University of Alberta

Relative effects of habitat cover versus configuration, and the existence of critical thresholds in ecology

By

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Doctor of Philosophy
in
Environmental Biology and Ecology
Department of Biological Sciences

Edmonton, Alberta
Fall 2007

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Your file Votre référence
ISBN: 978-0-494-33074-6
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ISBN: 978-0-494-33074-6

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Abstract

A major conservation concern is whether populations decline linearly in response to habitat loss, or whether they suddenly decline more rapidly below a "critical threshold" of habitat. Robust statistical methods are required to determine the shape of the relationship, and to estimate threshold values. A second concern is the relative importance of habitat loss versus fragmentation, since this will determine where conservation efforts should focus. I researched these issues through literature reviews, a comparison of statistical methods using artificially generated data, and analyses of empirical bird and mammal abundance data from an agricultural / southern boreal forest region of Alberta. Both linear and nonlinear ecological responses to habitat loss were evident among simulation and empirical studies from the literature, though the presence and value of critical thresholds was influenced by characteristics of the species (dispersal, reproduction, area / edge sensitivity) and landscape characteristics (fragmentation, matrix quality, rate of change). A comparison of piecewise regression and change-point analysis revealed that each was an unbiased estimator of the threshold only if the "true" threshold shape matched the shape assumed by the model (e.g. a "continuous" threshold like a sharply bent line, or a "discontinuous" threshold like a stair step, respectively). For choosing among a set of linear and nonlinear models, Akaike information criterion (AICc) was biased towards overfitting and Bayesian information criterion (BIC) towards underfitting. In my study area, the abundance of most forest-breeding birds and mammals changed linearly with habitat loss. However, *Picoides pubescens* declined only below a 10-20% forest cover threshold, and *Poecile atricapillus* peaked at a threshold of 34% forest. A review of the relative effects of habitat loss and fragmentation revealed that habitat loss had consistently large, negative effects. Fragmentation effects were usually weaker, but depended somewhat on characteristics of the species (vagility, reproduction) and landscape (habitat amount, scale), and the experimental / analytical approaches used by the researcher (response variable, definition of habitat). Empirical bird and mammal abundance data supported the idea that fragmentation was generally less important than habitat loss. However, relative fragmentation effects depended on spatial scale, and increased at lower levels of forest cover.

Acknowledgements

Sue! Thank you for your patience, time, thoughtful input, and bluntness. I really could not have asked for a better supervisor. I am also grateful to the rest of my committee, Jens Roland and Fiona Schmiegelow, for their insights and advice. Cindy McCallum, thank you for always being there to lend a hand or answer questions. Thank you to the small army of other folk who helped smooth the treacherous path towards this thesis: my lab mates for helpful discussions and advice (especially Judith Toms, who provided valuable statistical advice); Jason Young for providing GIS data, Charlene Nielsen for GIS technical assistance, Erin Bayne for statistical advice, and Neil Darlow for sharing the load in terms of GIS work and field accommodations.

The field portion of my research would not have been possible without the many kind landowners in the Ministik region who permitted me to access their land. Thank you for your generosity and trust. Permission was also granted for the use of Elk Island National Park, the Cooking Lake - Blackfoot Grazing, Wildlife and Provincial Recreation Area, Miquelon Lake Provincial Park, and the Ministik Game Bird Sanctuary. Elk Island National Park provided field housing, and the Sherwood Park Fish and Game Association provided a camp site. I greatly appreciate the support provided by all of these organizations. Field assistance was provided by Kelly Gray, Carmen Lefebvre, Alan Marsh, Julie Mills, Matthew Hanneman, and Jamille Heer. Matthew Hanneman also assisted in digitizing the study area, and did a wonderful job.

I deeply appreciate the love, encouragement and support of my friends, family, and extended family. Tony, thank you for your patience, for distracting me from my thesis, and for not asking me too many questions about it!

Research funding was provided by the Alberta Conservation Association, the North American Waterfowl Management Plan Biodiversity Initiative, the Alberta Sport, Recreation, Parks and Wildlife Foundation, and the Canadian Circumpolar Institute. Funding for travel to conferences was provided by the University of Alberta (Department of Biological Sciences Travel Award, and the Faculty of Graduate Studies and Research Gordin J. Kaplan Graduate Student Award). Trisha Swift was supported by Post-Graduate Scholarships from the National Sciences Engineering Research Council of Canada, a Province of Alberta Fellowship, Walter H. Johns Graduate Fellowships, a Province of Alberta Graduate Student Scholarship, a McAfee Estate Scholarship in Zoology, and teaching assistantships and a Science Graduate Scholarship from the University of Alberta.

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Chapter 1: Thesis introduction

1. Introduction

The introduction of agricultural land uses into forested-dominated landscapes leads to major changes in landscape structure. There is a reduction in total forest area, and concurrent changes in forest spatial configuration towards greater fragmentation (Hobson et al. 2002, Young et al. 2006). Forest remnants become more numerous yet smaller and more widely interspersed within the matrix, which may be inhospitable to many forest-dependent species (e.g. Bennett et al. 1994). Evidence from computer simulation suggests that population declines may follow a "critical threshold" relationship with habitat loss (e.g. Flather and Bevers 2002). Above this threshold, population declines are predictable from the amount of habitat loss. Below the threshold, however, populations abruptly decline more steeply. A threshold decline is expected if negative fragmentation effects compound those of habitat loss, once the amount of habitat in the landscape falls below a critical value (Andrén 1994). By the same token, if fragmentation effects are positive, then the increased fragmentation associated with habitat loss may compensate for mild to moderate habitat loss. For example, some species that benefit from edge habitats may be most abundant at medium levels of habitat, and exhibit a quadratic relationship with the proportion of habitat in the landscape. Species that are not strongly affected by habitat fragmentation might be expected to decline linearly with habitat loss.

A major concern for conservation is to quantify the relative importance of habitat amount versus its spatial configuration (Fahrig 1997). If fragmentation has large, negative effects over and above those due to forest loss, then reducing fragmentation in landscapes could be an effective conservation strategy (Kareiva and Wennergren 1995). However, if fragmentation has a very small effect relative to forest loss, then conservation resources would be much better spent on even moderate levels of habitat restoration or preservation (Fahrig 2003).

2. Thesis objectives

Two major topics are addressed in this thesis. The first deals with the shape(s) of the relationships between habitat proportion and ecological responses. Specifically, what is the evidence in the literature for linear and nonlinear ecological responses to habitat loss? What statistical methods are appropriate for the detection and estimation of critical thresholds and other shapes, both linear and nonlinear? Using these methods, what is the evidence for the shapes of the relationships between forest cover and the abundance of forest birds and mammals in an agricultural / boreal system of Alberta? The second topic focuses on quantifying the independent and relative effects of habitat proportion versus spatial configuration on populations. What insights does the ecological literature provide on the subject? What are the relative effects of habitat loss and fragmentation on the abundance and diversity of forest birds and mammals, and what is the effect of spatial scale and of the range of forest cover analyzed?

3. Study organisms

The empirical portions of my thesis deal with forest-breeding birds and mammals in an agricultural / southern boreal region of Alberta. I focused mainly on resident birds. With respect to habitat loss and fragmentation, resident birds have been less intensively studied than migratory species. These two migratory groups may respond to different aspects of habitat fragmentation. For example, most neotropical migrants are open-cup nesters, and may be more exposed to increased edge-related nest predation (Wilcove 1985) and brood parasitism (Strausberger and Ashley 1997), especially in agricultural landscapes (Chalfoun et al. 2002, Morrison and Caldwell 2002). In contrast, resident birds are cavity nesters and are not commonly parasitized. During the winter, they may instead face greater energetic costs (Dolby and Grubb 1999, Turcotte and Desrochers 2003) as well as reduced survivorship (Doherty and Grubb 2002) and nutritional condition (Doherty and Grubb 2003) at habitat edges and in small patches. Because population limitation of both migratory groups likely occurs during the winter (e.g. Herrera 1978, Newton 1994), resident populations in northern regions may be more responsive to the structure of these landscapes.

4. Thesis structure

The structure of this thesis is as follows. In the next chapter, I review the theoretical and empirical evidence for the existence of critical threshold responses to habitat loss. This review revealed a need for the use of formal statistical methods for distinguishing between linear and nonlinear relationships, and for identifying threshold values. In Chapter 3, I use simulated data to compare several such methods: piecewise regression and change-point analysis (for estimating threshold values), and Akaike information criterion (AICc) and Bayesian information criterion (BIC; for comparing the weight of evidence for different model shapes). Chapter 4 makes use of these methods to evaluate the shapes of the relationships between the abundance and diversity of forest breeding birds and mammals, and the proportion of forest in the landscape. In Chapter 5, I review the theoretical and empirical evidence for the relative effects of habitat proportion versus spatial configuration on population responses. I estimate the relative effects of these landscape characteristics on the abundance and diversity of the study species in Chapter 6. A summary of the major findings of the thesis is provided in Chapter 7.

References

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.

Bennett, A., Henein, K. & Merriam, G. 1994. Corridor use and the elements of corridor quality: Chipmunks and fencerows in a farmland mosaic. *Biological Conservation* 68: 155-165.

Chalfoun, A. D., Thompson, F. R. & Ratnaswamy, M. J. 2002. Nest predators and fragmentation: A review and meta-analysis. *Conservation Biology* 16: 306-318.

Doherty, P. F. & Grubb, T. C. Jr. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. *Ecology* 83: 844-857.

Doherty, P. F. Jr. & Grubb, T. C. Jr. 2003. Relationship of nutritional condition of permanent-resident woodland birds with woodlot area, supplemental food, and snow cover. *Auk* 120: 331-336.

Dolby, A. S. & Grubb, T. C. Jr. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. *Condor* 408-412.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603-610.

Flather, C. H. & Bevers, M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159: 40-56.

Herrera, C. M. 1978. On the breeding distribution pattern of European migrant birds: MacArthur's theme reexamined. *Auk* 95: 496-509.

Hobson, K., Bayne, E. & Van Wilgenburg, S. 2002. Large-scale conversion of forest to agriculture in the boreal plains of Saskatchewan. *Conservation Biology* 16: 1530-1541.

Kareiva, P. & Wennergren, U. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373: 299-302.

Morrison, M. L. & Hahn, D. C. 2002. Geographic variation in cowbird distribution, abundance, and parasitism. *Studies in Avian Biology* 25: 65-72.

Newton, I. 1994. Experiments on the limitation of bird breeding densities: A review . *Ibis* 136: 397-411.

Strausberger, B. M. & Ashley, M. V. 1997. Community-wide patterns of parasitism of a host "generalist" brood-parasitic cowbird. *Oecologia* 112: 254-262.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds . *Ecology* 66: 1211-1214.

Young, J. E., Sánchez-Azofeifa, G. A., Hannon, S. J. & Chapman, R. 2006. Trends in land cover change and isolation of protected areas at the interface of the southern boreal mixedwood and aspen parkland in Alberta, Canada. *Forest Ecology and Management* 230: 151-161.

Chapter 2: Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications

1. Introduction

Numerous studies have documented the detrimental effects of habitat loss on various ecological responses (e.g. bird body condition: Burton et al. 2006; amphibian populations: Cushman 2006; plant reproduction: Aguilar et al. 2006). Recently, there has been growing interest in the shapes of these relationships. Do ecological responses change linearly with habitat loss, or are there "critical threshold" levels of habitat? A critical threshold is "an abrupt, nonlinear change that occurs in some parameter across a small range of habitat loss" (With and King 1999a). The response variable undergoing this abrupt change may be individual behaviour, the abundance of a species, or community composition, among others. The key point is that its relationship (e.g. magnitude or slope) with habitat proportion changes at some critical proportion.

The existence of critical thresholds in habitat proportion is of conservation concern, because small additional losses of habitat below the critical threshold may lead to abrupt population declines or other important ecological changes. Unanticipated, such changes may preclude timely conservation measures. Such thresholds also indicate that some other factor (such as fragmentation, see below) may become substantive only below certain proportions of habitat, compounding the effects of habitat loss at low habitat proportions.

1.1. Purpose and structure of review

The purpose of this review is to present theoretical and empirical evidence for critical thresholds in species' responses to habitat proportion in the landscape. I will discuss a) possible explanations for critical thresholds, b) evidence for their occurrence and value in simulated and real landscapes, c) the effect of species and landscape characteristics on the existence and value of critical thresholds, and d) potential uses and misuses for critical threshold information in landscape management. The review will conclude with a summary of major trends and recommendations for future research.

Included are studies for which the authors explicitly address the presence or absence of "critical thresholds", "thresholds", "sudden changes", or "nonlinear" relationships, as well as a few which only presented data suggesting such relationships (e.g. data plots). Different authors seemed to estimate exact critical threshold values in different ways, or not at all. Therefore, when there was no formal statistical assessment of critical threshold values, I re-estimated them as either the point at which the slope changed (for sharp thresholds), the midpoint of the curve around which the slope changed (for more gradual thresholds), or the range over which the response value changed markedly (for categorical data), rounded to the nearest 5% (Fig. 2-1). This was done to make the results of different studies more comparable, not necessarily because this is the best or only way to define the value of a critical threshold, which in some cases may be considered as a range rather than an exact point (e.g. see Huggett 2005 for a broader view of "ecological thresholds").

Only studies conducted at the "landscape" level were reviewed (including studies for which species' responses were measured within individual habitat patches but habitat proportion was measured from the surrounding area). "Landscapes" were considered to be mosaics of habitat and non-habitat patches (or patches of varying quality), large enough to be relevant to the response variable and focal organism (McGarigal and McComb 1995, Chust et al. 2004).

2. Possible explanations for critical thresholds, and conservation implications

2.1. Configuration effects at low habitat cover

Ther are several explanations for critical threshold relationships with habitat cover. The most common is that at low levels of habitat, negative effects of habitat fragmentation compound those of habitat loss, such that the rate of change in the ecological response is greater than expected from habitat loss alone (e.g. Andrén 1994). Habitat fragmentation is distinct from habitat loss, reflecting aspects of habitat configuration (e.g. number of habitat fragments, edge density, patch shape), rather than the total amount of habitat in a landscape. Negative fragmentation effects may include increased predation and brood parasitism (Donovan et al. 1997), harsher microclimate (Dolby and Grubb 1999), decreased food (Zanette et al. 2000), and decreased ability of animals to move across the landscape between habitat patches (Bélisle et al. 2001).

Why might fragmentation effects compound those of habitat loss only at low habitat levels? Models based on percolation theory have shown that some aspects of structural fragmentation itself may increase abruptly below critical proportions of habitat. For example, when habitat is randomly distributed on a raster map, and a habitat "patch" is composed of habitat pixels adjacent to one another along at least one horizontal or vertical edge (the "four neighbour rule"), there are abrupt thresholds in the amount of habitat near which certain aspects of configuration change abruptly. Below a critical threshold of about 59% remaining habitat, the largest patch no longer spans the map (no longer "percolates"), and its size decreases abruptly (Gustafson and Parker 1992, Andrén 1994, Bascompte and Solé 1996). As well, mean inter-patch neighbour distance increases rapidly below about 40% (Gustafson and Parker 1992, Andrén 1994), and patch number peaks near 30% (Gustafson and Parker 1992). If a species is sensitive to these aspects of fragmentation, their responses to habitat proportion might also be expected to be nonlinear.

Another possible explanation for ecological threshold responses to habitat loss is that there may be a nonlinear relationship between habitat loss and *biological responses* to structural fragmentation (i.e. functional fragmentation). For example, when the proportion of habitat in a landscape is low, fragmentation of that habitat may result in interpatch distances that exceed the maximum distance that a certain species is willing or able to cross. Alternatively, habitat patches that fall below the minimum size can no longer support a population or territory. At high habitat proportions, a similar level of subdivision would result in a system of patches that are on average larger than those in the low habitat cover, and close enough together to allow frequent genetic exchange, recolonization (Fahrig 1998), or multi-patch home range movements. The amount of habitat loss required for these fragmentation effects to occur would depend on species characteristics, such as gap crossing distances and home range sizes.

The existence of a fragmentation-related threshold would mean that when habitat cover falls below the threshold, reducing fragmentation of the remaining habitat may be an effective management strategy. More specifically, reducing fragmentation should help to maintain the ecological parameter (e.g. population size) closer to what would be expected from habitat loss alone.

2.2. *Allee effects at low habitat cover*

Allee effects could also potentially lead to critical threshold relationships with habitat amount, even in the absence of fragmentation effects. Allee effects occur in small populations when per capita growth rates are inversely dependent on population density (reviewed by Courchamp et al. 1999). Proposed mechanisms to explain Allee effects include inbreeding depression, demographic stochasticity, and inhibition of social facilitation (e.g. sexual reproduction or predator avoidance tactics). Below a threshold population size, growth rates may even become negative (Courchamp et al. 1999). Because habitat loss reduces maximum population sizes, there may be a critical threshold proportion of habitat below which Allee effects come into play. Above this critical habitat / population threshold, population abundance has the potential to reach the carrying capacity of the habitat (Greene 2003). Below this amount, the population size would be less than expected from the amount of habitat.

A Levins metapopulation model incorporating both habitat loss and Allee effects (Amarasekare 1998) supports this idea. A Levins metapopulation model without Allee effects predicts that the total number of occupied patches will decrease linearly with habitat loss. Deterministic extinction occurs at some proportion of habitat, "x", equal to the proportion of patches that are unoccupied when habitat = 100%. However, if Allee effects occur once the number of occupied patches drops below a certain threshold, "t", then there is a range of habitat proportion (x to x + t) in which the predicted equilibrium proportion of occupied patches is unstable. Within this range, the population may go extinct, even if the amount of available habitat is above the eradication threshold, x (Amarasekare 1998). Thus, the decline in occupied patches may become non-linear (decline more steeply) below an "Allee threshold" proportion of habitat (x + t). An Allee effects-related critical threshold could occur as a response to pure habitat loss, in the absence of fragmentation. However, fragmentation could conceivably interact with habitat loss to divide a population into smaller, isolated subpopulations that are individually subject to Allee effects, thus increasing the critical threshold level of habitat that would otherwise be observed.

Allee effects-related habitat thresholds may be of particular conservation concern, because they may severely limit our ability to reverse the effects of habitat loss / fragmentation. In particular, habitat loss and fragmentation may cause populations to become demographically limited, rather than habitat limited (Schrott et al. 2005a). Thus, below some "restoration threshold" for population size / habitat amount, habitat restoration would not prevent further declines. Instead, effective management would require efforts to increase reproduction and decrease mortality (Schrott et al. 2005a).

2.3. Time lags

Simulation models have suggested that ecological time lags (Tilman et al. 1994, Hanski and Ovaskainen 2002) are pronounced when the rate of habitat loss is rapid relative to the demographic response time (e.g. generation time) of the organism (Schrott et al. 2005b). Indeed, several populations are better predicted by past than current habitat levels (Hanski and Ovaskainen 2002, Cowlishaw 1999, Gu et al. 2002). Time lags could lead to apparently nonlinear responses to habitat loss. Consider a population that would decline linearly with habitat loss when habitat loss was slow, disappearing below 20% habitat. If habitat loss was rapid enough to produce a time lag, then the population would initially decline less steeply with habitat loss than expected. The corollary is that if habitat loss is ongoing, then at some point (e.g. after habitat levels reach or fall below 20%), the decline must become steeper as the population moves towards extinction. This nonlinearity would be accentuated if the rate of habitat loss itself was nonlinear over time (i.e. initially rapid and then slower). The slower rate would allow the population to more rapidly "catch up" to current habitat levels, which would appear as a threshold decline. As well, for relationships that are already nonlinear for other reasons (e.g. fragmentation or Allee effects at low habitat cover), time lags may instead cause a decrease in the apparent threshold level of habitat.

