contribute to the positive relationship between distribution and abundance in this group of 33 boreal forest songbirds.

The results of this study suggest that the amount of habitat in the landscape influences local abundance and distribution and provides support for the idea that variation in disperser success can generate a positive abundance-distribution relationship. This is indirect support for the metapopulation hypothesis which relies on the same mechanism. However, I cannot draw any conclusions about whether or not there would be sufficient variation in species-specific dispersal parameters to generate the necessary variation in disperser success to account for a positive abundance-distribution relationship. Results here indicate that variation in degree of ecological specialization and variation in amount of habitat in the landscape are not mutually exclusive explanations for the positive abundance-distribution relationship. Both explanations could operate simultaneously to produce a stronger relationship than either one alone.

GENERAL DISCUSSION

The focus of this thesis has been to examine the influence of the amount of habitat in the landscape on both the abundance and distribution of species as a means of explaining the positive abundance-distribution relationship. Landscape structure affects dispersal success (Dunning *et al.* 1992, Taylor *et al.* 1993, Fahrig and Merriam 1994), and amount of habitat on a landscape is a fundamental component of landscape structure. Species within the assemblage that have been used to demonstrate the empirical abundance - distribution relationship are usually taxonomically related but show substantial differences in the kinds of habitat they use. Therefore any given landscape will offer a different amount of habitat to each species within a group of such organisms. I hypothesized that these differences in amount of habitat available on the landscape will affect the success rate of dispersers and will lead to a positive relationship between distribution and abundance. This mechanism is the same as that proposed by Gyllenberg and Hanski (1992) but I am proposing a different source for the variation in disperser success.

The positive relationship between abundance and distribution is a very general relationship in that it appears to be the common pattern in many groups of organisms, at many different scales and in the context of many different definitions of both abundance and distribution (Appendix 1). But most studies that have examined this abundance-distribution relationship and the possible explanations for it have ignored the fact that different species use different habitat types preferentially. This has had two major impacts on discussions of the abundance-distribution relationship. First, because each species in an

assemblage uses different habitat, each species perceives the same landscape differently. Therefore, landscape composition can be highly variable among species in an assemblage which generates associated variation in metapopulation dynamics among species. This source of variation has been previously ignored. Second, local habitat where abundance and distribution are measured has a very strong influence on abundance and the probability of occurrence. Therefore, the differences in habitat use and the distribution of habitat types in a sample must be considered when examining an abundance-distribution relationship if reasonable interpretations of the data are to be made.

Deterministic models such as those developed by Gyllenberg and Hanski (1992) have been used to demonstrate that variation in a number of dispersal related parameters have potential to generate a positive abundance-distribution relationship. These single species deterministic models hold the landscape composition and structure constant but vary species specific metapopulation dynamic parameters. In this way, the landscape influence on the dynamics is de-emphasized. In Chapter 1 I used simulation model experiments to emphasize the potential influence of variation in landscape composition and its related structure on local abundance and distribution by holding all species specific parameters constant and varying the landscape composition (amount of breeding habitat). Within these simulation experiments sufficient variation in dispersal success was generated through variation in amount of breeding habitat to positively influence both distribution and abundance and therefore, generate a positive relationship between distribution and abundance.