When habitat loss is rapid and ongoing or recent, time lagged responses make it more difficult to empirically assess habitat loss effects, since they initially mask the full ecological consequences (Schrott et al. 2005b, With et al. 2006). A population experiencing rapid habitat loss may appear to be relatively unaffected over a large range of habitat loss, compared to a population experiencing slower rates of loss. Yet, the former would go extinct sooner in time and the threshold would be more abrupt (Fig. 4 of Schrott et al. 2005b), thus reducing the potential for managers to restore population viability before it is too late.

2.4. Habitat loss

Habitat loss alone is likely to lead to nonlinear changes in some ecological responses. Conceivably, binomial population responses such as persistence or occurrence could remain at 100% over the initial range of habitat loss, particularly if the initial population size is large. However, as the amount of habitat moves closer to zero, persistence or occurrence probability must at some point also decline towards zero. Thus, a threshold relationship will be evident, with a steeper slope below than above the threshold. Community level responses such as species richness may also exhibit threshold declines in response to habitat loss alone. Consider a group of species, all of which are moderately abundant at 100% habitat cover (e.g. on average 5-20 individuals per landscape, depending on the species). Each species declines in exact proportion to (linearly with) habitat loss, and reaches an average abundance of zero for landscapes with no habitat remaining. Such linear responses imply that additional factors do not compound habitat loss at low habitat levels. For this community, species richness should decline little until a threshold of habitat loss is surpassed. This is because the "cloud" of scatter around each species' average abundance is unlikely to encompass zero until the average abundance (determined by habitat amount) becomes sufficiently low. Thus, as habitat amount decreases below some threshold, the average number of species that are absent from a given landscape should increase sharply. I confirmed this expectation by calculating "species richness" for a community of 15 artificially generated species' abundance data sets (Poisson distribution). Although each "species" declined linearly with habitat loss as described above, richness fell off sharply below a threshold level of habitat.

3. Evidence for critical thresholds

Evidence for the presence and value of critical thresholds comes from three types of studies: simulation models, and two empirical approaches that I call "micro-landscape" and "large-landscape". Simulations allow the experimenter to manipulate landscape and organism properties in the absence of environmental noise. They explore species or landscape characteristics associated with the occurrence of critical thresholds, and compare the relative effect of such characteristics on threshold values (Fahrig 2001). However, simulations do not capture the full range of environmental complexity present in real ecosystems, and thus cannot predict exact threshold values for real species (Lamberson et al. 1992).

"Micro-landscapes" studies are small manipulative experiments, which allow strong inference because non-treatment factors are held constant, and treatments / controls are applied randomly (McGarigal and Cushman 2002). However, such experiments may not reflect long-term responses to changes in real landscapes, because they tend to examine short-term responses in artificial landscapes.

"Large-landscape" studies of critical thresholds were mensurative experiments, measuring ecological parameters in real landscapes (McGarigal and Cushman 2002). They are subject to a greater amount of uncontrolled variation than micro-landscape studies. In addition, while many of the simulations and micro-landscape studies (Tables 2-1 and 2-2) focused on risk of extinction or details of movement patterns, these variables are more difficult to measure in large landscapes. Thus, most empirical large-landscape studies have used surrogate measures such as species occurrence, abundance, or diversity (Table 2-3), under the assumption that these reflect habitat quality and / or individual fitness. This assumption may not hold under some conditions (Van Horne 1983, Bock and Jones 2004). However, per capita and per land area recruitment was positively related to adult density in 72% and 85% of northern hemisphere studies (Bock and Jones 2004). As well, simulated population size (Fahrig 1998, Flather and Bevers 2002) and patch occupancy (Vos et al. 2001) were positively correlated with persistence, thus lending general support to the use of presence or abundance measures indicators of habitat quality.

Among the studies compiled for this review, there was a large amount of variation in terms of whether thresholds were found for the ecological response, and at what proportion of habitat (Tables 2-1, 2-2, and 2-3). Below, I outline the results from simulation, micro-landscape, and large landscapes studies, and examine some possible reasons for this variation.

3.1. Simulation studies of critical thresholds

Many simulation models have found critical threshold relationships between habitat loss and various ecological responses (Table 2-1), including: a) plant migration rates; b) population size; c) patch occupancy; d) population persistence probability; e) population demographic parameters; f) species extinction rates in communities; g) dispersal success; and h) individual movement parameters. The values of these thresholds range across nearly the entire continuum of habitat proportion, from about 1% to 99% (though most fall between 10-50%), and linear relationships also occur (Table 2-1). Some of this variation reflects different assumptions made about the simulated organism and landscape, the effects of which are discussed below.

3.1.1. Effects of simulated landscape characteristics on critical thresholds

In simulation models, habitat pattern influences the location of critical thresholds. For a given proportion of habitat, landscapes with fractal (clustered) patterns of habitat have fewer, bigger habitat patches with less edge than do random maps (With et al. 1997), and are thus less fragmented. For random maps the percolation threshold (see above) occurs at 59% habitat, but this threshold becomes smaller and more variable for fractal patterns (45-54% for a binary habitat / nonhabitat system, With and King 1999b; 29-50% for a 3 habitat system, With et al. 1997). Similarly, the thresholds for simulated ecological responses to habitat loss tend to decrease as the degree of habitat contagion increases (patch occupancy: Hill and Caswell 1999, With and King 1999b; population survival probability, Fahrig 2001; proportion of species pool persisting, McLellan et al. 1986; population growth rates: Schrott et al. 2005b; movement path complexity: With et al. 1999). For plant migration rates, the threshold *increased* as fragmentation decreased (Collingham and Huntley 2000). This is because faster migration requires that plant propagules spread quickly across the landscape to new, unoccupied habitat patches, not just to any suitable habitat such as within the parent patch. Smaller levels of fragmentation mean that although individual habitat patches are larger, they are also farther apart, and thus more difficult to reach (Collingham and Huntley 2000).

Matrix quality (as determined by mortality rates) may have an even larger effect on critical threshold values than habitat pattern. As the rate of mortality in the matrix decreases, the threshold location can be reduced by up to 58% habitat cover, compared with only 17% by reducing fragmentation (Fahrig 2001).

The rate of landscape change may also be important. For a given level of habitat, as patch turnover rates (Keymer et al. 2000, Wimberly 2006) or environmental variance (Lamberson et al. 1992) increase, the threshold level of habitat for long term patch occupancy or survival probability increases. This is because when patch turnover rates increase, the duration of local populations decreases. Past a critical turnover rate, the entire metapopulation cannot persist, even if the amount of habitat would otherwise be sufficient in a static landscape (Keymer et al. 2000). In contrast, as the rate of habitat *loss* increases, the apparent threshold level of habitat decreases, but occurs sooner in time (population growth rate: Schrott et al. 2005b).

3.1.2. Effects of species characteristics on critical thresholds

As the ability of an organism to move through and survive in nonhabitat increases, the critical threshold decreases or disappears. The percolation threshold for random landscapes is about 59% when movement follows the four-neighbour rule (Gustafson and Parker 1992, Andrén 1994, Bascompte and Solé 1996). However, the threshold decreases to 40% when movement can also occur between diagonally adjacent habitat cells (8-neighbour rule, Plotnick and Gardner 1993), and to 29% when even movement between habitat cells separated by the distance of one cell edge can occur (12-neighbour rule, With and King 1999b). Similarly, simulated "sand cybercrickets" following the four-neighbour rule exhibited sharp declines in movement-path complexity below 20-50% habitat, while movement parameters for a cybercricket following the 12-neighbour rule exhibited no threshold (With et al. 1999).

Critical threshold values are also influenced by dispersal characteristics, although this effect depends on whether dispersal ability is modeled as a purely species characteristic, or as an interactive effect of both species and landscape characteristics. For example, when colonization rates are assumed to reflect dispersal ability, then as species' dispersal distances (or number of territories searched) increase, critical thresholds either occur at lower proportions of habitat (proportion of species pool persisting: McLellan et al. 1986; patch occupancy: With and King 1999a, Lamberson et al. 1992, Carlson 2000) or are less precipitous (dispersal success: With and King 1999b). In contrast, if the risk of mortality is assumed to be higher in the matrix than in habitat, the critical threshold for population survival *increases* with increasing emigration rates (Fahrig 2001). Higgins et al. (2003) also found that the shape of the relationship between plant migration rates depended on a complex interaction between species dispersal and landscape characteristics. Such species-landscape interactions may be highly relevant in anthropogenically-modified systems, where organisms may encounter new sources of mortality or barriers to movement (e.g. roads, Trombulak and Frissel 2000, Bélisle and St. Clair 2001; urban development: Hitchings and Beebee 1997; habitat gaps: Desrochers and Hannon 1997, St. Clair et al. 1998), to which they may be poorly adapted.

Simulations have also demonstrated a strong negative relationship between reproductive rate and threshold value (patch occupancy: With and King 1999a, Keymer et al. 2000, Carlson 2000; persistence: Fahrig 2001, population size: Durell et al. 1997), suggesting that species with low reproductive rates are particularly sensitive to habitat loss / fragmentation. The importance of reproductive rate in determining critical threshold values may exceed that of dispersal, fragmentation, and matrix quality (Fahrig 2001).

Finally, threshold values for population growth rates increased with increasing sensitivity to patch area and habitat edge (Schrott et al. 2005b). These characteristics were intended to reflect empirically observed patterns for some bird species: area and edge sensitive simulants avoided settling in smaller patches, and had lower reproductive success in patches with a high edge:area ratio (Schrott et al. 2005b).

3.1.3. Evidence for causes of critical thresholds in simulations

Few studies were designed to investigate the causes of critical threshold relationships. However, several studies suggest that fragmentation effects become more important at low levels of habitat, which could potentially lead to threshold relationships with habitat loss. For example, at high levels of habitat, predicted population responses were the same regardless of the degree of fragmentation or spatial information; however, at low levels of habitat these population parameters declined more steeply for more fragmented or spatially explicit simulations, compared to less fragmented or spatially implicit simulations (McLellan et al. 1986, Bascompte and Solé 1996, Fahrig 1997, Hill and Caswell 1999, Collingham and Huntley 2000, Keymer et al. 2000, Flather and Bevers 2002, King and With 2002, Jager et al. 2006; see Table 2-1 for response types). Further, two simulation studies that found thresholds also tested for interactions between habitat loss and fragmentation effects; both were significant (Collingham and Huntley 2000, Flather and Bevers 2002). More direct evidence of a causational relationship is provided by Flather and Bevers (2002). Predicted population declines were nearly linear for the least fragmented landscapes, but became threshold-like when fragmentation levels were high (see Fig 4b of Flather and Bevers 2002).

The idea that Allee effects could compound habitat loss below a threshold level of habitat was supported by one study. Below a certain proportion of habitat, simulated patch occupancy declined more steeply (and extinction occurred sooner) when dispersing females were required to search for mates (Lamberson et al. 1992). This suggests that Allee effects have the potential to lead to threshold responses to habitat loss where linear relationships would otherwise occur. However, in this case patch occupancy declined in a threshold manner even in the absence of Allee effects (Lamberson et al. 1992), so direct evidence of this is lacking.

Most studies measured long-term, equilibrium responses to habitat proportion in static landscapes. Thus, time lags were not usually an issue, though as mentioned above time lags had the ability to decrease the threshold value (Schrott et al. 2005b). Many studies measured ecological response as a proportion or probability (e.g. proportion of species persisting or of females mated, birth/death rates, dispersal success, patch occupancy, persistence probability; Table 2-1). In these cases, it is possible that the presence of any thresholds was a response to habitat loss alone (see rationale in section 2.4.), with fragmentation or Allee effects influencing the threshold value in some cases.

3.2. Micro-landscape studies of critical thresholds

Do the critical thresholds predicted by simulation models appear in experimental micro-landscapes with real organisms? Recall that the percolation threshold for randomly arranged habitat is 59% under the four-neighbour rule. This scenario was replicated in an experiment involving a grid of randomly arranged agar "habitat" dots. The distances between these dots allowed the spread of a fungus only between neighbouring dots (Otten et al. 2004), akin to the four neighbour rule. The ability of the fungus to "percolate" from the center to the edge of the grid dropped strongly below 60% habitat (Otten et al. 2004), remarkably near the critical percolation threshold.

Other micro-landscape studies (Table 2-2) demonstrated either lower thresholds (20% for beetle movement in random habitat, Wiens et al. 1997; 20-40% for insect spatial aggregation in fractal arrangements, With et al. 2002), or linear responses (butterfly richness and frequency of patch visits, Summerville and Crist 2001, but note the high range of habitat: 20-100%). One micro-landscape study showed no effect at all of habitat loss or fragmentation on species richness or mean abundance of terrestrial invertebrates (Parker and Mac Nally 2002). This may be explained by the fact that both ecological responses reflected the combined (and possibly contrasting) responses of a variety of different species (Parker and Mac Nally 2002).

3.2.1. Evidence for causes of micro-landscape thresholds

As with most simulation studies, most micro-landscape studies were not designed to test for time lag or Allee effects on the occurrence or value of the threshold. In any case, these factors would have been irrelevant for several studies that found thresholds in individual movement parameters (Table 2-2); fragmentation effects are thus a more likely explanation for these studies. In one study the more mobile species tracked the distribution of habitat closely, with both habitat and species aggregation increasing more rapidly below about 20% habitat (i.e. larger and more variable distances between habitat patches or occupied patches, respectively, With et al. 2002). Thus, the species' threshold appeared to be related to a similar threshold for structural habitat configuration. In contrast, the less mobile species had a higher threshold (40%, With et al. 2002). This suggests that below this threshold, the ability of this species to locate and occupy empty habitat patches was compromised (i.e. landscapes were functionally fragmented).

3.3. Evidence from large-landscape studies

Andrén's (1994) meta-analysis of bird and mammal studies suggested a 10-30% critical habitat proportion threshold, below which the effects of habitat loss / fragmentation were greater than expected from habitat loss alone (but see Mönkkönen and Reunanen 1999 and Andrén 1999). Subsequent studies have varied in their support of Andrén 's (1994) proposed threshold. Linear and critical threshold relationships have been suggested for a variety of taxa, responses, habitat types, landscape types and spatial scales (Table 2-3). These large landscape studies are too variable and limited in number to clearly suggest whether the presence or value of thresholds depends on any of these factors. However, when thresholds were apparent, most occurred within Andrén's (1994) proposed 10-30% range (Table 2-3).

3.3.1. Evidence for causes of large-landscape thresholds

None of the large-landscape studies presented information on changes in growth rates with habitat loss, so it is uncertain whether Allee effects influenced the presence or value of thresholds in these cases. However, one patch level study (Groom 1998) suggests an interaction between habitat loss and fragmentation in producing an Allee-related threshold. Specifically, patches of a plant species experienced reproductive failure past a critical threshold distance from pollen donors. Because isolation distances reflect the amount of habitat loss around the focal patch (Fahrig 2003), this suggests that Allee effects occur below a threshold level of habitat in the landscape. Because the threshold occurred only for small patches (Groom 1998), this suggests that fragmentation interacted with habitat loss to produce the threshold.

The decline of the white-backed woodpecker (*Dendrocopos leucotos*) in Finland in response to several decades of habitat loss suggests a possible time lag related threshold. This species initially declined less than expected from the amount of habitat loss, and then much more rapidly below an apparent habitat threshold of about 10%, suggesting a time-lagged response for this long-lived species (Carlson 2000). The rate of habitat loss during the first 15 years immediately preceding the threshold was much more rapid (0.52% / year) than that in the subsequent 20 years (0.09% / year; calculated from Table 1 in Carlson 2000). As outlined previously, I speculate that this nonlinear change in the rate of habitat loss could have produced or accentuated the apparent threshold response to habitat loss.

None of the large landscape studies reviewed here compared the effects of habitat fragmentation at low versus high habitat cover. Two studies that found thresholds tested for interactions between habitat amount and fragmentation, which would be consistent with a stronger effect of fragmentation at low habitat cover (Fahrig 2003). Neither found significant interactions (Cushman and McGarigal 2003, Radford et al. 2005). However, comparisons within and among three amphibian studies indirectly suggest that greater fragmentation effects at low habitat cover may have played a role in the observed thresholds. First, two studies conducted in areas with urban or suburban matrices found threshold declines in occurrence, including two of the same species (Gibbs 1998, Homan et al. 2004). In contrast, a third study in an agricultural landscape found linear responses to habitat loss for these same two species (Guerry and Hunter 2002). Amphibians are vulnerable to traffic mortality (Fahrig et al. 1995, Carr and Fahrig 2001) and are more genetically isolated among ponds in urban than rural environments, suggesting that migration is inhibited (Hitchings and Beebee 1997). In other words, urban and suburban environments may enhance negative fragmentation effects for amphibians, leading to threshold declines that are otherwise absent in rural environments.

Second, Gibbs (1998) noted that among the species with threshold relationships (the two noted above plus a third), the threshold value increased with increasing dispersal tendency. This characteristic should increase sensitivity to fragmentation if mortality is greater in the matrix (Fahrig 2001). Indeed, Carr and Fahrig (2001) found that of two frog species, the more vagile one was more prone to traffic mortality. Gibbs (1998) further suggested that habitat specificity might mediate the influence of dispersal tendency on sensitivity to habitat loss and fragmentation: highly dispersive species may be more sensitive if habitat specificity is high, but a combination of high dispersal tendency and habitat flexibility may confer tolerance.

Finally, Homan et al. (2004) examined the occurrence of two amphibian species that migrated seasonally between breeding ponds and wintering forests. Thresholds in wintering habitat surrounding breeding ponds were apparent at scales of 1 and 28 ha (100 and 300m radii), but at the smaller or larger spatial extents the relationships appeared linear (see comments under "statistical considerations" below). Interestingly, the 300m extent corresponds to the distance from breeding ponds over which at least one of the species had the highest wintering densities (Regosin et al. 2005). The fact that a threshold occurred at this extent may have been related to an effect of fragmentation (e.g. movement inhibition or matrix mortality) during fall migration over this distance.

4. Utility of critical thresholds in conservation

There are several potential uses for critical threshold information, though some of these are subject to important practical and conceptual limitations. The idea of using critical thresholds in habitat proportion to make broad management decisions has been criticized because threshold values are expected to vary by species, landscape type, and spatial scale, and thus the results of one study do not necessarily apply to another situation (Huggett 2005, Lindenmayer et al. 2005, Lindenmayer and Luck 2005). This review supports this idea. However, such variation doesn't preclude the possibility that useful generalizations can be found. For example, simulations suggest that critical thresholds are closely related to life-history and landscape characteristics (see above). If sufficient empirical support existed, such trends could be used to predict: a) the presence and / or value of critical thresholds for different species, assemblages, and landscapes, b) the relative sensitivity of different species (see caveat below), c) the range of habitat proportions over which it may be most fruitful to look for (and potentially manage or account for) habitat fragmentation effects, Allee effects, or other factors, or d) the form of landscape management (e.g. reducing fragmentation, increasing matrix quality, or increasing the demographic potential) with the largest potential to decrease the threshold, and thus ameliorate the effects of landscape change. Such information could help to more efficiently target conservation efforts to the appropriate landscapes, species, and methods.