The ecological specialization hypothesis (Brown 1984) suggests that generalists

will be more widely distributed because they are more likely to find suitable habitat than specialists. This is an intuitively satisfying idea. But in conjunction with this, generalists are also assumed to be more abundant which implies that they must be more efficient at using resources than specialists. This idea is less intuitively satisfying and has been questioned in the literature (Kouki and Häyrinen 1991). Part of Brown's (1984) argument rests on the assumption that sets of environmental variables are distributed independently of each other and that variation in these variables is autocorrelated such that the probability of sites having similar combinations of environmental variables is an inverse function of the distance between them. At larger scales this is probably true and is reflected in the commonly found, normally distributed population density over space (Hengeveld and Haack 1981, Brown 1984). Brown (1984) also noted that any examination of abundance at a small enough scale would be multimodal, but that if the scale was averaged over large enough areas a unimodal pattern would be apparent. I expect abundance, sampled within habitat type, to be multimodal. Habitat type scaled for forest songbirds reflects the small scale influences of topography. If the abundance is averaged over a larger scale then the pattern of abundance probably reflects the average availability of habitat not the efficiency with which a species can use habitat. Species that are generalists will be able to occupy more of the area because of their wider niche. If local abundance is measured over an area that includes more than one habitat type then generalists will be more abundant than specialists. This will result in a positive abundance-distribution relationship but not because generalists use habitat more efficiently; it will be due to the fact that there is more area where generalists can live and so their average

abundance over some small area will be larger than specialists. It is probable that in many studies that have averaged samples over large areas to generate measures of average abundance (see Bock and Ricklefs 1983, for example), abundance reflects the area of the abundance sample that the species can use.

Because my abundance samples were at a small, within-habitat scale, it was obvious that local habitat would influence local abundance and the probability of occurrence and therefore local habitat type needed to be controlled for before trying to examine any other relationships. For abundance-distribution relationships within single species it was possible to control for local habitat type statistically by including it as a covariate. This is not as simple in the interspecific case because each species responds differently to local habitat. Instead I examined the local abundance and proportion of sites occupied for only sites of the most preferred vegetation type for each species. Therefore, the abundance of each species should reflect the highest abundance that the species reaches at the point count scale. I found that species with wider niches were more locally abundant in their preferred habitat type suggesting that generalists are more efficient at using resources than specialists. I also found that different variation in local abundance and distribution was explained by amount of habitat in a 200 m radius landscape around the site (Chapter 5). Both the ecological specialization mechanism and the amount of habitat mechanism were operating at the same time to contribute to a positive abundance-distribution relationship.

I examined the abundance-distribution relationship within a single species in Chapters 2-4 as a means of controlling for species specific differences. As a result, I was

able to clearly demonstrate a landscape driven phenomenon that was not confounded by other species specific explanations. This in no way suggests that species specific differences are not operating in the commonly found multi-species abundance-distribution relationship. These within species studies are analagous to the simulation experiments in that only the landscapes were changed from one data point to the next.

My approach in this thesis has been to describe the variation in the landscape that is due to differences in the way that species perceive the landscape; and to use this variation to explain the pattern of abundance and distribution to organisms. It is common practice in comparative studies to look for correlations between life history traits of species and ecological patterns and processes (Hanski and Tiainen 1989, O'Connor 1989, Hanski *et al.* 1993 for example) while ignoring the landscape influence. Often, when landscape effects are examined it is within simplified landscapes where species within the assemblage are expected to respond similarly to habitat and non-habitat (Opdam 1991). Boreal forests are composed of a mosaic of many types of habitat and it has been argued that a landscape perspective usually has to be applied to studies in these areas (Hansson 1992). Songbird species within boreal forest use a wide variety of habitat types in different proportions so it is essential to consider the specific habitats that each species uses when examining the patterns of distribution and abundance. And it would be impossible to examine the influence of landscape on the abundance and distribution of these species without describing the landscape separately for each species in terms of their specific habitat use.

For dispersal success to function to generate the abundance-distribution

relationship, each measure of distribution and abundance must be taken where the landscape is expected to influence both measures in the same way. Variation in amount of habitat in the landscape as a generator of variation in disperser success can occur for a single species over a variety of landscapes or for an assemblage of species on a single landscape. Habitat is only available when it is within the dispersal distance of individuals within the local population in question. Therefore this mechanism is not expected to operate at all scales. Results of Chapter 4 and Chapter 5 suggested that it would be inappropriate to apply this mechanism to explain a positive distribution-abundance relationship that is found at biogeographic scales. Each pair of distribution and abundance measures must be taken over an area where amount of habitat is definable as a single measure, applicable to both abundance and distribution. The area of influence for ecological (or genetic) processes has been termed an ecological neighbourhood (Southwood 1977, Antonovics and Levin 1980, Addicott et al. 1987 and others). For mobile organisms the dispersal distance will usually define the neighbourhood for most ecological processes (Cunningham 1986, Ford and Krumme 1979, Jumars 1976, Koeppel et al. 1978, Southwood 1977). Certainly the dispersal distance should define the neighbourhood size for the influence of amount of habitat on abundance and distribution.

The relationship between regional habitat availability and both distribution and local abundance is significant to problems of conservation. For example, the relationship between population size and the amount of available habitat is not linear if the mean local abundance decreases with decreasing amount of habitat regionally. Loss of habitat due to human action is significant globally (Vitousek 1994) and also more specifically within the

boreal forests of Canada (Schmieglow and Hannon 1993). Results here suggest that local population sizes are influenced by the amount of habitat available regionally. Therefore, it is necessary to understand the form and magnitude of the relationship between local abundance and amount of habitat in the landscape to make estimates of the impact of habitat removal on local population size and viability. These estimates will be essential if land management is to attempt to maintain sustainable ecosystems.

The impact of habitat removal on local abundance should operate at the scale of the ecological neighbourhood. Results from this study indicate that there is variation in the size of the neighbourhood for dispersal mediated processes among boreal forest songbirds. Generally, for the group of species examined, the size of the neighbourhood is defined by a radius of less than 10 km and for most species less than 2 km.

The results presented in this thesis suggest strongly that variation in disperser success can and does operate to generate a positive distribution-abundance relationship. This variation in disperser success is at least in part a function of variation in the amount of habitat in the landscape. Some evidence has been presented here that variation in ecological specialization also generates a positive abundance-distribution relationship in part because generalists are more efficient at using resources. Explanations for the abundance-distribution relationship include sampling artifact (Bock and Ricklefs 1983), random distribution (Wright 1991), variation in ecological specialization (Brown 1984), variation in disperser success due to species specific differences (Gyllenberg and Hanski 1992) and variation in disperser success due to variation in amount of habitat in the landscape (Venier and Fahrig in press). All of these explanations have been demonstrated

directly or indirectly to operate in some cases and not in others (see Brown 1984, Gaston and Lawton 1990b, Kouki and Häyrinen 1991, Hanski *et al.* 1993 for examples). It is logical to conclude that none of these explanations are solely responsible for the commonly observed abundance-distribution relationship. Therefore, any distribution-abundance relationship must be explained in the context of the way in which the data were collected including considerations of scale, operational definitions of abundance and distribution, and the influence of local habitat on both abundance and the probability of occurrence.

APPENDIX 1

Studies examining the relationship of abundance versus distribution. Data for many of these studies originated in other studies that I have not cited here. Relationship between abundance and distribution is positive unless otherwise noted. Studies are organized by taxonomic group and then chronologically.

Study	Species	Distribution	Abundance	Additional Scale Information
Plants				
Fowler and Lawton 1982	British umbellifera	% occupied 10 km squares - estimate of geographic range	proportion of occupied 2 km squares of available squares	Britain
Gotelli and Simberloff 1987	tallgrass prairie plants	# of 10m ² plots occupied	average abundance (%cover) in 10m ² quadrats	total area of study 3487ha
Hanski <i>et al.</i> 1993 no relationship	freshwater aquatic plants from southern Finland (56 species)	# of sites occupied	% cover at occupied sites	20 sites in southern Finland
Hanski <i>et al.</i> 1993	coastal meadow plants (51 species)	# of sites occupied	% cover at occupied sites	22 sites in southern Finland
Hanski <i>et al.</i> 1993 no relationship	of rich fen plants (18 species)	# of sites occupied	% cover at occupied sites	35 sites in southern Finland
Insects				
Hanski 1982a	bumble bees (15 species)	# of sites occupied	mean abundance in occupied sites	parks in a single city
Hanski 1982b	leafhoppers	# of sites occupied	mean abundance in occupied sites	meadows in East Finland
Hanski 1982b	soil mites	# of sites occupied	mean abundance in occupied sites	north Finland (50 sites)
Hanski 1982b	dung and carrion beetles	# of trapping sites occupied	mean catch from a single site	12 sites at least 0.5 km from each other