The presence of a critical threshold relationship does not necessarily indicate greater "sensitivity" of a population, compared to one exhibiting linear responses to habitat loss. Consider two species, one which declines gradually as habitat is lost from a landscape, then declines more rapidly below a critical threshold of 20% habitat cover, and disappears below 10% habitat; and another which declines linearly (but steeply) with habitat loss, disappearing below 40% habitat. The latter species exhibits no *critical* threshold in habitat cover (as defined above), but is arguably the more sensitive to habitat loss because it becomes extinct below 40% habitat (versus 10% for the former).

Critical thresholds are often viewed as a potential tool to set conservation targets for habitat retention or restoration (Huggett 2005). However, there are some important conceptual considerations, such as what the response variable is, what a critical threshold means, and what the management goal is. For example, a critical threshold for species richness represents the level of habitat loss by which several species have declined to zero, and thus the target level should be well above this threshold (Radford et al. 2005, Lindenmayer and Luck 2005). Indeed, Schmidt and Roland (2006) found that while a threshold for moth species diversity occurred near 20% forest, total moth abundance declined below a threshold of 40-50% forest. Further, community-level or average threshold values may underestimate the habitat requirements of the more sensitive species (Mönkkönen and Reunanen 1999). Even population-level thresholds may not be reliable targets for individual species. For example, just because habitat fragmentation may compound the effects of habitat loss on population size below 30%

habitat (thus producing a threshold), it does not follow that habitat loss alone has not already had a profound effect on population viability above this threshold (or conversely that the population is not viable below this threshold). This may be particularly true if time lags are operating.

If the management goal is population persistence, the most reliable target level of habitat is the threshold for population persistence itself, and then only if persistence probability is acceptably high above this threshold. However, persistence probability is difficult to measure empirically. Whether it is acceptable to use threshold values from substitute measures of persistence is debatable, though measures of fitness such as reproductive success (Gunn et al. 2000) may be better than prevalence. Regardless, even a fitness threshold should be interpreted cautiously, since persistence probability is determined by many different factors.

5. Statistical considerations

Assuming that the threshold for some ecological response is an acceptable criterion for setting a management target (given the particular management goal), there are still the practical problems of distinguishing threshold from linear relationships, and estimating threshold values. The majority of studies reviewed here did not use any formal statistical method to do so. Visual estimates of threshold presence and value from data plots are likely to be inconsistent among observers (personal observation) and possibly biased. Methods to estimate the best threshold value included piecewise regression (Radford et al. 2005, Lindenmayer et al. 2005, Homan et al. 2004), and change-point analysis (Homan et al. 2004). One study tried both methods (Homan et al. 2004). For a given species and spatial scale, the threshold value depended on the statistical technique used (Homan et al. 2004). Because the "true" threshold was unknown, it is uncertain which technique was more accurate.

Methods to distinguish linear from threshold / non-linear shapes included: a) comparing linear versus piecewise regression and other non-linear regressions models (based on the Akaike information criterion (AIC): Radford et al. 2005; unspecified criterion of "fit": Lindenmayer et al. 2005), b) a t-test comparing observed values versus predicted values under the assumption of linearity (Imbeau and Desrochers 2002), c) significance of the difference between the upper and lower slopes of piecewise regression models (Homan et al. 2004), and d) testing the significance of quadratic and cubic effects (Summerville and Crist 2001). Although Homan et al. (2004) suggested that a significant "change-point test" indicates a non-linear relationship, this is incorrect. It merely indicates a significant *change* (i.e. a non-null relationship). In fact, many of the relationships for which Homan et al. (2004) found a significant change-point appeared (visually) to be linear, and did not show a significant difference between the upper and lower piecewise slopes. The other methods are legitimate tests of "nonlinearity". Most are based on traditional significance testing, while the AIC method is a form of multi-model selection (see Johnson 1999 and Anderson et al. 2000 for an in depth criticism of former and promotion of the latter). One major advantage of multi-model selection is that it allows simultaneous comparison of a set of models that need not be nested (Johnson and Omland 2004). For example, one could compare the weight of evidence for a linear, change-point, piecewise, and polynomial relationship.

Even when statistical estimates are used, these are subject to uncertainty, as are all such estimates, and the variability inherent in most ecological data sets will increase this uncertainty. This may not be of great concern when the object is to find general trends between threshold presence or values and life-history traits, or to approximate the range of habitat proportions in which to look for fragmentation or Allee effects. However, if the object is to set a minimum target for conservation, then accuracy is more important, and underestimation of the threshold value could have profound consequences. Statistical issues related to estimation of threshold values for management targets are discussed in more detail in Chapter 3.

6. Summary and Conclusions

Threshold responses to habitat loss were common among the studies reviewed here, although their exact value depended on many factors. For example, simulation studies suggested that threshold values tend to increase with various landscape characteristics: a) increasing fragmentation of habitat; b) decreasing matrix quality; c) increasing environmental variance or patch turnover rates; and d) decreasing rates of habitat loss. Threshold values may also depend on species characteristics, increasing with: a) decreasing ability to enter the matrix; b) decreasing dispersal distance (assuming no matrix mortality); c) increasing emigration rate (assuming matrix mortality); d) decreasing reproductive rate; and e) increasing sensitivity to fragmentation. These trends have yet to be rigorously tested empirically.

While evidence was limited, some of these same patterns were supported in empirical studies. When present, most empirical thresholds fell near Andrén's (1994) proposed range of 10-30% habitat cover. Higher critical habitat threshold values have occasionally been reported, notably for fungal spread in a percolation-like laboratory model with random habitat (60%, Otten et al. 2004), for total moth abundance (40-50%, Schmidt and Roland 2006), and for amphibian occurrence with urban / suburban disturbances (up to 55 or 60%, Gibbs 1998, Homan et al. 2004). For the fungus, the high threshold probably reflects the random habitat arrangement and the "four neighbour rule" manner of fungal spread (reflecting a percolation model). For moths and amphibians, the high thresholds may reflect a sensitivity to fragmentation after only moderate habitat loss. Linear relationships occurred somewhat more frequently in empirical than in modeling studies, perhaps reflecting greater behavioural flexibility of real organisms (e.g. ability to move through non-habitat) than is sometimes parameterized in simulation models.

The study of critical thresholds in landscape ecology is still new, and many questions remain for future research. How common are critical thresholds, and what are their causes? Many simulations have suggested that increasing fragmentation effects at low levels of habitat can produce threshold relationships with habitat proportion. Empirical studies rarely test for this, or consider the possibility of time lags or Allee effects. Which species are likely to exhibit critical thresholds, and in what types of landscapes? At what spatial scales should we expect to find critical thresholds, and can these be predicted from species characteristics (e.g. dispersal distances)? There is also a need for the use of statistical methods to detect and estimate thresholds, both to increase objectivity within individual studies, and to facilitate comparison among studies. This is essential if the questions above are to be addressed. Answers to these questions would help land managers to more efficiently direct resources to where they would have the greatest impact.

Table 2-1. Simulation studies of the shape of the relationship between habitat proportion and ecological responses

Source	Response variable	Taxon	Landscape characteristics		Relationship(s) found		
			Habitat pattern	Range of habitat cover (%)	Threshold (%)? A	Linear?	Depended on species (S) or landscape (L) characteristics?
McLellan et al. 1986	community (proportion of species pool persisting)	generic	clustered	0-80	10-40	no	S, L
Solé et al. 2004	community (species richness)	generic	random	10-80	10-40	no	
Schrott et al. 2005b	demographic (growth rate)	birds	clustered	0-100	5-90	yes	L
Jager et al. 2006	demographic (proportion females mated)	mammal	clustered	50-100	n/a	yes	
Jager et al. 2006	demographic (births, death rate)	mammal	clustered	50-100	80-90	yes	L
King and With 2002	movement (dispersal success)	generic	random, clustered	1-90	<5-40	yes	S, L
With and King 1999b	movement (dispersal success)	generic	clustered	1-99	10	no	
Ruckleshaus et al. 1997	movement (dispersal success)	generic	clustered	2-24	8	no	
Higgins et al. 2003	movement (migration rate)	plant	clustered	1-90	~1-7	yes	S, L
Collingham and Huntley 2000	movement (migration rate)	plant	clustered	1-90	10-25	no	L
With et al. 1999	movement (individual patterns)	insect	clustered	0-80	20 | 50	yes	S, L
Keymer et al. 2000	prevalence (patch occupancy)	generic	random	10-90	25-50	no	S, L
Lamberson et al. 1992	prevalence (patch occupancy)	bird	random	0-100	20-30	no	S, L
Carlson 2000	prevalence (patch occupancy)	bird	random	0-100	25-40	no	S
Bascompte and Solé 1996	prevalence (patch occupancy)	generic	random	0-100	25-95	yes	S, L
Wimberly 2006	prevalence (patch occupancy)	generic	random, clustered	10-90	20-70	no	S, L
Hill and Caswell 1999	prevalence (patch occupancy)	generic	clustered	10-100	10	yes	
With and King 1999a	prevalence (patch occupancy)	generic	clustered	20-80	5-85	yes	S, L
Durell et al. 1997	prevalence (population size)	bird	n/a	5-100	10-50	no	S
Jager et al. 2006	prevalence (population size)	mammal	clustered	50-100	n/a	yes	
Flather and Bevers 2002	prevalence (population size)	bird	clustered	10-90	30-50	no	L
Flather and Bevers 2002	persistence (probability)	bird	clustered	10-90	30-50	no	L
Fahrig 1997	persistence (probability)	generic	clustered	0-100	20	no	
Jager et al. 2006	persistence (probability)	mammal	clustered	50-100	n/a	yes	

A. Threshold ranges separated by a | indicate that habitat proportion was categorical, so that a more precise threshold estimate was not possible

Table 2-2. Micro-landscape studies of the shape of the relationship between habitat proportion and ecological responses

Source	Response variable	Taxon	Landscape characteristics			Relationship(s) found		
			Habitat pattern	Range of habitat cover (%)	Landscape size	Threshold (%)?[A]	Linear?	Depended on species (S) or landscape (L) characteristics?
Summerville and Crist 2001	community (species richness)	insects	random	20-100	15x15m	no	yes	
Parker and Mac Nally 2002	community (species richness)	insects	uniform	10-100	15x15m	no	not sig.	
With et al. 2002	distribution (lacunarity)	insect	clustered	10-80	16x16m	10|20, 20|40	yes	S, L
Summerville and Crist 2001	movement (# patch visits)	insects	random	20-100	15x15m	no	yes	
With et al. 1999	movement (patterns)	insect	clustered	0-80	5x5m	50|80	yes	
Wiens et al. 1997	movement (patterns)	insect	random	0-80	5x5m	0|20	yes	
Otten et al. 2004	movement (percolation)	fungus	random	40-100	154cm^2	60	no	

A. Threshold ranges separated by a | indicate that habitat proportion was categorical, so that a more precise threshold estimate was not possible

Table 2-3. Large-landscape studies of the shape of the relationship between habitat proportion and ecological responses

			Landscape characteristics			Relationship(s) found		
Source	Response variable	Taxon	Disturbance type	Range of habitat cover (%)	Landscape size (ha)	Threshold (%)? [A]	Linear?	Depended on species (S) or landscape (L) characteristics?
Cushman and McGarigal 2003	community (species evenness)	birds	forestry	0-100	250-300	no	yes	
Cushman and McGarigal 2003	community (species richness)	birds	forestry	0-100	250-300	0|20[B]	no	
Lindenmayer et al. 2005	community (species richness)	birds, lizards	forestry	0-100	314, 1256	no	yes	
Radford et al. 2005	community (species richness)	birds	agric. > forestry	2-60	10,000	10	no	
Schmidt and Roland 2006	community (species richness)	insects	agriculture	5-95	12.6	20	no	
Schmidt and Roland 2006	community (total abundance)	insects	agriculture	20-95	50-113	40-50	no	S
Carlson 2000	prevalence (abundance)	bird	various	8-18	Finland	10	no	
Thies and Tscharntke 1999	prevalence (parasitism rate)	insects	agriculture	3-65	177	20	yes	S
Imbeau and Desrochers 2002	prevalence (presence)	bird	forestry	8-100	28	no	yes	
Lindenmayer et al. 2005	prevalence (presence)	birds, lizards	forestry	0100	314, 1256	no	yes	
Bergman et al. 2004	prevalence (presence)	insects	agriculture	0-30	7850	5-15	no	S
Radford and Bennett 2004	prevalence (presence)	bird	agriculture	0-40	10,000	10-20	no	L
Guerry and Hunter 2002	prevalence (presence)	amphibians	agriculture	10-98	314	no	yes	
Kerkhoff et al. 2000	prevalence (presence)	mammal	agric., urban	3-70	90,000	no	yes	
Homan et al. 2004	prevalence (presence)	amphibians	suburban, agric.	0-100	0.3-314	10-50[C], 34-55[D]	yes	S, L
Gibbs 1998	prevalence (presence)	amphibians	urban	8-98	180?	50-60	yes	S
Reunanen et al. 2004	prevalence (presence)	mammal	forestry	0-90	100	40	no	
Andrén 1994	consistency of results with random sample hypothesis[E]	birds, mammals	various	5-70	various	10|30	no	

A. Threshold ranges separated by a | indicate that habitat proportion was categorical, so that a more precise threshold estimate was not possible

B. An observed threshold decrease in richness above 80-100% late-seral forest corresponded to an abrupt loss of several early-seral species below 0-20% early-seral habitat (Cushman and McGarigal 2003).

C. According to piecewise regression (for each species / scale, threshold value with largest test statistics only)

D. According to change-point analysis

E. Meta-analysis

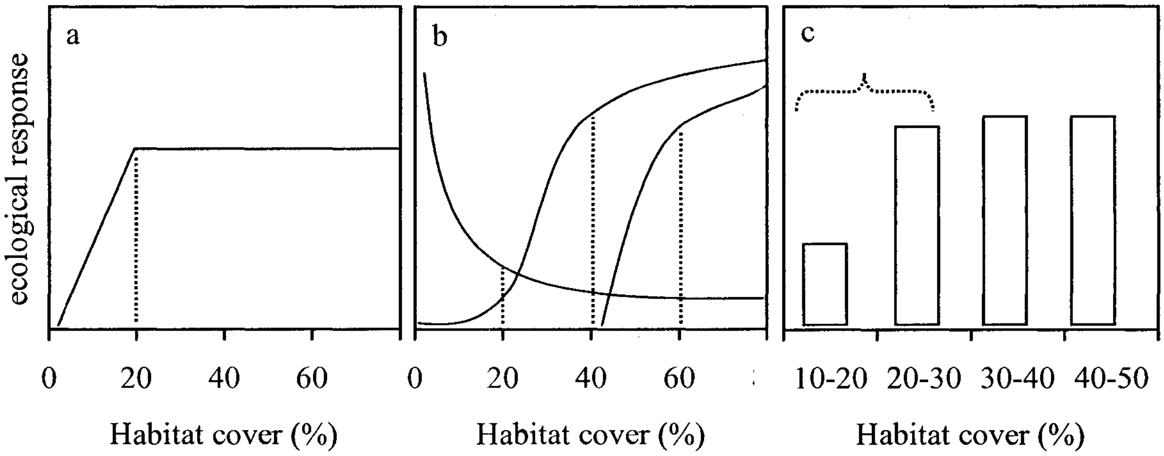

Fig. 2-1. Various types of critical threshold relationships, and estimation of critical threshold value: a) sharp threshold; b) smooth thresholds; c) categorical threshold. Dashed line or bracket indicates estimated threshold value or range, respectively.

References

Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M. A. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters* 9: 968-980.

Amarasekare, P. 1998. Allee effects in metapopulation dynamics. *American Naturalist* 152: 298-302.

Anderson, D. R., Burnham, K. P. & Thompson, W. L. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. *Journal of Wildlife Management* 64: 912-923.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.

Andrén, H. 1999. Habitat fragmentation, the random sample hypothesis and critical thresholds. *Oikos* 84: 306-309.

Bascompte, J. & Solé, R. V. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology* 65: 465-473.

Bélisle, M. & St. Clair, C. C. 2001. Cumulative effects of barriers on the movements of forest birds. *Conservation Ecology* 5: 9.

Bergman, K.-O., Askling, J., Ekberg, O., Ignell, H., Wahlman, H. & Milberg, P. 2004. Landscape effects on butterfly assemblages in an agricultural region. *Ecography* 27: 619-628.

Bock, C. E. & Jones, Z. F. 2004. Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment* 2: 403-410.

Burton, N. H. K., Rehfisch, M. M., Clark, N. A. & Dodd, S. G. 2006. Impacts of sudden winter habitat loss on the body condition and survival of redshank *Tringa totanus*. *Journal of Applied Ecology* 43: 464-473.

Bélisle, M., Desrochers, A. & Fortin, M.-J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82: 1893-1904.

Carlson, A. 2000. The effect of habitat loss on a deciduous forest specialist species: the white-backed woodpecker (*Dendrocopos leucotos*). *Forest Ecology and Management* 131: 215-221.

Carr, L. W. & Fahrig, L. 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15: 1071-1078.

Chust, G., Pretus, J. Ll., Ducrot, D. & Ventura, D. 2004. Scale dependency of insect assemblages in response to landscape pattern. *Landscape Ecology* 19: 41-57 .

Collingham, Y. C. & Huntley, B. 2000. Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications* 10: 131-144.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. 1999. Inverse density dependence and the Allee effect . *Trends in Ecology & Evolution* 14: 405-410.

Cowlishaw, G. 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. *Conservation Biology* 13: 1183-1193.

Cushman, S. A. & McGarigal, K. 2003. Landscape level patterns of avian diversity in the Oregon Coast Range. *Ecological Monographs* 73: 259-281.

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128: 231-240.

Desrochers, A. & Hannon, S. J. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11: 1204-1210.

Dolby, A. S. & Grubb, T. C. Jr. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. *Condor* 408-412.

Donovan, T. M., Jones, P. W., Annand, E. M. & Thompson, F. R. I. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78: 2064-2075.

Durell, S. E. A. l. V. d., Goss-Custard, J. D. & Clarke, R. T. 1997. Differential response of migratory subpopulations to winter habitat loss. *Journal of Applied Ecology* 134: 155-1164.

Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100: 65-74.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603-610.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modeling* 105: 273-292.

Fahrig, L., Pedlar, J. H., Pope, S. E., Taylor, P. D. & Wegner, J. F. 1995. Effect of road traffic on amphibian density. *Biological Conservation* 73: 177-182.

Flather, C. H. & Bevers, M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159: 40-56.

Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* 13: 263-268.

Greene, C. M. 2003. Habitat selection reduces extinction of populations subject to Allee effects. *Theoretical Population Biology* 64: 1-10.

Groom, M. 1998. Allee effects limit population viability of an annual plant. *The American Naturalist* 151: 487-496.

Gu, W., Heikkila, R. & Hanski, I. 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. *Landscape Ecology* 17: 699-710.

Guerry, A. D. & Hunter, M. L. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology* 16: 745-754.

Gunn, J. S., Desrochers, A., Villard, M.-A., Bourque, J. & Ibarzabal, J. 2000. Playbacks of mobbing calls of black-capped chickadees as a method to estimate reproductive activity of forest birds. *Journal of Field Ornithology* 71: 472-483.

Gustafson, E. J. & Parker, G. R. 1992. Relationship between landcover proportion and indices of landscape spatial pattern. *Landscape Ecology* 7: 101-110.

Hanski, I. & Ovaskainen, O. 2002. Extinction debt at extinction threshold. *Conservation Biology* 16: 666-673.

Higgins, S. I., Lavorel, S. & Revilla, E. 2003. Estimating plant migration rates under habitat loss and fragmentation. *Oikos* 101: 354-366.