Appendix 1 (continued)

Study	Species	Distribution	Abundance	Additional Scale Information
Gaston 1988	moths (263 species)	# of traps occupied	population density in occupied sites	light traps at 53 sites throughout Great Britain in a wide range of environments (950 km north to south, 500 km east to west)
Gaston and Lawton 1988a	herbivorous insects that feed on bracken (27 species)	sites occupied	mean abundance in occupied sites	216 sites spread widely throughout Britain
Gaston and Lawton 1988b	aphids (97 species)	regional distribution (# of traps occupied)	annual mean population density in occupied sites	18 sites throughout Britain; sites selected to cover island fairly evenly, environmentally uniform as possible, suction traps (sample over a large area) used to smooth out irregularities in the density surface over the area
Gaston and Lawton 1988b	carabids	# of 10 km squares occupied from Atlas data	mean annual abundance from pitfall catches at 4 sites	Netherlands
Spitzer and Lepš 1988 no relationship	noctuid moths (89 species)	qualitative categories from the literature - from cosmopolitan (largest) to Europe (smallest)	mean annual catch at each of 3 locations	long term census using light traps at 3 different locations in Bohemia, Czechoslovakia
Hanski <i>et al.</i> 1993	British butterflies (49 species)	# of sites occupied	mean abundance in occupied sites	42 sites located throughout England, Scotland, and Wales; excluding sites which were clearly atypical habitat e.g. seashores and mountains
Hanski <i>et al.</i> 1993	dung beetles (35 species)	# of sites occupied	mean abundance in occupied sites	20 sites in Africa (authors describe as local scale)

Appendix 1 (continued)

Study	Species	Distribution	Abundance	Additional Scale Information
Hanski <i>et al.</i> 1993	dung beetles (119 species)	# of sites occupied	mean abundance in occupied sites	6 sites in Africa (authors describe as regional scale)
Hanski <i>et al.</i> 1993	carbid beetles (25 species)	# of sites occupied	mean abundance in occupied sites	9 sites from southern Norway
Crustaceans				
Brown (1984)	freshwater planktonic crustaceans	# of lakes inhabited	average density in those lakes where it occurs	45 lakes in Ontario, Canada
Helminths				
Hanski <i>et al.</i> 1993	helminth parasites of lesser scaup (15 species)	# of sites inhabited	mean abundance of occupied sites	45 sites
Gastropods				
Russell and Lindberg 1988	recent prosobranch gastropods	linear dimension (or range) along coastline where they occurred	qualitative assessment (abundant, common, occasional, rare)	analysis restricted to species occurring between the western most Aleutian Islands and the southern tip of Baja California
Hanski <i>et al.</i> 1993	terrestrial gastropods (12 species)	# of sites occupied	mean abundance in occupied sites	32 sites from northern Finland
Fish				
Gaston and Lawton 1983a no relationship	freshwater fish of the British Isles	# of occupied 10 km squares	abundance measured at a single reference point (50 km stretch)	British Isles

Appendix 1 (continued)