Hill, M. F. & Caswell, H. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecology Letters* 2: 121-127.

Hitchings, S. P. & Beebee, T. J. C. 1997. Genetic substructuring as a result of barriers to gene flow in urban *Rana temporaria* (common frog) populations: implications for biodiversity conservation. *Heredity* 79: 117-127.

Homan, R. N., Windmiller, B. S. & Reed, J. M. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians . *Ecological Applications* 14: 1547-1553.

Huggett, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation* 124: 301-310.

Imbeau, L. & Desrochers, A. 2002. Area sensitivity and edge avoidance: the case of the three-toed woodpecker (*Picoides tridactylus*) in a managed forest. *Forest Ecology and Management* 164: 249-256.

Jager, H. I., Carr, E. A. & Efroymson, R. A. 2006. Simulated effects of habitat loss and fragmentation on a solitary mustelid predator. *Ecological Modelling* 191: 416-430.

Johnson, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63: 763-772.

Johnson, J. B. & Omland, K. S. 2004. Model selection in ecology and evolution . *Trends in Ecology and Evolution* 101-108.

Kerkhoff, A. J., Milne, B. T. & Maehr, D. S. 2000. Toward a panther-centered view of the forests of South Florida. *Conservation Ecology* 4.

Keymer, J. E., Marquet, P. A., Velasco-Hernandez, J. X. & Levin, S. A. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *American Naturalist* 478-494.

King, A. W. & With, K. A. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147: 23-39.

Lamberson, R. H., McKelvey, R., Noon, B. R. & Voss, C. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. *Conservation Biology* 6: 505-512.

Lindenmayer, D. B., Fischer, J. & Cunningham, R. B. 2005. Native vegetation cover thresholds associated with species responses. *Biological Conservation* 124: 311-316.

Lindenmayer, D. B. & Luck, G. 2005. Synthesis: Thresholds in conservation and management. *Biological Conservation* 124: 351-35.

McGarigal, K. & Cushman, S. A. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* 12: 335-345.

McGarigal, K. & McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* 65: 236-260.

McLellan, C. H., Dobson, A. P., Wilcove, D. S. & Lynch, J. F. 1986. Effects of forest fragmentation on new and old world bird communities: empirical observations and theoretical implications. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates (pp. 305-313). Madison, Wisconsin: University of Wisconsin Press.

Mönkkönen, M. & Reunanen, P. 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84: 302-306.

Otten, W., Bailey, D. J. & Gilligan, C. A. 2004. Empirical evidence of spatial thresholds to control invasion of fungal parasites and saprotrophs. *New Phytologist* 163: 125-132.

Parker, M. & Mac Nally, R. 2002. Habitat loss and the habitat fragmentation threshold: an experimental evaluation of impacts on richness and total abundances using grassland invertebrates. *Biological Conservation* 105: 217-229.

Plotnick, R. E. & Gardner, R. H. 1993. Lattices and landscapes. Predicting spatial effects in ecological systems (pp. 129-157).

Radford, J. Q. & Bennett, A. F. 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. *Biological Conservation* 117: 375-391.

Radford, J. Q., Bennett, A. F. & Cheers, G. J. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124: 317-337.

Reunanen, P., Mönkkönen, M., Nikula, A. & Nivala, V. 2004. Assessing landscape thresholds for the Siberian flying squirrel. *Ecological Bulletins* 51: 277-286.

Ruckelshaus, M., Hartway, C. & Kareiva, P. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* 11: 1298-1306.

Schrott, G. R., With, K. A. & King, A. W. 2005a. Demographic limitations of the ability of habitat restoration to rescue declining populations. *Conservation Biology* 19: 1181-1193.

Schrott, G. R., With, K. A. & King, A. W. 2005b. On the importance of landscape history for assessing extinction risk. *Ecological Applications* 15: 493-506.

Schmidt, B. D. & Roland, J. 2006. Moth diversity in a fragmented habitat: importance of functional groups and landscape scale in the boreal forest. *Ecology and Population Biology* 99: 1110-1120.

Solé, R., Alonso, D. & Saldana, J. 2004. Habitat fragmentation and biodiversity collapse in neutral communities. *Ecological Complexity* 1: 65-75.

St. Clair, C. C., Belisle, M., Desrochers, A. & Hannon, S. 1998. Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology[online]* 2: 13.

Summerville, K. S. & Crist, T. O. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* 82: 1360-1370.

Thies, C. & Tscharntke, T. 1999. Landscape structure and biological control in agroecosystems. *Science* 285: 893-895.

Tilman, D., May, R., Lehman, C. & Nowak, M. 1994. Habitat destruction and the extinction debt. *Nature* 371: 65-66.

Trombulak, S. C. & Frissel, C. A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18-30.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.

Vos, C. C., Verboom, J., Opdam, P. F. M. & Ter Braak, C. J. F. 2001. Toward Ecologically Scaled Landscape Indices. *American Naturalist* 157: 24-41.

Wiens, J. A., Schooley, R. L. & Weeks, R. D. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78: 257-264.

Wimberly, M. C. 2006. Species dynamics in disturbed landscapes: when does a shifting habitat mosaic enhance connectivity? *Landscape Ecology* 21: 35-46.

With, K. A. & King, A. W. 1999a. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314-326.

With, K. A. & King, A. W. 1999b. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* 14: 73-82.

With, K. A., Cadaret, S. J. & Davis, C. 1999. Movement responses to patch structure in experimental fractal landscapes. *Ecology* 80: 1340-1353.

With, K. A., Gardner, R. H. & Turner, M. G. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78: 151-169.

With, K. A., Pavuk, D. M., Worchuck, J. L., Oates, R. K. & Fisher, J. L. 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications* 12: 52-65.

With, K. A., Schrott, G. R. & King, A. W. 2006. The implications of metalandscape connectivity for population viability in migratory songbirds. *Landscape Ecology* 21: 157-167.

Chapter 3: A comparison of statistical methods for identifying ecological thresholds

1. Introduction

Habitat loss is becoming a major conservation concern, and the concept of critical thresholds in ecology is receiving increased attention. A critical threshold is an abrupt change that occurs in an ecological response, at a critical proportion of habitat in the landscape (With and King 1999). A major challenge is to determine the best methods to identify the proportion of habitat representing the critical threshold, and to distinguish critical threshold relationships from other nonlinear and linear relationships.

A meta-analysis of bird and mammal studies suggested there was a critical threshold level of habitat cover between 10-30% for species richness and population size (Andrén 1994). Empirical work has found both linear (e.g. Imbeau and Desrochers 2002, Guerry and Hunter 2002, Thies and Tscharntke 1999) and threshold relationships (e.g. Gibbs 1998, Radford and Bennett 2004, Bergman et al. 2004, Schmidt and Roland 2006) for various bird, amphibian, and insect taxa. However, formal statistical analyses have rarely been used either to identify the threshold value, or to distinguish a linear from a critical threshold relationship or other shapes. Determining the presence and value of a critical threshold based on visual examination of data is problematic, since different observers may have very different opinions. Rigorous statistical methods to identify threshold presence and value would greatly facilitate comparison among studies. This would allow ecologists to better address important issues, such as whether there is a common critical threshold value for all species, or whether critical thresholds can be predicted based on characteristics of the landscape (e.g. agricultural versus forestry) or species (e.g. dispersal traits).

Few statistical methods are suitable for the detection of environmental thresholds (Qian et al. 2003, Guénette and Villard 2005). However, both piecewise regression (Toms and Lesperance 2003) and a version of change-point analysis based on deviance reduction (Qian et al. 2003) have recently been recommended. While both methods assume there is a discrete value of the independent variable at which there is a sudden change in the response, the assumed relationship shapes are quite different. Piecewise models assume a "continuous threshold" (Fig. 3-1a). The predicted response forms two lines with (potentially) different slopes that join at the threshold value of the independent variable (Toms and Lesperance 2003). For example, forest-dependent species might be expected to decline continuously with forest loss, and perhaps more quickly below a threshold level of forest if some other factor (such as fragmentation) becomes detrimental only below this threshold (Andrén 1994, Radford and Bennett 2004). In contrast, change-point models assume a "discontinuous threshold" (Fig. 3-1b); the response variable has a different mean and/or variance below versus above the threshold, but is homogenous within each group (King and Richardson 2003). For example, if different communities exhibit tolerance within relatively non-overlapping ranges of an environmental gradient, a discontinuous threshold in community-level responses might be expected (e.g. community dissimilarity versus phosphorus concentration, Fig. 1 in Qian et al. 2003). Alternatively, a species that requires both treed and open habitats may prefer (be more abundant over) a certain range of forest proportion, but exhibit tolerance to changes within each range. Another difference between piecewise and change-point models is that the former requires more parameters to be estimated, which will become more difficult as sample size decreases and/or variance increases.

Receiver operating characteristic (ROC) analysis has also been suggested for detecting ecological threshold values (Guénette and Villard 2005). For a fitted model (e.g. logistic regression), a ROC analysis finds the predicted value of the dependent that best classifies the dependent as present (to one side of the threshold) or absent (to the other side). This cut-off point can then be translated into the corresponding "threshold" value of the independent, which may be useful for establishing certain decision thresholds (Guénette and Villard 2005). However, ROC analysis is restricted to binary data. Further, a ROC analysis always finds a threshold value, but the predictive model on which the threshold is based may be any shape, including linear. Hence, ROC analysis does not constitute a "threshold model" that can be compared to other linear and nonlinear models.

Recently, a few studies have applied piecewise regression (Radford et al. 2005, Lindenmayer et al. 2005), change-point analysis (Deluca et al. 2004), or both methods (Homan et al. 2004 used a non-parametric version of change-point) to identify the location of critical thresholds in landscape level habitat loss or land use, for various ecological responses. Homan et al. (2004) found quite different threshold estimates depending on the estimator used. No formal comparison has been done of the performance of piecewise versus change-point methods, in terms of accurately estimating a threshold value. While one method might be "better" than the other, this may depend on the characteristics of the data. The first objective of my study was to determine whether change-point or piecewise threshold estimates were closer to the "true" threshold for artificially generated count data intended to reflect variation in real data (continuous or discontinuous threshold, threshold value, sample size, distribution).

Change-point and piecewise models assume the presence of a threshold, but are not evidence that the true relationship has a threshold. There are several statistical methods available for choosing one model from among a set (e.g. linear versus threshold etc.). Multi-model selection methods, such as Akaike information criterion (AIC and a version corrected for small samples, AICc) and Bayesian information criterion (BIC), are gaining popularity over traditional significance tests which generally require that the models under consideration be nested. For example, likelihood ratio tests can select among a piecewise, linear, and null models (because each simpler model is a subset of the more complex model(s)). Similarly, a deviance reduction test (Qian et al. 2003) indicates whether a change-point model results in a significantly smaller deviance than a null model, but cannot compare a change-point to a linear model (because one is not a subset of the other). In contrast, AIC, AICc and BIC do not require models to be nested, and provide a measure of *relative* support for each model (versus the "significant or not" approach of significance tests, Burnham and Anderson 2004).

AIC, AICc and BIC are widely used in ecology (Johnson and Omland 2004). Burnham and Anderson (2004) recommend routine use of AICc over AIC, since it converges with AIC as sample size increases. Both AICc and BIC rank a set of models according to a measure of model fit, plus a penalty term for each parameter. However, AICc tend to select more complex models than does BIC, and BIC penalizes more strongly as sample size increases (Zucchini 2000). These differences can lead to markedly different conclusions about the shape of a relationship. A linear and a continuous threshold model, for example, differ by only two parameters (see below). Further, the number of parameters that can be reliably estimated will depend in part on sample size and the variability of the data. The second objective of my study, therefore, was to compare the ability of BIC and AICc to select the "correct" model shape for artificially generated data sets. More specifically, I determined whether the relative performance of AICc versus BIC depended on characteristics of the data (shape, sample size, and error distribution).

2. Methods

2.1. Artificial data generation

Artificial data were generated to simulate several possible relationships between the number of an organism ("y") and the proportion of habitat in a landscape ("x"). X ranged from 0.01 to 1, with half of the observations falling at or below 0.3. This was intended to represent a scenario in which sampling was more intensive over the range of habitat proportions in which critical thresholds are expected to occur (Andrén 1994). Two sets of x were generated, representing sample sizes of 50 and 250.

Thirteen different models were created to reflect hypothetical relationships between y and x . These varied by shape (null, linear, fractional polynomial, discontinuous threshold and continuous threshold), threshold value (0.1 or 0.3), and "strength" (weak or strong; Table 3-1, Fig. 3-1a-d). The meaning of "strength" depended on shape: a) linear: shallow versus steep slope, b) continuous threshold: small or large difference in slope below/above the threshold , c) fractional polynomial: gradual or more sudden curve, or d) discontinuous threshold: small or large difference in mean value below/above the threshold. This was intended to reflect variation in real data, but since its meaning was not consistent, "shape" was not used in formal statistical analyses. For each of the 13 generating models and two sample sizes, data were generated according to two distributions (Poisson, or negative binomial with a dispersion parameter near 3). This resulted in 13x2x2=52 "data types", for which 50 replicate "data sets" were generated each (52x50=2600 data sets in total).

2.2. Model types and modeling approach

Six types of models (null, linear, degree-1 and degree-2 fractional polynomials, piecewise, and change-point) were fit to each of the 2600 data sets. All model estimates and statistics were obtained using weighted least squares regression (see explanation in section 2.3) in version 9 of Stata (StataCorp 2005).

2.2.1 Null, linear, and fractional polynomial models

Null models fit the mean value of y and do not vary with x ($y = \hat{y}$, Fig. 3-1c). Linear models fit the best straight line with some slope ($y = B0 + B1*x$, Fig. 3-1c).

Degree-1 fractional polynomial models are the best-fitting regression of y against the best log or power transformation of x ($y = B0 + B1*\ln(x)$ or $y = B0 + B1*x^{(p)}$; p = -2, -1, -0.5, 0.5, 1, 2, or 3). Degree-2 fractional polynomial models (Fig. 3-1d) are similar, but y is regressed on two log or power transformations of x, and the range of possible curves is more extensive.

2.2.2. Piecewise models

Piecewise regression models (Toms and Lesperance 2003) fit one slope for values of x at/below some threshold value, and another (potentially different) slope above the threshold. If each segment is linear and the two segments join sharply at the threshold ("continuous threshold"; Fig. 3-1a), the piecewise equation is expressed as

$$
\begin{array}{ll}
y_i = B0 + B1*x_i & \text{if } x_i <= T_{pw} \\
y_i = B0 + B1*x_i + B2*(x_i - T) & \text{if } x_i > T_{pw}
\end{array}
$$

where i represents the observation number, y is the dependent, x is the independent, B0 is the y-intercept, B1 is the first slope, B2 is the change in slope between the first and second segments, and T_{pw} is the piecewise threshold - the value of the independent at which the two segments join. When the threshold is known, model estimates and statistics can be obtained easily from most statistical software packages simply by regressing y against x and a threshold term (E. Bayne, personal communication). The threshold term is calculated as

$$
\begin{array}{ll}
tterm_{pw} = x_i - T_{pw} & \text{if } x_i \geq T_{pw} \\
tterm_{pw} = 0 & \text{if } x_i < T_{pw}
\end{array}
$$

where $tterm_{pw}$ is the piecewise threshold term, and x_i and T are as above. The regression coefficient for $tterm_{pw}$ is interpreted as the change in slope between the two segments (i.e. equivalent to B2 above). When T is unknown, two approaches can be used to estimate it. One involves using a model estimation program that incorporates the piecewise equation and requires the user to provide initial starting "guesses" for each coefficient (Toms and Lesperance 2003 outline how to find good initial values). While this method can provide very precise estimates of the threshold value (i.e. down to several decimal places), it is sensitive to the starting guess provided (Toms and Lesperance 2003). As well, such programs are not available in many commonly used statistical packages, and must be written by the user. A somewhat coarser approach requiring less expertise is to try a range of threshold values and choose the best fitting model (Radford et al. 2005, Schmidt and Roland 2006).

I opted for the latter approach, and used an existing least squares regression function to estimate a series of piecewise models (y versus x and $tterm_{pw}$) for each of the 2600 data sets, trying threshold values at intervals of 0.01 (i.e. 1% habitat cover). Threshold values resulting in fewer than 3 observations either at/below or above the threshold were not considered. The model chosen was that with the largest log-likelihood. Given the large number of data sets, I wrote a program to find the piecewise threshold values (Appendix 3-1), and another to record the threshold values and other relevant statistics for the chosen model.

2.2.3. Change-point models

Change-point analysis finds the threshold value of x ("change-point") that divides y into the two groups with the smallest within-group deviances (analogous to the first division of a tree model, Qian et al. 2003). For this method, data are ordered by x and divided into two groups at all possible change-points, which are limited to observed values of x. For each potential change-point, the deviance of each of the two groups is calculated, and added together. The final change-point chosen is that which results in the smallest summed value of the two group deviances. Deviance is calculated as

$$D^2 = \Sigma_i (d_i^2)$$

where d_i^2 is the squared deviance residual for observation i. The formulae for the squared deviance residuals for Poisson and negative binomial data can be found in Hardin and Hilbe (2005).

For each of the 2600 data sets, the change-point threshold was calculated using Poisson or negative binomial deviance, as appropriate. As with the piecewise models, change-point threshold values resulting in fewer than three observations at/below or above the threshold were not considered. The change-point model and its associated statistics, were estimated by running a weighted least-squares regression of y against the appropriate threshold term:

$$\begin{array}{ll} \text{tterm}_{cp} = 1 & \text{if } x > T_{cp} \\ \text{tterm}_{cp} = 0 & \text{if } x <= T_{cp} \end{array}$$

where T_{cp} was the change-point threshold value estimated as above. The coefficient for tterm_{cp} is interpreted as the change in the predicted value of y when the threshold is surpassed. Due to the large number of data sets, I wrote programs to calculate the change-point threshold (Appendices 3-2a and b) and to record the estimated threshold and other statistics for each data set.

2.2.4. Rationale for weighted least-squares regression approach

Although the data were drawn from either Poisson or negative binomial distributions, I did not use Poisson or negative binomial regression. As mentioned above, all model statistics were instead obtained from weighted least squares regression, for the following reasons. When there is a particular interest in the shape of a relationship, then the scale of analysis must be considered carefully, because the shape will depend on the scale (Lindenmayer et al. 2005). Poisson and negative binomial regression are performed on natural log-transformed values of y; thus if x and y are linearly related, x and ln(y) will have a curved relationship. I was interested in addressing such questions as, for example, whether or not bird populations decline in proportion to (i.e. linearly with) forest cover. Hence, the relevant scale was the natural scale, and the shape of the relationship between x and ln(y) would be difficult to interpret.

Least squares regression is based on untransformed values of y, but the data are assumed to be normally distributed and homoscedastic. Data drawn from Poisson or negative binomial distributions tend to be right skewed and heteroscedastic. Fortunately, linear regression is robust to all but "severe" violations (Zar 1999), and the 2600 data sets appeared to be only slightly to moderately skewed. In contrast, heteroscedasticity was quite pronounced for some data types (particularly for strong linear shapes or negative binomial distributions). This was dealt with by using weights that increased as variance decreased (Toms and Lesperance 2003), for all non-null data sets. Specifically, I used smoothed values of 1/(variance + 0.5), where variance was calculated for groups of five consecutive observations, ordered by x (E. Bayne, personal communication).

2.3. Analyses comparing piecewise versus change-point threshold value estimates

The ability of change-point versus piecewise methods to accurately estimate the true threshold value was compared for the 1800 threshold data sets only. A measure of their relative accuracy was calculated as: the absolute difference between the change-point estimated and the true threshold, minus the absolute difference between the piecewise estimated and the true threshold ("cp_pw"). Thus, cp_pw was positive if the piecewise threshold estimate was closer to the true threshold than the change-point estimate, and negative if the change-point estimate was closer. Because the median was a better estimate of central tendency for cp_pw, a nonparametric median regression was used to explore whether cp_pw was influenced by threshold shape, distribution, sample size, and threshold value. These variables were first converted to dummy variables (reference level for shape: discontinuous; distribution: Poisson; sample size: 50; threshold value: 0.1). Standard errors were bootstrapped using 500 replications. The final model was derived by modifying the methods of Hosmer and Lemeshow (2000), as follows. The four independent variables were used as candidate variables in a forward stepwise regression, using fairly permissive α values (0.15 for entry and 0.2 for exclusion). The least significant main effects were dropped sequentially until all were significant at $\alpha=0.05$. From these main effects, all two-way interactions were considered. Any interactions that were individually significant at $\alpha=0.05$ were then added (as a group) to the main effects model. Finally, any interaction effects that were no longer significant (at $\alpha=0.05$) in the presence of these others were dropped (as a group), followed by the least significant main effect until all terms were significant at $\alpha=0.05$.

The above analysis explored whether change-point versus piecewise was a *relatively* better estimator of the true threshold. To examine whether each estimator was "good" in an absolute sense, for each data type: a) the median difference between the estimated and true threshold value were plotted (negative values indicated underestimation, and positive values overestimation), along with b) the raw threshold estimates (to show variation about the median).

After examining some of the results, it seemed likely that a bias in the piecewise estimates for discontinuous threshold data would be reversed if the true threshold value was high (see rationale in results/discussion). To explore this possibility, one extra data type (50 replicates) was generated with a high (70%) discontinuous threshold (Poisson, sample size = 250 each), and the piecewise-estimated thresholds were examined. These estimates were not included in any formal statistical analyses, or in the general results and discussion except where explicitly stated.

2.4. AICc and BIC

2.4.1. Calculation of AICc and BIC "best" models and confidence sets

For least-squares models, AICc and BIC add a "penalty term" (2*k or k*ln(n), respectively) to a measure of fit (n*ln(population variance)), where n is sample size, and k is the number of parameters (including the constant and variance estimates, Burnham and Anderson 2004). For the non-linear models here, the threshold value and fractional polynomial power(s) (Royston and Altman 1994) were also counted as parameters, since these values were estimated. Thus, the number of parameters for the all model types were: 2 (null); 3 (linear); 4 (change-point), 4 (degree-1 fractional polynomial), 5 (piecewise), and 6 (degree-2 fractional polynomial).

For each of the 2600 data sets, AICc and BIC were calculated for a set of five models (null, linear, change-point, piecewise, and one of the fractional polynomials). The fractional polynomial model included was that with the smallest AICc or BIC, but the degree-2 model was excluded if its predicted values were implausible (e.g. sharp "hooks" at small values of x and y). The five models in each set were ranked from "best" to worst in increasing order of AICc or BIC score. The best AICc or BIC model was considered "correct" if its shape matched that of the generating model (excluding exact coefficient values). While this suited the practical purpose of this study, this definition of "correctness" is not of theoretical interest, since AICc and BIC have different target models (Burnham and Anderson 2004). Briefly, the target model of BIC is the most parsimonious model that minimizes Kullback-Leibler information loss, and does not depend on sample size. The target model of AICc is that which is best for inference given the data, and will depend on sample size and variance (which influence the number of coefficients that can be reliably estimated, Burnham and Anderson 2004).

The Akaike weight or posterior probability was calculated for each model in each of the 2600 AICc or BIC model sets, respectively. These values sum to one across the models in each set, and indicate the relative support for each model (Burnham and Anderson 2004). For each data set, an AICc and a BIC "confidence set" was also generated, by adding models to the confidence set in order of rank until their cumulative weights / posterior probabilities were at least 90%. These "declared" confidence levels ($\geq$90%) indicated the proportion of confidence sets that should contain the "correct" model if the experiment were repeated many times (Alfaro and Huelsenbeck 2006).

2.4.2. Analyses comparing the performance of AICc versus BIC

Multiple logistic regression was used to explore whether the tendency for the "best" AICc or BIC model to be better at identifying the "correct" model depended on the type of data considered. A dichotomous response variable was coded as 0 if only

AICc identified the correct mode, and 1 if only BIC did so (i.e. cases where both were right or wrong were ignored). Only explanatory variables that applied to all data sets were considered - sample size, distribution, and shape (as dummy variables). Sample size and distribution were of interest since these will be known or readily estimated by the researcher. If their effects on the relative performance of AICc and BIC are large, this information could potentially be used to choose between the two methods. While the relationship shape will obviously not be known, its effect on the relative performance of AICc and BIC could help to choose between the two criteria, given the particular research goals (for example, whether it is more important to "catch" threshold or linear relationships). Null and linear shapes were grouped because null shapes predicted a response of 1 perfectly, resulting in estimation problems. Significant main effects and interactions were determined following a similar procedure as for cp_pw above, except that likelihood ratio tests were used to test the statistical significance of each effect (Hosmer and Lemeshow 2000).

Frequency of "misidentification" was calculated as the number of data sets for which a certain shape was chosen as "best" (by AIC or BIC), among data sets whose true shape did *not* match the chosen shape. For example, how often was the chosen shape "linear", when the true shape was not linear? Misidentification occurred relatively infrequently, so sample sizes were insufficient to support a multiple regression. Instead, five sign tests for paired observations were used to test whether misidentification (as null, linear, polynomial, continuous or discontinuous threshold) was more frequent for AICc or BIC ($\alpha = 0.05$). It appeared as though the misidentified shape was not random with respect to the true shape (for example, the true shape of most data sets misidentified as polynomials was usually a continuous threshold, but rarely a discontinuous thresholds). Thus, these five sign tests were repeated once for each of the four relevant true shapes (i.e. excluding the true shape corresponding to the misidentified model shape; $\alpha = 0.05/4 = 0.0125$).

To examine whether agreement between AICc and BIC best models indicated greater reliability of the best model, rates of correct and misidentification were compared for AICc or BIC alone, versus the subset of cases for which AICc and BIC agreed.

The performance of AICc versus BIC confidence sets were compared by calculating the proportion of confidence sets that contained the "correct" model, for a) all data sets and b) for data sets for which the number of models in the AICc and BIC sets differed. Sign tests were used to compare the number of models in the confidence set between AICc versus BIC.

3. Results and Discussion

3.1. Comparison of change-point versus piecewise threshold estimates

Several main effects (threshold shape, value, and sample size) and two interactions (shape*threshold value, shape*sample size) were significantly related to the relative accuracy of change-point versus piecewise estimates of the true threshold value (cp_pw; Table 3-2). Error distribution was not significant. Main effects will not be discussed since all were involved in significant interactions. By far the most important interaction was that between shape and threshold value (Table 3-2). Piecewise threshold estimates were more accurate than were change-point estimates (cp_pw positive) when the true shape was a continuous threshold, and change-point estimates were more accurate (cp_pw negative) when the shape was a discontinuous threshold, but these differences were more pronounced when the true threshold was 0.3 versus 0.1 (Fig. 3-2). The other interaction was more subtle. For continuous threshold data only, the relative accuracy of piecewise threshold estimates (compared to change-point estimates) was slightly greater for sample sizes of 250 than for 50 (Fig. 3-2). Specifically, at the larger sample size, piecewise estimates were closer to the true threshold than were change-point estimates by an additional 0.033 (i.e. 3.3% habitat), compared to the smaller sample size.

A scatter plot of the distances of the raw threshold estimates from the "true" threshold value (Appendices 3-3a-b) shows the *absolute* accuracy of piecewise and change-point estimates: a) the median change-point estimates tended to be very near the "true" discontinuous thresholds, while median piecewise estimates were very near the "true" continuous thresholds, b) change-point tended to underestimate continuous thresholds (but overestimate weak continuous thresholds of 0.1), whereas piecewise overestimated discontinuous thresholds (or more occasionally underestimated, for an overall pattern of avoidance), and c) for either estimation method on either threshold data type, the threshold estimates were more tightly clustered for the larger sample size and for Poisson distributed data.

Therefore, if there is a mismatch between the true shape of the data and the assumed shape in the model, the threshold estimate will be biased, although this bias will be reduced when the threshold value is close to the lower end of the gradient. For change-point estimates, this resulted at least in part because the tendency to underestimate continuous thresholds was constrained by the lower boundary of x. The explanation for piecewise estimates is more complicated. The piecewise models, having only one threshold, could only fit one portion of discontinuous threshold data well, by fitting a near zero slope in one segment. For the best overall fit, the zero slope should be (and tended to be) fitted to the longest segment (for the present data, the upper one). For lower thresholds (i.e. one segment very short and the other very long), the sloped portion of the fit was necessarily steeper (Fig. 3-3a) than for higher thresholds (Fig. 3-3b), and thus "overshot" the true threshold value less severely. More rarely this pattern was reversed, with the shorter (lower) segment being fit with the near zero slope, and in these cases the true threshold was underestimated. Thus, while piecewise on average overestimated the true discontinuous threshold, a more general pattern was one of *avoidance*, particularly for the more central true threshold value (Appendix 3-3a).

By a similar rationale, one would expect that for a high discontinuous threshold, the biased avoidance pattern would be reversed: the lower (longer) segment would usually be fit with the near zero slope, and the true threshold would usually be underestimated (or occasionally overestimated). Indeed, this pattern was observed in the piecewise estimates for the 70% discontinuous data sets (data not shown).

Within the range of distributions and sample sizes considered here, neither distribution nor sample size should influence the decision of whether to use change-point or piecewise methods to estimate of a threshold value. However, the relative accuracy of change-point threshold estimates for continuous threshold data increased with decreasing sample size (even though piecewise estimates were better for either sample size). Judging from a scatter plot of the raw data, this seemed to result mainly from a decrease in the accuracy of piecewise but not change-point threshold estimates at the smaller sample size (Appendix 3-3b). This probably reflects the fact that when sample sizes are small, a more complex model will be less reliably estimated than will a simpler model. Although both models estimate a threshold value, piecewise models additionally estimate slopes, while change-point models predict simple group means. At very small sample sizes, it may only be possible to estimate group means, but not slopes, and in this case change-point models may estimate a continuous threshold nearly as well as (or perhaps better than) a piecewise model.

3.2. Uncertainty in threshold estimates

Even when the threshold model (change-point or piecewise) was appropriate to the type of data (discontinuous or continuous threshold, respectively), there was sometimes a large spread in the threshold estimates. Not surprisingly, this spread was greater for weaker thresholds, smaller sample sizes, and for negative binomial rather than Poisson dispersion (Appendices 3-3a-b), conditions which make any parameter more difficult to estimate.

Such uncertainty is expected for ecological threshold values, and a more complete examination of a threshold model would include a confidence interval to reflect this uncertainty (Lindenmayer et al. 2005). Three types of confidence intervals (including bootstrapped) have been described for piecewise thresholds (Toms and Lesperance 2003), and a bootstrapped method was described for change-point thresholds (Qian et al. 2003). However, bootstrapped 95% confidence intervals for the change-point were later found to encompass the "true" threshold for only about 70% of data sets, and thus the declared confidence level is wrong (S. Qian, personal communication).

One of the most desired uses of critical threshold information is for setting minimum habitat retention or restoration targets for land management (Guénette and Villard 2005, Radford et al. 2005, Huggett 2005). The boundaries of a 95% confidence interval might at first seem to provide a conservative estimate for such target values. However, the correct interpretation of such a confidence interval is *not* that the probability of the true threshold falling outside of the interval is only 5% (S. Qian, personal communication). The confidence level is correctly interpreted as the proportion of confidence intervals that would contain the threshold if the experiment were repeated many times. A single confidence interval either does or does not contain the true threshold (unfortunately there is no way to know which is the case), and thus no probability can be assigned to a single confidence interval (Littlewood et al. 2002, Lin et al. 2000). For setting environmental targets based on a change-point problem, S. Qian (personal communication) recommends using a Bayesian method of calculating the change-point and Bayesian credible intervals (Qian et al. 2003), which do have the appropriate probablistic interpretation (S. Qian, personal communication).

3.3. AICc versus BIC

3.3.1. Comparison of AICc versus BIC "best" models

Summary statistics suggest that both criteria tended to select the "correct" model, though generally less often for the smaller sample size and for negative binomially distributed data (Appendix 3-4). Among the 461 data sets for which only one criterion's best model was "correct", sample size and shape were significant predictors of whether the correct model was that of AICc (response=0) or BIC (response=1), in a logistic regression (Table 3-3). Predicted values were higher (i.e. BIC performance improved) for the larger sample size, but the most important effect was that of shape (Fig. 3-4). Specifically, BIC chose the correct model more often than AICc if the true shape was null/linear or fractional polynomial (predicted responses >0.5), while AIC was correct more often than BIC if the shape was a continuous or discontinuous threshold (predicted responses <0.5, Fig. 3-4).

Summary statistics show that the proportion of data sets misidentified by either criterion increased with decreasing sample size and for increasing dispersion in the data (Appendix 3-4). Paired sign tests indicated that compared to the best BIC model, the best AICc model more frequently misidentified non-continuous-threshold data sets as continuous thresholds, and non-discontinuous-threshold data sets as discontinuous thresholds. This was most pronounced when the true shape had one or two fewer parameters than the incorrectly chosen shape (Table 3-4). Thus, AICc was biased towards overfitting, in relation to the "correct" model. In contrast, the best BIC model misidentified non-null data sets as null, non-linear data sets as linear, and non-polynomial data sets as polynomial, significantly more often than did AICc. This was most pronounced when the true shape had one or two *more* parameters than the incorrectly chosen shape (Table 3-4). Thus, BIC was biased towards underfitting. Note that since the fractional polynomial model included in the AICc or BIC model set was primarily degree-1 (4 parameters), the tendency for BIC to misidentify true continuous thresholds (5 parameters) as fractional polynomials still represents underfitting.

Thus, AICc and BIC were each biased towards selecting certain shapes. Specifically, AICc chose continuous and discontinuous thresholds more often than BIC, both correctly and incorrectly. BIC chose null, linear, and polynomial shapes more often than AICc, both correctly and incorrectly. Given these biases, the choice between AICc or BIC for selecting the best model shape may therefore depend on the research goals. For example, if the primary concern is to identify species with critical threshold relationships with habitat loss, AICc might represent a more conservative criterion from a conservation perspective, if misidentification of some linear or smooth nonlinear shapes as sharp thresholds is acceptable. On the other hand, if there is a cost to managing for critical thresholds, and misidentification of some nonlinear relationships as simpler shapes is acceptable, then BIC might be a more conservative approach from an economic standpoint.

The opposite biases of AICc and BIC also suggests that considering both criteria together may be useful. Specifically, agreement between both criteria may indicate greater confidence for the chosen model. Indeed, when AICc and BIC agreed on the best shape, the rate of correct identification was higher, and misidentification lower, than the rates for AICc or BIC alone (averaged over the rates for each of the 5 shapes, Table 3-5). This was because, for each individual shape, the rates of correct and misidentification when AICc and BIC agreed tended to fall between the overall rates for AICc and BIC alone, but closer to the better of the two (Table 3-5). For example, AICc correctly identified 59.5% of 200 null data sets, and BIC 93.5%. However, of the 132 null data sets for which AICc and BIC agreed on the best model, 90.2% of the chosen shapes were correct (closer to the better (BIC) rate). Similarly, AICc misidentified only 2.7% of the 2400 non-null data sets as null, compared to 5.8% for BIC. Of the 1935 non-null data sets for which the AICc and BIC best models agreed, only 3.3% were misidentified as null (closer to the better (AICc) rate). However, the exact rates of correct and misidentification will depend on the particular data, and agreement between the AICc and BIC best models will not necessarily mean that there is a low (absolute) probability of misidentification or a high probability of correct identification.

3.3.2. Comparison of AICc versus BIC confidence sets

Rather than depending only on the one "best" model chosen by AICc or BIC (or even by both), one should also consider a confidence set. Both AICc and BIC confidence sets were larger for the smaller sample size and for negative binomial data (data not shown). However, AICc sets were larger significantly more often than were BIC sets, overall and for most true shapes (Table 3-6). At first glance, this appears to suggest that BIC sets were better in terms of narrowing down the shape of a relationship. However, AICc confidence sets contained the "correct" model for slightly more data sets (94%) than did BIC sets (92%). These values were both slightly below the average "declared" confidence levels of about 97% (i.e. the average cumulative weights or posterior probabilities for each model set). This small discrepancy may result from violations of model assumptions, affecting the Bayesian based confidence sets more strongly than AIC (Alfaro and Huelsenbeck 2006).

The negative effect of assumption violations on this discrepancy can be substantially more severe (e.g. see Alfaro and Huelsenbeck 2006) than the 3-5% observed here. This suggests that using weighted least squares regression to model count data can produce fairly reliable confidence sets despite the violation of assumptions. For example, if a confidence set were to contain only one model, there would be a high level of confidence that it was the best one. Larger sets could also be useful if the models shared similar characteristics. For example, while fractional polynomial and continuous threshold shapes were not well distinguished from one another by either AICc or BIC (in terms of their "best" model, Appendix 3-4), they commonly occurred together in confidence sets of two. Such a set would indicate a high level of confidence that y declines faster at lower values of x, though whether with a sharp or smooth transition would be uncertain. Even large confidence sets containing dissimilar models can be informative, implying strongly that the data are not sufficient to describe the functional relationship.

In contrast, traditional significance tests would yield more simplistic results. Consider two data sets, both with non-significant linear slopes (failure to reject the null hypothesis of a zero slope reflects *lack* of confidence that the slope is not zero, not confidence that the slope *is* zero). For the first data set, the confidence set contains only a null model (reflecting a high level of confidence that the best model of the set *is* a zero slope model), while the second contains a null, linear, and discontinuous threshold model (reflecting a low level of confidence about both the linear slope and functional form). Both confidence sets are more informative than are either significance test.

As with the AICc and BIC best models, considering the AICc and BIC confidence sets together may be useful. Among data sets for which the number of models in the two confidence sets differed, the confidence set with fewer models contained the correct model in only 83% (AICc) or 84% (BIC) of cases, while the one with more models (whether AICc or BIC) contained the correct model in 98% of cases. This reflected the contrasting biases of AICc and BIC: AICc sets were smaller than BIC sets and lacking the correct model mainly when the true shape was null, linear, or polynomial (for which BIC had a greater rate of correct identification). A similar pattern occurred for BIC sets mainly for continuous or discontinuous threshold data sets (for which AICc had a higher rate of correct identification). Thus, the more conservative approach would be to consider the larger of the two confidence sets. In contrast, when the number of models in the two confidence sets was the same, AICc and BIC sets contained the correct model for a similar proportion of data sets (94.1% and 94.5%, respectively).