Study	Species	Distribution	Abundance	Additional Scale Information
Birds				
Järvinen and Sammalisto (1976)	birds in Finnish peatland bogs	proportion of areas inhabited by a given species	mean abundance	112 open bogs in 5 regions of Finland
Bock and Ricklefs (1983)	seed eating songbirds (65 species)	range size is # 5° blocks occupied	average within range abundance on non-zero Christmas Bird Counts (CBCs) ¹ in occupied 5° blocks	wintering in USA and Canada
Bock 1984	apodiform, piciform and passerine landbirds	# of 5° blocks occupied (CBC data)	mean birds counted per census hour across all occupied blocks (CBC data)	bird whose ranges are 75% or more restricted in winter to the contiguous US and southern Canada
Bock 1984	same as above	same as above	maximum # of birds per census hour in a single block (CBC data)	same as above
Bock 1984	same as above	same as above	maximum # of birds per census hour on a single CBC	same as above
Brown 1984	North American hawks	area of winter geographic range from range maps	average local population density from CBC	North America
Lacy and Bock 1986	seed eating songbirds (65 species)	range size is # 5° blocks occupied (CBC data)	average within range abundance on non-zero CBCs in occupied CBC samples	wintering in USA and Canada same data as Bock and Ricklefs (1983) but with modifications for measuring abundance
Bock 1987	landbirds (62 species)	# of 35 m radius plots occupied	mean abundance in occupied plots	124 plots in 24 habitat types in and near Huachuca Mountains, Arizona

Appendix 1 (continued)

Study	Species	Distribution	Abundance	Additional Scale Information
Bock 1987	same as above	CBC counts in Arizona in which species was counted at least once	mean # counted per 1000 party-hours of field effort on all CBC's in each occupied block	27 CBC counts in Arizona
Bock 1987	same as above	# of 5° blocks occupied (CBC data) in the western United States	average # counted per 1000 party-hours of field effort on all CBC's in each occupied block	20 5° blocks
Brown and Maurer 1987	North American terrestrial avifauna (400 species)	total area from range maps	Breeding Bird Survey (BBS) ² data 50 census locations per route, # of detections per route	approximately 2,000 BBS routes
Ford 1990	negative relationship 77 Australian bird species	distribution throughout Australia measured as # of 1° squares in which the species was recorded (Atlas data)	density of individuals per hectare based on transect censuses in seven sites where the species occurred	Australia
Maurer 1990	boreal bird species (23 species)	# of sites occupied	mean density in occupied sites	Great Smoky Mountains (4 census plots)
Maurer 1990	boreal bird species (38 species)	# of sites occupied	mean density in occupied sites	northern Manitoba
Kouki and Häyrynen 1991	wading and passerine birds breeding in Finnish mires	distance between the northernmost and southernmost Finnish breeding record	mean abundance at occupied sites based on single visit sample plot censuses	327 censuses covering almost the entire north-south range of Finland (1130 km and 190 km ²)

Appendix 1 (continued)

Study	Species	Distribution	Abundance	Additional Scale Information
Mammals				
Frown 1984	desert rodents (12 species)	# of sites where the species was observed	mean population density at occupied sites	115 sites in southern Nevada

Footnotes

¹ The basic sampling unit of the Christmas Bird Count (CBC) is a 24 km diameter circle. Birds are counted for an entire day and are standardized for effort (Bock and Root 1981).

² The basic sampling unit of the Breeding Bird Survey (BBS) is a route. Each route is conducted on secondary roads and consists of 50 3-minute counting locations 0.8 km apart (Bystrak 1981).

APPENDIX 2: Boreal forest bird species included in the thesis with selected life history traits. Migration strategies are : year round residents in Canada (res) , nomadic (nom), short distance migrant-wintering range primarily north of the United States-Mexico border (sdm) and neotropical migrants - wintering range primarily south of the US-Mexico border (neo). The Food category represents the primary food during the breeding season (in=insectivore, om=omnivore- a variety of foods including both animal and plant foods - the less common food making up at least 10% of the diet, gr=granivore -seeds and nuts. The return rate is the average arrival date for the Thunder Bay region. Wing is the average length in mm of an adult male wing. Weight is the average weight in grams of an adult male. References for Appendix 2 include DeGraff *et al.* 1985, Denis 1961, Ehrlich *et al.* 1987, Peck and James 1987.