4. Summary and conclusions

A growing interest in ecological thresholds brings with it a need for robust statistical methods of identifying threshold values and the shape of the relationship. I compared the performance of two methods for identifying threshold values, piecewise regression and change-point analysis (Table 3-7). Piecewise regression estimated continuous thresholds most accurately. However, for discontinuous threshold relationships, this method tended to either overestimate or underestimate the threshold value, when the true threshold value was low or high, respectively. Similarly, change-point analysis estimated discontinuous thresholds most accurately, and tended to underestimate the value of continuous thresholds. Therefore, if only one type of threshold model is considered, this should correspond to the type of threshold that is most likely to occur (given ecological or theoretical considerations). If both threshold types are plausible, multi-model selection methods such as AICc or BIC are useful for choosing between these (and other) models. The "significance" of the piecewise or changepoint threshold does not indicate whether the true shape is a continuous or discontinuous threshold, respectively. A piecewise model would likely indicate a significant threshold even for a data set with a discontinuous threshold, as would a changepoint model for a data set with a continuous threshold.

Further, traditional significance tests do not allow the comparison of a set of non-nested models. Therefore, I also compared the ability of AICc and BIC to choose the correct shape, from a set of models that could plausibly describe the relationship between the abundance of an organism and the proportion of some habitat type (Table 3-7). BIC tended to correctly choose null, linear, and simple polynomials more often than AICc, but was somewhat biased towards underfitting. As well, the BIC confidence set was somewhat more sensitive to violations of model assumptions. In contrast, AICc tended to correctly choose continuous and discontinuous thresholds more often than BIC, but was somewhat biased towards overfitting. Thus, managers might choose AICc over BIC if the emphasis was on correctly identifying threshold relationships (or if model assumptions are violated), and BIC if it was more important to correctly identify simple linear and polynomial shapes. However, if there is no such bias in management goals, AICc and BIC results should both be examined. Agreement between the AICc and BIC best models suggested greater reliability of the chosen model. However, a more complete consideration of the evidence would involve an examination of the confidence set of models. When the number of models in the confidence sets differed, the smaller set (whether AICc or BIC) was less reliable on average, containing the correct model less often (83-84%) than the larger set (98%). When the confidence sets were the same size, the confidence set contained the correct model for a high proportion (~94%) of data sets. Thus, because the respective biases of AICc and BIC were in opposite directions, an examination of both criteria together may be more informative than either criterion alone.

Table 3-1. Characteristics and formulas of the 13 models from which artificial data were generated. Poisson or negative binomial scatter (sample size 50 or 250) was added to each model (n=50 for each combination of model shape, sample size, and error distribution)

Shape	Strength	Threshold	Formula	
Continuous threshold	Weak	0.1	y = 32.6*x |x<=T|	y = 32.6*x - 25.11(x-0.1) |x>T|
		0.3	y = 20*x |x<=T|	y = 20*x - 14.29 (x-0.3) |x>T|
	Strong	0.1	y = 76.3*x |x<=T|	y = 76.3 - 73.67 (x-0.1) |x>T|
		0.3	y = 30*x |x<=T|	y = 30*x - 28.57 (x-0.3) |x>T|
Discontinuous threshold	Weak	0.1	y = 7 |x<=T|	y = 10 |x>T|
		0.3	y = 7 |x<=T|	y = 10 |x>T|
	Strong	0.1	y = 4 |x<=T|	y = 10 |x>T|
		0.3	y = 4 |x<=T|	y = 10 |x>T|
Fractional polynomial	Weak		y = 11.64 + 3.88*ln(x+0.05) - 1.66 (x+0.05)^2	
	Strong		y = 18.21 - 3.86 (x+0.05)^-0.5 - 4.34 (x+0.05)^0.5	
Linear	Weak		y = 10 * x	
	Strong		y = 5+5*x	
Null	n/a		y = 10	

Table 3-2. Final median regression model for influence of threshold shape, threshold value, sample size and interactions (as dummy variables1) on the relative accuracy of change-point versus piecewise threshold estimates (cp_pw). Cp_pw was positive if the piecewise estimate averaged closer to the true threshold, and negative if the change-point estimates averaged closer (n=1600, pseudo r2 = 0.3137)

Variable[1]	Coefficient	S.E.	P-value
Threshold shape	0.0584	0.0056	<0.001
Threshold value	-0.1788	0.0067	<0.001
Threshold shape * value	0.2308	0.0093	<0.001
Threshold shape * sample size	0.0277	0.0060	<0.001
Constant	-0.0489	0.0026	<0.001

1. Reference levels for dummy variables: threshold shape: discontinuous; threshold value: 0.1; sample size: 50

Table 3-3. Final logistic regression model of the effect of sample size and true shape (dummy variables[1]) on the probability that only the BIC-chosen model shape was correct, among cases where only one criterion was correct (response = 1 if BIC correct, 0 if AICc was correct; n = 461, pseudo r2 = 0.6563).

Variable	Coefficient	S.E.	P-value
Sample size = 250	0.8626	0.3566	0.016
Shape = discontinuous threshold	-5.383	0.7561	<0.001
Shape = fractional polynomial	-3.065	0.7698	<0.001
Shape = continuous threshold	-8.3076	0.9291	<0.001
Constant	3.7975	0.7303	<0.001

[1] Reference levels for dummy variables: sample size: 50; shape: null/linear

Table 3-4. Frequency with which AICc versus BIC misidentified data sets as null, linear, fractional polynomial, discontinuous threshold, or continuous threshold (i.e. true shape was different than the chosen shape). Data sets for which both criteria agreed were not included. Bold values indicate the criterion for which misidentification frequency for one criterion was significantly greater than for the other criterion, in a paired sign test (alpha = 0.05 when all data sets included; alpha= 0.0125 for subsets of individual true shapes).

Chosen shape	True shape (# data sets)	Frequency of misidentification by:	
		AICc only	BIC only
Null	all (76)	0	**76**
	continuous threshold (5)	0	5
	discontinuous threshold (60)	0	**60**
	fractional polynomial (2)	0	2
	linear (9)	0	**9**
Linear	all (109)	11	**98**
	continuous threshold (51)	1	**50**
	discontinuous threshold (40)	6	**34**
	fractional polynomial (14)	0	**14**
	null (4)	4	0
Fractional polynomial	all (164)	48	**116**
	continuous threshold (130)	20	**110**
	discontinuous threshold (13)	8	5
	linear (17)	**16**	1
	null (4)	4	0
Discontinuous threshold	all (77)	**56**	21
	continuous threshold (15)	6	9
	fractional polynomial (14)	3	11
	linear (26)	**25**	1
	null (52)	**52**	0
Continuous threshold	all (157)	**151**	6
	discontinuous threshold (33)	**33**	0
	fractional polynomial (73)	**67**	6
	linear (43)	**43**	0
	null (8)	**8**	0

Table 3-5. Proportion of data sets correctly or misidentified (as null, linear, polynomial, discontinuous threshold, or continuous threshold) by AICc, BIC, and for the subset of data sets for which AICc and BIC best models agree

True shape	Proportion correctly identified (out of # data sets)		
	AICc	BIC	AICc + BIC in agreement [1]
Null	0.595 (200)	0.935 (200)	0.902 (132)
Linear	0.630 (400)	0.813 (400)	0.796 (314)
Fractional polynomial	0.475 (400)	0.568 (400)	0.554 (314)
Discontinuous threshold	0.790 (800)	0.725 (800)	0.822 (680)
Continuous threshold	0.696 (800)	0.513 (800)	0.659 (618)
average (of 5)	**0.637**	**0.711**	**0.733**
	Proportion misidentified (out of # data sets)		
	AICc	BIC	AICc + BIC in agreement [1]
Non-null	0.027 (2400)	0.058 (2400)	0.033 (1935)
Non-linear	0.054 (2200)	0.094 (2200)	0.062 (1753)
Non-fractional polynomial	0.083 (2200)	0.114 (2200)	0.075 (1799)
Non-discontinuous threshold	0.109 (1800)	0.073 (1800)	0.080 (1387)
Non-continuous threshold	0.159 (1800)	0.079 (1800)	0.094 (1449)
average (of 5)	**0.086**	**0.084**	**0.068**

1. Restricted to data sets for which the AICc and BIC best models agree (correctly or incorrectly)

Table 3-6. Frequency with which AICc versus BIC confidence set contained more models, for all data sets together and for each simulated shape. Bold indicates the criterion that had the larger set for significantly more data sets, in a paired sign test (alpha = 0.05 for all data sets together; alpha = 0.0125 for each individual shape)

True shape (# data sets)	AICc set larger	BIC set larger
All (2600)	**787**	295
Null (200)	**176**	6
Linear (400)	**290**	12
Fractional polynomial (400)	55	59
Discontinuous threshold (800)	**182**	71
Continuous threshold (800)	84	**147**

Table 3-7. Recommendations for statistical methods of estimating threshold presence, type and value

Method for estimating threshold value:	Choose this method when:	Biases:
Piecewise regression	Threshold shape is expected to be or clearly appears to be a "continuous threshold"	If true shape is a discontinuous threshold, the estimate of the threshold value will be biased in relation to the true threshold (towards higher values, if the true threshold value is low, or towards lower values if the true threshold value is high)
Change-point analysis	Threshold shape is expected to be or clearly appears to be a "discontinuous threshold"	If true shape is a continuous threshold, the estimate of the threshold value will be biased towards lower values than the true threshold
Piecewise regression and changepoint analysis	Either type of threshold may plausibly describe the relationship; use AICc and / or BIC to determine the weight of evidence for each shape	
Method for estimating shape of relationship	Choose this method when:	
AICc	Priority is to "catch" threshold relationships	Slight bias towards overfitting (tendency to choose more complex shapes than the true shape)
BIC	Priority is to "catch" linear or simply polynomial relationships; if there is an economic cost to managing for thresholds, and "missing" some less obvious thresholds is acceptable	Slight bias towards underfitting (tendency to choose simpler shapes than the true shape)
AICc & BIC	Priority on estimating the "true" shape, with no emphasis on "catching" certain shapes; agreement between AICc and BIC suggests greater confidence in the best model or confidence set, while disagreement can be interpreted in light of the respective biases of AICc and BIC.	

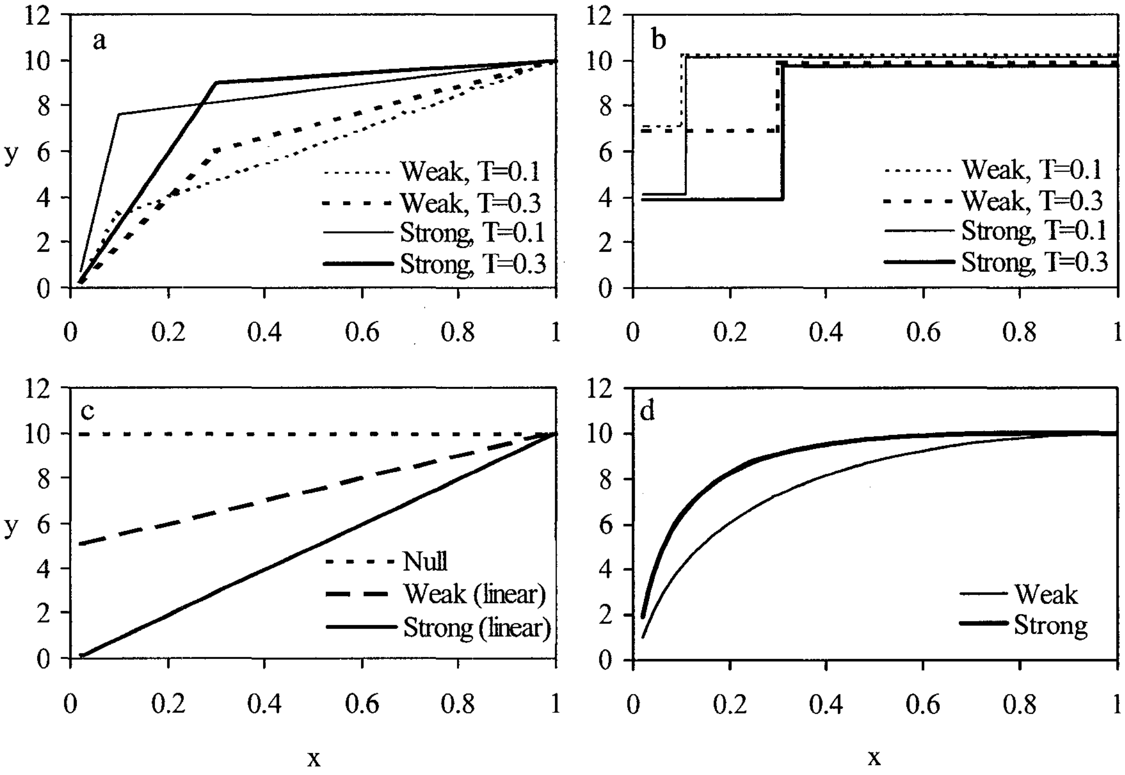

Fig. 3-1 a-d. Appearances of the 13 models around which artificial count data were generated. Continuous thresholds (a); discontinuous thresholds (b); null and linear (c); fractional polynomials (d). T = threshold value.

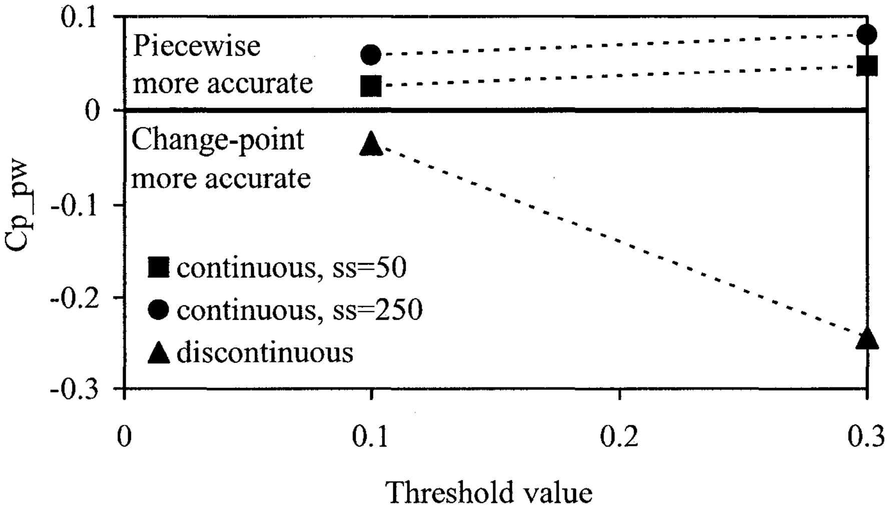

Fig. 3-2a – Predicted values for a median regression of the influence of threshold shape, threshold value, sample size, and interactions on the relative accuracy of change-point versus piecewise estimated threshold values (cp_pw; positive values indicate piecewise was more accurate). Since independent variables were categorical, only the point markers represent predicted values (dashed lines are for convenience only, to group like shapes)

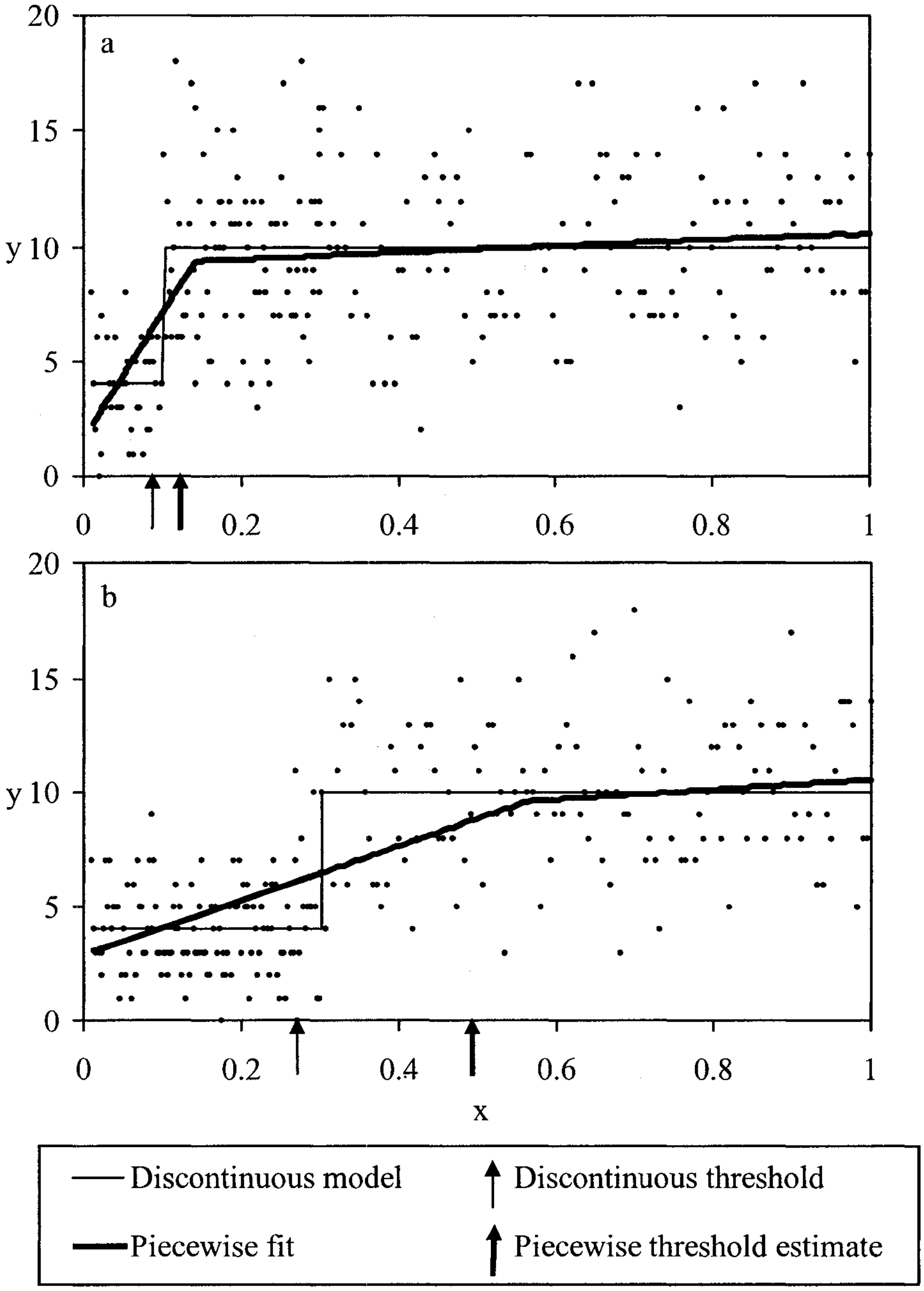

Fig. 3-3a-b. Typical fit of a piecewise model on discontinuous threshold data where the true threshold = 0.1 (a) or 0.3 (b).

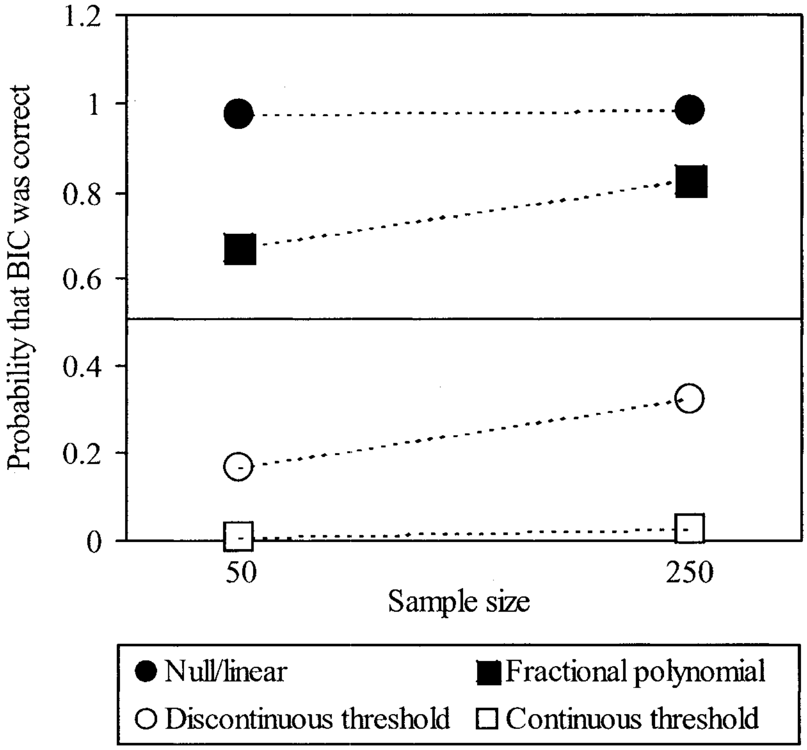

Fig. 3-4. Predicted values for logistic regression of the influence of sample size and true shape on the probability that only the BIC best model was correct, among cases where only one criterion was correct (response = 1 if BIC was correct, 0 if AICc was correct). Horizontal line indicates an equal probability of AIC or BIC being correct.

References

Alfaro, M. E. & Huelsenbeck, J. P. 2006. Comparative performance of Bayesian and AIC-based measures of phylogenetic model uncertainty. *Systematic Biology* 55: 89-96.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.

Bergman, K.-O., Askling, J., Ekberg, O., Ignell, H., Wahlman, H. & Milberg, P. 2004. Landscape effects on butterfly assemblages in an agricultural region. *Ecography* 27: 619-628.

Burnham, K. P. & Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261-304.

DeLuca, W. V., Studds, C. E., Rockwood, L. L. & Marra, P. P. 2004. Influence of land use on the integrity of marsh bird communities of Chesapeake Bay, USA. *Wetlands* 24: 837-847.

Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* 13: 263-268.

Guerry, A. D. & Hunter, M. L. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology* 16: 745-754.

Guénette, J.-S. & Villard, M.-A. 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. *Conservation Biology* 1168-1180.

Hardin, J. and Hilbe, J. 2005. Glm - generalized linear models. In: Stata Base Reference Manual 1: Release 9. Stata Press, College Station, Texas, pp 392-420.

Homan, R. N., Windmiller, B. S. & Reed, J. M. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians . *Ecological Applications* 14: 1547-1553.

Hosmer, D. W. & Lemeshow, S. 2000. Applied Logistic Regression, 2nd Edition. United States of America: John Wiley & Sons, Inc.

Huggett, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation* 124: 301-310.

Imbeau, L. & Desrochers, A. 2002. Area sensitivity and edge avoidance: the case of the three-toed woodpecker (*Picoides tridactylus*) in a managed forest. *Forest Ecology and Management* 164: 249-256.

Johnson, J. B. & Omland, K. S. 2004. Model selection in ecology and evolution . *Trends in Ecology and Evolution* 101-108.

King, R. S. & Richardson, C. J. 2003. Integrating bioassessment and ecological risk assessment: An approach to developing numerical water-quality criteria. *Environmental Management* 31: 795-809.

Lin, P.-E., Meeter, D. & Niu, X.-F. A nonparametric procedure for listing and delisting impaired waters based on criterion exceedances. 2000.

Lindenmayer, D. B., Fischer, J. & Cunningham, R. B. 2005. Native vegetation cover thresholds associated with species responses. *Biological Conservation* 124: 311-316.

Littlewood, B., Popov, P. & Strigini, L. 2002. Assessing the reliability of diverse fault-tolerant software-based systems. *Safety Science* 40: 781-796.

Qian, S. S., King, R. S. & Richardson, C. J. 2003. Two statistical methods for the detection of environmental thresholds. *Ecological Modelling* 166: 87-97.

Radford, J. Q. & Bennett, A. F. 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia . *Biological Conservation* 117: 375-391.

Radford, J. Q., Bennett, A. F. & Cheers, G. J. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124: 317-337.

Royston, P. & Altman, D. G. 1994. Regression using fractional polynomials of continuous covariates: parsimonious parametric modelling. *Applied Statistics* 43: 429-467.

StataCorp 2005. Stata Statistical Software: Release 9. College Station, Texas: StataCorp LP.

Thies, C. & Tscharntke, T. 1999. Landscape structure and biological control in agroecosystems. *Science* 285: 893-895.

Toms, J. D. & Lesperance, M. L. 2003. Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84: 2034-2041.

With, K. A. & King, A. W. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314-326.

Zar, J. H. 1999. Biostatistical Analysis, 4th Edition. Upper Saddle River, New Jersey: Prentice-Hall, Inc.

Zucchini, W. 2000. An introduction to model selection. *Journal of Mathematical Psychology* 44: 41-61.

Chapter 4: Linear and nonlinear changes in the abundance of forest-breeding birds along a gradient of forest proportion in an agricultural region of Alberta

1. Introduction

Habitat loss and fragmentation affect species persistence on landscapes. A major research concern is whether species' abundance declines linearly with habitat loss, or whether it declines more rapidly below a critical threshold of habitat amount. A critical threshold is "an abrupt, nonlinear change that occurs in some parameter across a small range of habitat loss" (With and King 1999). Strong, negative fragmentation effects are hypothesized to occur once the amount of habitat in the landscape falls below a threshold amount. If so, populations should initially decline in proportion to habitat loss, but decline more steeply below this threshold ("fragmentation threshold hypothesis"). For example, Andrén's (1994) meta-analysis suggested that below a threshold of 10-30% habitat in the landscape, patch size and isolation had an effect on bird and mammal presence, abundance, density, or richness (but see Fahrig 2003).

Alternatively, a critical threshold might take the form of a "discontinuous threshold", with an abrupt jump at the threshold in the mean value of the ecological response, which is otherwise constant (Fig. 4-1b). For example, aquatic macroinvertebrate communities often appeared to respond to increasing phosphorus concentration in this manner, reflecting an abrupt shift from mainly phosphorous intolerant to phosphorous tolerant species (Qian et al. 2003). Published accounts of discontinuous threshold responses to landscape-level habitat loss are rare. However, a discontinuous threshold could occur for a community metric such as species evenness, if a subset of species became rare or absent below the same level of habitat, while others declined less strongly. Individual species could also exhibit discontinuous thresholds. Radford et al. (2004) report this type of threshold for large-patch specialists in response to loss of forest in the landscape. Below the threshold, these species are uniformly absent because large patches are absent; above the threshold, incidence (akin to density) is greater but not strongly related to percent forest (Radford et al. 2004). At the other extreme, The abundance of a species that uses both forest (e.g. for nesting) and open habitats (e.g .for foraging) may not respond in a continuous manner to the amount of forest in a landscape. They may have a preferred and non-preferred *range* of forest cover, within which abundance is uniformly high or low, respectively.

Several empirical studies have demonstrated threshold responses to habitat loss for species' occurrence, diversity, or movement, but rarely for individual species' abundances (reviewed in Chapter 2). Further, few used statistical methods to find the threshold value and to test whether a threshold shape was better than linear or other shapes. I used such methods to examine the response of forest-breeding organisms (birds and squirrels) to landscape-level forest proportion. I focused on resident birds. The effects of landscape habitat proportion and fragmentation may be more evident for residents than for migrants, because a) some habitat loss and fragmentation effects may occur mainly during the winter (e.g. Dolby and Grubb 1999), and b) population limitation likely occurs in the winter (Nilsson 1987, Herrera 1978, Newton 1994, Sherry and Holmes1996, Lahti et al. 1998), for both resident birds (which are present year-round) and for migratory birds (which over-winter elsewhere). My main questions were: 1) What is the shape of the relationship between each species abundance and the proportion of forest in the landscape? 2) If a thresholds occurs, what is its value? and 3) If a threshold occurs, is it consistent with the fragmentation threshold hypothesis?

2. Methods

2.1. Study area

The 75x55 km study area was located about 40 km east of Edmonton, Alberta, Canada (Fig. 4-2a), in an "island" of boreal dry mixedwood surrounded by central parkland. Forest covers about 24% of the study area. The forest is primarily deciduous (mainly trembling aspen, *Populus tremuloides;* with smaller amounts of other species such as balsam poplar, *Populus balsamifera,* and paper birch, *Betula papyrifera).* There are also a few areas of mixed deciduous-coniferous forest and rarely, conifer dominated stands (mainly white spruce, *Picea glauca*). The most highly forested areas occur in several parks and reserves, including Elk Island National Park, Miquelon Lake Park, the Cooking Lake - Blackfoot Grazing, Wildlife and Provincial Recreation Area, and the Ministik Lake Game Bird Sanctuary. The Cooking Lake reserve has some grazing activity, and Elk Island Park contains bison, *Bison bison.* Outside of such areas, non-forested land is largely agricultural, including pasture, hay, and row crops (Young et al. 2006). There are several small towns and suburban areas within the study area, though the most highly developed areas were avoided as study sites (e.g. all towns and much of the area immediately surrounding Cooking Lake).

I selected fifty sites (800 by 800m) for bird surveys (see below). The dominant tree species for all study sites was trembling aspen. Within 1km or 3km radius landscapes surrounding these sites, forest cover ranged from about 2.5 to 62%. The proportion of forest in the 1km and 3km radius landscape surrounding each survey site was measured using the Fragstats extension in ArcView 3.2, from a digitized map with a 5m grain size (see Chapter 6 for details and rationale for choice of landscape sizes).

2.2. Study species and survey methods

Resident birds surveyed included: black-capped chickadee, white-breasted nuthatch (*Sitta carolinensis*), downy woodpecker, hairy woodpecker, ruffed grouse (*Bonasa umbellus*), black-billed magpie, and blue jay. Two short distance migrants were also included: American crow (*Corvus brachyrhynchos*) and yellow-bellied sapsucker (Sphyrapicus varius). There were several reasons for including these species.. They are fairly easily detected, and are both taxonomically related to and share certain habitat requirements with one or more of the residents. Red squirrels (*Tamiasciurus hudsonicus*) were also recorded, because they are forest dependent residents, and readily detected. Of these ten species, only crows and magpies make extensive use of both forest (for nesting, safety, and occasionally foraging or caching) and nonforest (for foraging; Trost 1999, Verbeek and Caffrey 2002). For convenience, the other species will be referred to as "forest species" or "forest birds".

Bird surveys were conducted on the fifty sites during four rounds between April and July (2002 and 2003), on days without heavy rain or winds (> 25km / hour). Each surveyor (2-3 each year) surveyed two sites per day, one starting at dawn, the second in the late morning, and each lasting 3-4 hours. Surveys were scheduled such that in each round the mean and range of forest proportion was similar a) between landscapes surveyed at dawn or in the late morning, and b) among landscapes surveyed by different observers. On a given day, survey landscapes were selected to represent a relatively wide range of forest proportion. As well, a landscape surveyed at dawn in one round was usually surveyed in the late morning in the next round, and vice versa. In each site, the survey route consisted of 2.4km of transects, and nine survey stations spaced 300m apart in a 3x3 grid (Fig. 4-2b). Surveyors walked along the transects and stopped at each survey station for 12 minutes. Birds (or squirrels) seen or heard within 100m of the observer (either on transects or survey stations) were recorded. Thus, a total of about 50ha was actively sampled in each site (i.e. the area within a 100m buffer around the transect pathway, using square rather than rounded ends and corners). Each individual was recorded by location, species, sex (if sexually dimorphic), and age (adult, or in the last round, fledgling; data were substantial for chickadees only). Stations lacking tree cover within 100m were surveyed silently. At forested stations, recordings of chickadee mobbing calls, downy woodpecker calls and drums, and hairy woodpecker calls and drums were broadcast, in that order. Each species' recording was broadcast for two one-minute intervals, each followed by one minute of silence. The volume was adjusted for ambient noise conditions to be audible within a 100m radius. These broadcasts attract birds to the observer (e.g. Hurd 1996) and improve detection rates.

2.3 The response variables - species' abundance and community indices

The dependent variable for each species was its average yearly abundance (sapsuckers were surveyed only in 2003). Since most of the species either have small territory sizes (e.g. chickadee, downy woodpecker), or did not respond to broadcasts (e.g. crow, magpie), the risk of double-counting the same bird at two different stations was probably small. Thus for most species, yearly abundance in each landscape was the total count from all survey stations and transects, for the round with the highest count.

However, two species that responded to broadcasts have territories of about 20ha (white breasted nuthatch, Butts 1931 cited in Pravosudov and Grubb 1993; hairy woodpecker, based on a 500m wide territory, Kilham 1969). For each year and landscape, abundance was estimated as follows. The location and sex of each observed individual (including movements) was mapped in ArcView, for each year and round. It was assumed that each territory was occupied either by a single individual or by a male-female pair, and was 20 ha in size and round (i.e. diameter = 505m). Birds of the same species and sex were counted as different individuals if a) their observed locations were more than 505m apart, or b) they were seen or heard concurrently. Otherwise, two birds of the same species and sex (or unknown sex) could represent the same individual. Birds were then "grouped" by 20 ha round territories into the fewest individuals possible, according to these criteria. Fig. 4-3 shows a hypothetical example that illustrates all of these criteria.

Two abundance-based forest bird community metrics were calculated for each study site. These were intended to guage whether responses to forest proportion and configuration that were consistent among species. Potentially, this could include effects that were difficult to detect at the single-species level, but became more apparent when present for several or all species. The first community metric was the number of species that were "abundant" in the landscape. A species was considered abundant in a landscape if its average 2-year abundance was greater than the median abundance for that species among all landscapes. This metric was used instead of species richness, because several species were present over most or all landscapes. Although their abundances changed with forest proportion, occurrence data would have failed to reflect these changes. The second community metric was the "evenness" of species' abundances. Evenness decreases when some species become relatively more rare or dominant compared to other species. Evenness was calculated in Multi-Variate Statistical Package version 3.13b (Kovach 1985), as the Shannon diversity index divided by the maximum possible Shannon diversity index (given the number of species present, Krebs 1999). Prior to calculating evenness, each species' abundance was standardized to a 0-1 scale, so that each species could have equal influence. Otherwise, evenness was strongly influenced by the most abundant species (chickadee). With each species' abundance standardized, changes in evenness along the gradient of a forest metric would reflect differences among species in the relative strength of their response to the metric (e.g. some decrease more steeply than others).

2.4. Statistical analyses

Statistical analyses were performed using Intercooled Stata 9.2 (StataCorp. 2005). Regression models were estimated using the least-squares method, and were weighted if data were heteroscedastic. Heteroscedasticity means that the variance of the dependent increases with its mean predicted value. This is a violation of least-squares model assumptions. In least-squares regression, using weights that increase as variance decreases can be used to correct for heteroscedasticity (e.g. Toms and Lesperance 2003). For each model, weights were calculated as the smoothed values of 1/(variance + 0.5). Variance was estimated for groups of five consecutive observations, ordered by percent forest (E. Bayne, personal communication). Smoothed values were the best degree-1 fractional polynomial (see details for estimating the best power in the following section).

2.4.1. Fitting different model shapes and estimating threshold values

For each species or community index (hereafter "dependent"), forest proportion was analyzed at either the 1km or 3km extent, depending on which extent was previously found to be most important (Chapter 6, all-landscapes multi-scale models). Estimating the shape of the relationship between forest proportion and each dependent variable involved two steps. The first was to fit a set of up to 6 models for each dependent. Each model assumed a different shape: null, linear, degree-1 and degree-2 fractional polynomials, piecewise regression ("continuous threshold", Fig. 4-1a), and a change-point model ("discontinuous threshold"; Fig 4-1b). The piecewise and change-point models both estimate a threshold value. For each dependent, the best polynomial power(s) were determined as those resulting in the lowest residual deviance, from a set of powers ranging from -2 to 3. Although fractional polynomials can be non-linear, a threshold value is not estimated as a model parameter. However, visual examination of predicted values can suggest an approximate threshold value.

Models were sometimes excluded from the set if their shape was biologically implausible (e.g. sharp "hooks") or if the degree-1 polynomial was linear (power=1). Change-point models were fit only for community level indices and for the abundance of species that extensively use both forested and open habitats (crow, magpie).

2.4.2. Comparison of different model shapes

The next step was to compare the fit of the models in each model set. Two different comparison methods were employed. The first method involved traditional significance testing. Specifically, fractional polynomial analysis was used to test whether the relationship was better modelled as a linear, degree-1 or degree-2 fractional polynomial shape (alpha = 0.05). The test is based on the difference in deviance between two or more nested models (Royston and Altman 1994). The sequence of tests was as follows. First, the linear and degree-2 models were compared. If the difference was not significant, the linear model was chosen. If the difference was significant, the degree-2 and degree-1 models were compared. If this difference was significant, the degree-2 model was chosen. If not, the degree-1 model was chosen. This sequence yields type I error rates near the declared alpha level, so no correction for multiple tests is required (StataCorp 2005).

The second method involved multi-model comparison methods, which do not require models to be nested. The AICc weight and BIC posterior probability (hereafter "weights") were calculated for each of the 5-6 models in each set (Burnham and Anderson 2004, Johnson and Omland 2004). These weights reflect the relative evidence that each model is the "best" of the set, and sum to 1 over the model set. An AICc and a BIC $\geq$90% confidence set of models (Alfaro and Huelsenbeck 2006) was then constructed for each dependent, Models were added to the confidence set in order of decreasing weight, until the cumulative weight was at least 0.90. A larger confidence set (more models) reflects a relationship whose shape is more difficult to define (e.g. large variance, small sample size, subtle non-linearities, etc.).

3. Results

3.1. Fractional polynomial analyses

Individual species responses: The abundance of most species changed linearly with forest loss (forest birds decreased, while forest-open birds increased; Table 4-1). Only one species had a significantly nonlinear relationship at $\alpha = 0.05$: chickadee abundance peaked at moderate levels of forest (degree-2 polynomial). However, downy woodpeckers and ruffed grouse had nearly significant nonlinear declines (p=0.12 and p = 0.08, respectively, for comparison of degree-2 and linear models; Table 4-1). To determine whether this reflected a tendency towards degree-1 or degree-2 polynomials, I tried substituting a higher alpha level in the analyses. These results suggested that (with marginal significance) downy woodpeckers and ruffed grouse declined shallowly over the initial range of habitat loss, followed by a steeper decline at low forest cover (degree-1).

Community responses: The number of abundant forest bird species appeared to decrease somewhat shallowly over the initial range of forest loss, and more rapidly below about 20% forest (degree-1). The evenness of standardized forest bird abundances declined linearly with habitat loss, with only a slight slope.

3.2 AICc, BIC analyses

For each dependent variable, the predicted values of each model in the AICc or BIC confidence set are presented in Fig. 4-4 (colour and thickness reflects the average of the AICc and BIC weights for each model). Weights for all models are given in Table 4-1. AICc and BIC almost always agreed on the "best" and second best model in each set. Most $\geq$90% confidence sets contained more than one model, suggesting that the precise shape was unclear. Regardless, for most species / community index, there was fairly strong evidence for the general shape. For each relationship, the following summary focuses on the model(s) with the greatest weights.