Species Common Name	Latin Name	Family	Migration Strategy	Food	Clutch Size	Return Date	Wing	Weight
American Robin	<i>Turdus migratorius</i>	Muscicapidae	sdm	om	3-4	April 4	129.9	80.2
Bay-breasted Warbler	<i>Dendroica castanea</i>	Emberizidae	neo	in	4-5	May 21	73.1	11.8
Black-capped Chickadee	<i>Parus atricapillus</i>	Paridae	res	in	6-7	overwinters	66.0	11.36
Blackburnian Warbler	<i>Dendroica fusca</i>	Emberizidae	neo	in	4	May 17	67.8	10.1
Boreal Chickadee	<i>Parus hudsonicus</i>	Paridae	res	in	6	overwinters	65.8	11.2
Brown Creeper	<i>Certhia americana</i>	Certhiidae	sdm	in	6	April 16	65	8.3
Black-throated Green Warbler	<i>Dendroica virens</i>	Emberizidae	neo	in	3-4	May 15	63.8	9.4
Black-and-White Warbler	<i>Mniotilta varia</i>	Emberizidae	neo	in	4-5	May 25	68.8	10.15
Canada Warbler	<i>Wilsonia canadensis</i>	Emberizidae	neo	in	4-5	May 26	64.8	10.1
Cape May Warbler	<i>Dendroica tigrina</i>	Emberizidae	neo	in	6-7	May 19	67.2	9.5
Chipping Sparrow	<i>Spizella passerina</i>	Emberizidae	sdm	om	4	May 5	70.1	12.5
Connecticut Warbler	<i>Oporornis agilis</i>	Emberizidae	neo	in	4-5	May 20	71.2	19.1
Dark-eyed Junco	<i>Junco hyemalis</i>	Emberizidae	sdm	om	4	April 10	78.4	18.2 ⁷⁵

Appendix 2 (continued)

Species	Common Name	Latin Name	Family	Migration Strategy	Food	Clutch Size	Return Date	Wing	Weight
Eastern Wood-Pewee		<i>Contopus virens</i>	Tyrannidae	neo	in	3	May 30	84.1	14.4
Golden-crowned Kinglet		<i>Regulus satrapa</i>	Muscicapidae	sdm	in	8-9	April 16	57.1	5.4
Hermit Thrush		<i>Catharus guttatus</i>	Muscicapidae	sdm	in	4	April 24	92.2	29.8
Least Flycatcher		<i>Epidinax minimus</i>	Tyrannidae	neo	in	4	May 20	64.3	11.1
Magnolia Warbler		<i>Dendroica magnolia</i>	Emberizidae	neo	in	4	May 17	61.25	8.8
Nashville Warbler		<i>Vermivora ruficapilla</i>	Emberizidae	neo	in	4-5	May 15	59.2	8.8
Orange-crowned Warbler		<i>Vermivora celata</i>	Emberizidae	sdm	in	4-5	May 17	61.4	8.5
Olive-sided Flycatcher		<i>Contopus borealis</i>	Tyrannidae	neo	in	3	May 27	106.9	31.1
Ovenbird		<i>Seiurus aurocapillus</i>	Emberizidae	neo	in	4-5	May 22	76.6	22.5
Pine Siskin		<i>Carduelis pinus</i>	Fringillidae	nom	om	3-5	May 3	72.8	12.5
Purple Finch		<i>Carduelis purpureus</i>	Fringillidae	sdm	gr	3-4	April 13	82.3	24.8
Red-breasted Nuthatch		<i>Sitta canadensis</i>	Sittidae	res	in	5-6	overwinters	67.3	10.3
Ruby-crowned Kinglet		<i>Regulus calendula</i>	Muscicapidae	sdm	in	8-9	April 22	58.3	6.9
Red-eyed Vireo		<i>Vireo olivaceus</i>	Vireonidae	neo	in	3-4	May 23	80.5	17.7
Solitary Vireo		<i>Vireo solitarius</i>	Vireonidae	sdm	in	4	May 19	72.7	16.5
Swainson's Thrush		<i>Catharus ustularius</i>	Muscicapidae	neo	om	3-4	May 11	99.1	30.3
Tennessee Warbler		<i>Vermivora peregrina</i>	Emberizidae	neo	in	4-6	May 19	64.9	9.3

Appendix 2 (continued)

Species Common Name	Latin Name	Family	Migration Strategy	Food	Clutch Size	Return Date	Wing	Weight
Veery	<i>Catharus fuscescens</i>	Muscicapidae	neo	om	4	May 16	99.9	32.26
Winter Wren	<i>Troglodytes troglodytes</i>	Troglodytidae	sdm	in	5-6	May 7	47.4	9.0
White-throated Sparrow	<i>Zonotrichia albicollis</i>	Emberizidae	sdm	om	4	April 26	73.9	26.4
Yellow-bellied Flycatcher	<i>Epidonax flaviventris</i>	Tyrannidae	neo	in	4	May 29	67.2	12.5
Yellow-rumped Warbler	<i>Dendroica coronata</i>	Emberizidae	sdm	in	3-4	April 22	72.7	12.0

APPENDIX 3

Brief descriptions of the 38 Vegetation types of the Forest Ecosystem Classification of northwestern Ontario from Sims *et al.* 1989.

Vegetation Type	Description
1	balsam poplar hardwood and mixed wood (mainly hardwood); understory is typically herb and shrub rich with a broad diversity of species
2	black ash hardwood and mixedwood (mainly hardwood); understory is typically dense and floristically diverse
3	hardwood and mixedwood stands dominated by species other than aspen/poplar, white birch or black ash (mainly hardwood); infrequent and of limited areal extent
4	white birch hardwood and mixedwood (mainly hardwood); generally herb and shrub rich
5	aspen hardwood; understory is characteristically herb and shrub rich
6	trembling aspen (white birch) - balsam fir/mountain maple; balsam fir as the main conifer species, canopy is typically diffuse and two-tiered with aspen or aspen-birch in the overstory and balsam fir in the secondary layer; understory is generally herb and shrub rich
7	trembling aspen - balsam fir shrub; typically two-tiered canopy; in general, trembling aspen form the overstory with balsam fir in the secondary canopy; understory development is variable
8	trembling aspen (white birch) / mountain maple; abundance of broadleaved herbs and shrubs in the understory
9	trembling aspen mixedwood; shrub and herb rich understory; trembling aspen is the main tree species balsam fir can be abundant in the understory
10	trembling aspen - black spruce - jack pine/low shrub; mainly hardwood but with black spruce and jack pine as the main conifer tree species; herb and shrub layers are usually rich in broad leaved species
11	trembling aspen -conifer/blueberry/feathermoss; mainly hardwood with black spruce or jack pine as the main conifer tree species; understory dominated by conifer and ericaceous shrubs; large patches of feathermoss
12	white pine mixedwood; tall overstory of white pine and a secondary canopy of other tree species; understory is typically herb and shrub rich
13	red pine mixedwood; mainly red pine in the conifer component of the overstory; understory variable; large patches of feathermoss
14	balsam fir mixedwood; canopy mostly balsam fir but may contain a mixture of several species; variable understory
15	white spruce mixedwood; white spruce as the main canopy tree species; variable understory with balsam fir common in shrub layer

Appendix 3 continued

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16	balsam fir- white spruce mixedwood/ feathermoss; balsam fir and/or white spruce as the main tree species; balsam fir in the understory; extensive feathermoss
17	jack pine mixedwood/shrub rich; spruce and fir occasional in the canopy; the understory is typically rich in herb and low shrub species
18	jack pine mixedwood/feathermoss; often with black spruce in the overstory; herb and shrub poor relative to other mixedwoods; extensive feathermoss
19	black spruce mixedwood / herb rich; several potential species in overstory; understory is dominated by a rich herb / dwarf shrub layer; usually balsam fir and black spruce are important components of the understory; variable forest floor
20	black spruce mixedwood; commonly with white birch constituting the hardwood component of the canopy; understory is typically dominated by low, ericaceous shrubs; extensive feathermoss
21	cedar /mountain maple; white cedar in conifer and mixedwood stands; shrub layer is usually dominated by balsam fir, white cedar but not dense; high diversity in herb layer
22	cedar / speckled alder / sphagnum; lowland white cedar including mixedwoods often containing black spruce in the canopy; shrub layer dominated by balsam fir, white cedar; moss cover (feathermoss and sphagnum)
23	tamarack (black spruce)/speckled alder/labrador tea; wet tamarack stands with black spruce in the overstory; shrub layer is typically dominated by low, ericaceous species although thickets of speckled alder, balsam fir or black spruce may occur; sphagnum and feathermoss
24	white spruce-balsam fir/shrub rich; white spruce and/or balsam fir as the main canopy species; understory tends to be shrub rich with balsam fir, mountain maple, beaked hazel and speckled alder; variable herb layer
25	white spruce - balsam fir / feathermoss; white spruce and/or balsam fir stands, often with black spruce in the canopy; balsam fir is often abundant in shrub layer; bunchberry in herb layer; feathermoss and conifer litter
26	white pine conifer; overstory composition ranges from white pine to a diverse conifer mix; understory tends to be shrub rich with balsam fir, mountain maple and beaked hazel; sparse herb layer
27	red pine conifer; often pure stands although some other conifer species occur; understory variable; pine needle litter, feathermoss
28	jack pine /low shrub; even-aged jack pine stands; typically well-developed in the low shrubs; mountain maple, green alder, beaked hazel in tall shrubs; feathermoss
29	jack pine /ericaceous shrub/ feathermoss; open even-aged jack pine stands; shrub layer dominated by blueberry species; feathermoss
30	jack pine - black spruce/blueberry/lichen, sparse jack pine and/or black spruce stands; understory is open with black spruce; blueberry species in herb and shrub layer; lichen cover

Appendix 3 continued

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31	black spruce - jack pine/tall shrub/feathermoss; black spruce and jack pine in the canopy; shrub and herb layers are moderately dense; balsam fir and black spruce in shrub layer; extensive feathermoss
32	jack pine - black spruce /ericaceous shrub/feathermoss; jack pine and black spruce in the canopy; open understory; scattered clumps of black spruce and green alder in shrub layer; herb and low shrub layer dominated by bunchberry and ericaceous species; extensive feathermoss
33	black spruce /feathermoss; black spruce stands with occasional occurrences of other conifers; understory typically open with clumps of black spruce; ericaceous species dominate the herb and low shrub layer; continuous feathermoss mat
34	black spruce/labrador tea/feathermoss (sphagnum); black spruce stands with occasional occurrences of other conifers in the canopy; ericaceous species typically dominate the understory; black spruce, balsam fir and speckled alder form a dense shrub cover, continuous feathermoss and sphagnum
35	black spruce /speckled alder/sphagnum; wet, shrub rich black spruce stands with other conifers in the canopy; speckled alder with black spruce and balsam fir in the shrub layer; high diversity in herb layer; sphagnum, feathermoss and broadleaf litter
36	black spruce/bunchberry/sphagnum(feathermoss) - black spruce stands occasionally with other conifers in the canopy; shrubs dominated by low, ericaceous species with scattered clumps of black spruce and balsam fir; sphagnum and feather moss
37	black spruce/ericaceous shrub/sphagnum: lowland black spruce stands, understory dominated by ericaceous species, labrador tea abundant, scattered clumps of black spruce in understory
38	black spruce/leatherleaf/sphagnum; poor, wetland black spruce stands with stunted, widely spaced trees; shrub layer composed of leatherleaf and labrador tea, low diversity in herb layer; continuous sphagnum/feathermoss mat

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OF/DE

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PM-1 3 1/2" x 4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

PRECISIONSM RESOLUTION TARGETS

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