Forest species: Among the forest species, there was strong support that hairy woodpecker, sapsucker, and red squirrel abundance declined linearly with forest cover (Figs. 4-4a-c). Similarly, nuthatch and blue jay abundance declined either linearly or with a slight curve (Figs. 4-4d-e). Chickadees exhibited a continuous threshold relationship that peaked near 34% forest (Fig. 4-4f). For downy woodpeckers (Fig. 4-4g), AICc suggested little decline until below about 10-20% forest (either a degree-1 or continuous threshold model). The "best" BIC model also suggested a polynomial shape (weight = 0.46), but a close contender was for a linear decline (weight = 0.33). Combined with the nearly significant fractional polynomial analysis, the evidence overall suggests that downy woodpecker abundance followed a weak threshold relationship with habitat cover. For ruffed grouse, the best shape was unclear (Fig. 4-4h). A peak in abundance at moderate forest cover was favored by AICc and BIC (weights = 0.62, 0.42), but there was also moderate evidence for a monotonic polynomial increase with forest cover (weights = 29, 0.40). Recall that fractional polynomial analysis favored a linear relationship, or a marginally significant degree-1 polynomial.

Forest - open species: Magpie abundance dropped above a discontinuous threshold of about 35% forest (Fig- 4.4i). This type of shape is not well approximated by fractional polynomials (personal observation), so it is not too surprising that the fractional polynomial analyses chose a linear model in this case. For crows, the strongest evidence was for a linear decrease with increasing forest cover, but this was followed closely by model indicating a discontinuous threshold decline above 47% forest (Fig. 4-4j).

Forest bird community responses: The number of abundant forest birds declined slowly over the initial range of forest loss, and more rapidly below about 25% forest (degree-1 or continuous threshold model; Fig. 4-4k). In contrast, the evenness of standardized forest bird abundances did not change strongly with forest cover, and tended to be only slightly lower at low forest cover (linear or null model was best; Fig. 4-41).

4. Discussion

4.1. Shape of the relationships with forest proportion

The "fragmentation threshold hypothesis" predicts that if negative fragmentation effects compound those of forest loss below a threshold amount of forest, then species abundance should decline disproportionately with forest loss below the threshold. Above the threshold, abundance should decline in proportion with forest loss. I did not observe this pattern among any of the eight forest species. Most declined in a linear or nearly linear fashion (hairy woodpecker, yellow-bellied sapsucker, red squirrel, white-breasted nuthatch, blue jay). These patterns may appear inconsistent with my findings in Chapter 6. These showed that for most of these six species, the relative effects of three forest configuration metrics (compared to proportion) were greater below 30% forest (except for the nuthatch, which had no configuration effects). However, these effects were small in an absolute sense (8-22% variance explained), and thus any resulting thresholds would be subtle. Indeed, Flather and Bevers (2002) found only a subtle threshold in the abundance of a simulated organism (see Fig. 3a of Flather and Bevers 2002), despite the fact that fragmentation explained 33-39% of the variation in abundance below that threshold. Further, the variation inherent in ecological data would make subtle thresholds difficult to detect (Flather and Bevers 2002, Lindenmayer et al. 2005). Since no thresholds were detected for the above species, this suggests that forest configuration either had little effect, or that its importance was constant over the entire gradient of forest cover.

The abundance of two forest species changed nonlinearly with forest amount. Downy woodpecker abundance suggested a threshold decline below about 10-20% forest, but was relatively constant above this threshold. Chickadee abundance peaked in landscapes with about 34% forest, and decreased above and below this level. Thus, above the threshold, neither species declined in proportion to forest loss. This is inconsistent with what the fragmentation threshold hypothesis would predict. Further, other analyses (Chapter 6) showed that the importance of forest configuration did not increase at lower levels of forest cover (<30%) for these species.

What, then, explains these nonlinear relationships between forest cover and the abundance of chickadees and downy woodpeckers? I suggest that these shapes resulted from a strong increase in chickadee density and a moderate increase in downy woodpecker density, in response to increasing fragmentation as forest cover decreased. Both species prefer forest edges (downy woodpeckers: Jackson and Ouellet 2002, chickadees: Smith 1993). As forest cover decreases, there is an increase in forest edge density. A corresponding linear increase in bird *density* (e.g. Fig 4.5a-b) would necessarily translate into a nonlinear relationship between abundance and forest cover (Fig. 4.5c-d). As the density-forest cover slope became steeper, the abundance-forest cover slope would become increasingly quadratic (Fig. 4.5d). A stronger increase in chickadee than in downy woodpecker density would be consistent with a personal observation in the field that chickadees in particular appeared more abundant near forest edges. The hypothetical abundance-forest cover shape in Fig. 4.5d (calculated from the strong linear density-forest cover slope) is qualitatively similar to the quadratic shape estimated for chickadees. The abundance shape in Fig. 4.5c (calculated from the moderate density slope) shows a less pronounced abundance "hump" preceding a steep decline at lower forest levels. The abundance-forest cover shape estimated for downy woodpeckers only loosely approximates this shape. However, the relatively subtle hump of Fig. 4.5c should make this shape more difficult to model accurately, particularly when variability is high and sample size is relatively small. Indeed, when I tried adding randomly generated sets of Poisson data (n=50) around the predicted values of Fig. 4.5c, these data often resembled those for downy woodpecker. Specifically, the hump was often obscured, suggesting instead a shallow slope preceding a more rapid decline below about 20% forest (e.g. Fig. 4.6). Thus, the asymptotic shape estimated for downy woodpecker abundance may have resulted from the combination real ecological patterns (a positive response to fragmentation) and experimental / statistical limitations (high variation and small sample size, which limit the ability to accurately model subtle nonlinearities).

The number of forest bird species that were abundant (i.e. present at greater than their median observed abundances) also declined shallowly until below a threshold of 25% forest. This nonlinearity was probably driven mainly by the nonlinear responses of chickadees and downy woodpeckers, since the relationship appeared nearly linear when these two species were removed (data not shown).

Discontinuous thresholds between species' abundance and forest proportion may be expected if the organism is tolerant to changes within broad ranges of forest proportion. Magpie and possibly crow abundance exhibited a discontinuous threshold with forest proportion, with a constant high mean abundance below 35% or 47% forest, respectively, and a constant low mean abundance above these thresholds. While both species use trees for nesting, roosting, and predator escape, open areas are important for foraging (Verbeek and Caffry 2002, Trost 1999). Thus, forest loss is not synonymous with either a loss or gain of "habitat", so one would not necessarily expect a direct (continuous) relationship between forest proportion and abundance. I speculate that for these species, a discontinuous threshold may be explained as follows. Over the range of forest cover below the threshold, any advantages gained by increasing forest may be balanced by a loss of foraging habitat (open areas, mainly agricultural land), so that abundance is uniform over this range of forest cover. The threshold may represent the point above which the advantages of greater forest cover plateaus, while the amount of good quality foraging habitat abruptly becomes too low to support a large population. Interestingly, above a discontinuous threshold of about 40% forest, open habitats become dominated by non-agricultural openings (up to about 45% of the 1km radius landscape; data not shown). These "natural" openings are mainly small forest gaps and wetland perimeters dominated by nonwoody vegetation, which may be less productive foraging habitats for crows and magpies than agricultural land.

4.2. Summary and management implications

The lack of thresholds in the decline of most forest species (hairy woodpecker, yellow-bellied sapsucker, red squirrel, blue jay, white-breasted nuthatch; shape unclear for ruffed grouse) suggests that fragmentation effects did not have a large absolute effect on species' abundances when the proportion of forest was low. This supports an analysis from Chapter 6 which suggested that the influence of three configuration metrics was small for these species, despite a *relatively* larger effect (compared to forest proportion) below 30% forest. Thus, there appears to be little potential for the negative effects of habitat loss on the abundance of these forest species to be lessened by managing for particular configurations of the remaining forest. The lack of threshold responses may seem disappointing to individuals who misinterpret threshold values to reflect adequate levels of habitat for the persistence of a population. However, persistence may be compromised well above the threshold, particularly if abundance declines with decreasing habitat prior to reaching the threshold.

In contrast, the nonlinear relationships between the abundance of downy woodpeckers and chickadee abundance suggests above 19 or 34% forest, respectively, forest loss either may have no detrimental effect or is compensated for by positive fragmentation effects. Thus, these thresholds *may* represent approximate target levels of forest for these species. Several notes of caution must follow this statement. As with all statistical estimates, these threshold estimates are only an approximation of the "true" threshold value, which could be higher (or lower). Second, high abundance may not always reflect reproductive fitness (Van Horne 1983, Bock and Jones 2004), and so may not always reflect the probability that a population will persist in the long term. Greater chickadee abundance did appear to be related to a larger ratio of fledglings to adults (Chapter 6), but this information was lacking for the other study species, as were demographic data such as growth rates. Finally, even if 19% and 34% forest reflects adequate targets for downy woodpeckers and chickadees, species-specific management is not usually realistic except in special cases (e.g. endangered species, game species). Nor would it be desirable for common species (such as downy woodpeckers and chickadees), since this approach may fail to maintain adequate levels of habitat for rarer or more sensitive species. Of the present study species, those with linear relationships may be the more sensitive, since their declines occurred over the full range of habitat proportion (~2-62%), rather than mainly over the lower range.

Corvids may be important nest predators for some forest nesting birds in agricultural areas (Andrén 1992, Rodewald and Yahner 2001, Herranz et al. 2002). Zanette and Jenkins (2000) suggested that the proportion of forest in the landscape may be more important than patch characteristics in determining the risk of nest predation by corvids. The discontinuous threshold decline of magpies above about 35% forest suggests that even moderate forest cover at the 1km radius scale could reduce this risk. Although a sharp threshold was less clear for crows, observed numbers were always relatively low above about 47% forest. For the reasons outlined above, these approximate thresholds should not be used as the sole factor in determining habitat retention / restoration targets for forest birds. However, where detailed demographic or fitness data are lacking, this information could be used (in conjunction with relevant ecological knowledge such as habitat preferences, home range sizes, reproductive rates, dispersal ability etc.) to help to identify real or hypothetical landscapes that are more likely to maintain viable populations for species that are susceptible to corvid predation.

Table 4-1. AICc and BIC weights for different model shapes describing species' abundance or community indices versus forest proportion.

		Model details			Model comparisons		
Species / community index	Model[A, B]	Coefficient(s) (S.E.)[C]	Constant (S.E.)	r^2	Final polynomial analysis model (α=0.05)	AICc weight[D]	BIC weight[D]
Hairy woodpecker	Null	n/a	2.05 (0.184)	0		0.00	0.00
	Linear	5.44 (0.651)	0.71 (0.200)	0.59	linear	**0.78**	**0.95**
	D1 (1)	(see linear model)	(see linear)	n/a)		n/a[F]	n/a[F]
	D2 (-0.5, 3)	-0.43 (0.151), 9.46 (2.379)	2.73 (0.478)	0.61		0.06	0.01
	C thresh (0.56)	4.98 (0.743), 18.2 (14.65)	0.77 (0.207)	0.61		0.16	0.04
	D thresh	n/a[E]	n/a[E]			n/a[E]	n/a[E]
Yellow-bellied sapsucker	Null	n/a	1.85 (0.251)	0		0.01	0.02
	Linear	5.90 (1.671)	0.981 (0.335)	0.21	linear	**0.69**	**0.82**
	D1 (2)	10.7 (2.914)	1.42 (0.253)	0.22		0.30	0.17
	D2 (-2, 0.5)	3.23e-3 (1.348e-3), 8.10 (1.965)	-1.62 (0.9104)	0.27		n/a[F]	n/a[F]
	C thresh (0.06)	-62.9 (34.04), 69.8 (34.49)	4.86 (1.942)	0.27		n/a[F]	n/a[F]
	D thresh	n/a[E]	n/a[E]	n/a[E]		n/a[E]	n/a[E]
Red squirrel	Null	n/a	0.79 (0.184)	0		0.00	0.00
	Linear	6.73 (1.252)	-0.15 (0.229)	0.38	linear	**0.97**	**1.00**
	D1 (1)	(see linear model)	(see linear)	n/a		n/a	n/a
	D2 (0, 3)	0.70 (0.288)	2.21 (0.704)	0.39		0.03	0.00
	C thresh (0.57)	6.34 (1.335), 47.7 (54.59)	47.7 (54.59)	0.37		n/a[F]	n/a[F]
	D thresh	n/a[E]	n/a[E]	n/a[E]		n/a[E]	n/a[E]
Blue jay	Null	n/a	0.97 (0.173)	0		0.00	0.00
	Linear	4.67 (1.071)	0.183 (0.234)	0.28	linear	**0.54**	**0.76**
	D1 (0.5)	4.24 (0.933)	-0.64 (0.384)	0.30		0.30	0.20
	D2 (0, 3)	0.69 (0.254), 3.90 (5.700)	2.35 (0.628)	0.31		0.03	0.00
	C thresh (0.07)	23.0 (13.76), -19.1 (14.28)	-0.91 (0.851)	0.31		0.12	0.04
	D thresh	n/a[E]	n/a[E]	n/a[E]		n/a[E]	n/a[E]
White-breasted nuthatch	Null	n/a	1.83 (0.182)	0		0.00	0.00
	Linear	4.91 (0.717)	0.62 (0.220)	0.49	linear	**0.56**	**0.77**
	D1 (0.5)	4.95 (0.706)	-0.46 (0.351)	0.51		0.31	0.19
	D2 (-0.5, 1)	-0.276 (0.255), 3.50 (1.489)	1.67 (1.000)	0.51		0.03	0.00
	C thresh (0.14)	10.3 (4.692), -6.19 (5.309)	8.79e-2 (0.503)	0.51		0.10	0.03
	D thresh	n/a[E]	n/a[E]	n/a[E]		n/a[E]	n/a[E]
Black-capped chickadee	Null	n/a	17.5 (1.217)	0		0.00	0.00
	Linear	19.3 (6.971)	14.1 (1.680)	0.14		0.00	0.00
	D1 (-0.5)	-3.97 (0.876)	29.8 (2.912)	0.30		0.00	0.00

Table 4-1. AICc and BIC weights for different model shapes describing species' abundance or community indices versus forest proportion.

		Model details			Model comparisons		
Species / community index	Model$^{A, B}$	Coefficient(s) (S.E.)^{C}	Constant (S.E.)	r^2	Final polynomial analysis model (α=0.05)	AICc weight^{D}	BIC weight^{D}
	D2 (1, 2)	140 (23.22), -208 (38.98)	4.93 (2.180)	0.46	degree-2	0.11	0.06
	C thresh (0.34)	74.2 (11.29), -150 (26.96)	8.44 (1.666)	0.48		**0.89**	**0.94**
	D thresh	n/a^{E}	n/a^{E}	n/a^{E}		n/a^{E}	n/a^{E}
Downy woodpecker	Null	n/a	4.28 (0.254)	0		0.00	0.02
	Linear	4.06 (1.279)	3.25 (0.393)	0.17	linear^{G}	0.15	0.33
	D1 (-0.5)	-0.83 (0.209)	6.37 (0.580)	0.25		**0.46**	**0.46**
	D2 (-2, -2)	-4.47e-2 (1.427e-2), -1.25e-2 (4.39e-3)	5.30 (0.341)	0.27		n/a^{F}	n/a^{F}
	C thresh (0.19)	17.1 (5.180), -17.0 (6.600)	1.81 (0.670)	0.28		0.38	0.18
	D thresh	n/a^{E}	n/a^{E}	n/a^{E}		n/a^{E}	n/a^{E}
Ruffed grouse	Null	n/a	0.73 (0.127)	0		0.00	0.01
	Linear	2.25 (0.753)	0.352 (0.172)	0.16	linear^{G}	0.05	0.14
	D1 (-0.5)	-0.40 (0.101)	2.00 (0.336)	0.25		0.29	0.40
	D2 (0, 3)	0.800 (0.2167), -5.21 (3.300)	2.56 (0.537)	0.27		0.04	0.02
	C thresh (0.39)	5.59 (1.245), -12.6 (3.894)	7.50e-3 (0.190)	0.31		**0.62**	**0.42**
	D thresh	n/a^{E}	n/a^{E}	n/a^{E}		n/a^{E}	n/a^{E}
American crow	Null	n/a	5.88 (0.521)	0		0.01	0.02
	Linear	-7.82 (2.364)	8.33 (0.880)	0.19	linear	**0.32**	**0.53**
	D1 (3)	-20.6 (5.833)	7.32 (0.621)	0.21		0.19	0.14
	D2 (1, 1)	-10.7 (3.225), -12.8 (9.503)	5.58 (2.268)	0.21		0.02	0.00
	C thresh (0.15)	22.8 (17.04), -34.9 (19.3)	5.16 (1.948)	0.24		0.15	0.06
	D thresh (0.47)	-3.70 (1.000)	7.04 (0.560)	0.22		0.31	0.24
Black-billed magpie	Null	n/a	2.94 (0.403)	0		0.00	0.00
	Linear	-9.58 (1.408)	6.41 (0.588)	0.49	linear	0.02	0.02
	D1 (2)	-14.1 (2.041)	5.39 (0.458)	0.50		0.01	0.00
	D2 (3, 3)	5.24 (16.18), 54.8 (31.13)	5.55 (0.521)	0.51		0.00	0.00
	C thresh (0.28)	-2.13 (4.900), -11.8 (7.410)	5.38 (0.866)	0.52		0.01	0.00
	D thresh (0.35)	-4.25)0.542)	5.25 (0.400)	0.56		**0.96**	**0.97**
# abundant forest bird species	Null	n/a	2.96 (0.293)	0		0.00	0.00
	Linear	7.71 (1.178)	1.05 (0.362)	0.47		0.02	0.05
	D1 (ln)	1.84 (0.239)	6.109 (0.454)	0.55	degree-1	0.36	**0.50**
	D2 (-2, -1)	01.12e-2 (3.621e-3), -0.49 (9.126e-2)	5.62 (0.432)	0.57		0.07	0.03
	C thresh (0.25)	17.8 (3.117)	-16.2 (4.694)	0.58		**0.47**	0.31
	D thresh (0.16)	2.97 (0.409)	1.42 (0.295)	0.52		0.08	0.10

Table 4-1. AICc and BIC weights for different model shapes describing species' abundance or community indices versus forest proportion.

		Model details			Model comparisons		
Species / community index	Model[A, B]	Coefficient(s) (S.E.)[C]	Constant (S.E.)	r^2	Final polynomial analysis model (α=0.05)	AICc weight[D]	BIC weight[D]
Forest bird evenness	Null	n/a	0.93 (3.900e-3)	0	linear (slope not sig.)	0.23	**0.51**
	Linear	3.60e-2 (2.094e-2)	0.93 (6.437e-3)	0.06		**0.34**	0.32
	D1 (3)	0.10 (5.645e-2)	0.93 (4.547e-3)	0.06		0.12	0.05
	D2 (-2, 3)	7.60e-6 (2.620e-5), 9.60e-2 (6.167e-2)	0.93 (5.849e-3)	0.07		0.01	0.00
	C thresh (0.21)	-3.30e-2 (7.837e-2), 9.62e-2 (0.1053)	0.94 (1.084e-2)	0.07		0.05	0.01
	D thresh (0.35)	1.834e-2 (8.363e-3)	0.93 (4.425e-3)	0.09		0.25	0.11

A. D1, D2 (degree-1, degree-2 polynomials); c thresh (continuous threshold); d thresh (discontinuous threshold)

B. Powers are given in brackets

C. Coefficients and standard errors are for: forest proportion (linear models); power transformation(s) of forest proportion (polynomial models); forest proportion and threshold term (continuous threshold models); threshold term (discontinuous threshold models).

D. Bold indicates the highest AICc or BIC weight, and grey highlights indicate models within the ≥90% confidence sets

E. Model not fit for this species

F. Model was fit, but either shape was biologically implausible, or the degree-1 polynomial was linear; dropped from AICc, BIC model sets

G. Initial comparison of the degree-2 and linear model was nearly significant (p=0.12 for downy woodpecker, 0.09 for grouse). A degree-1 model is selected if a more permissive alpha is used

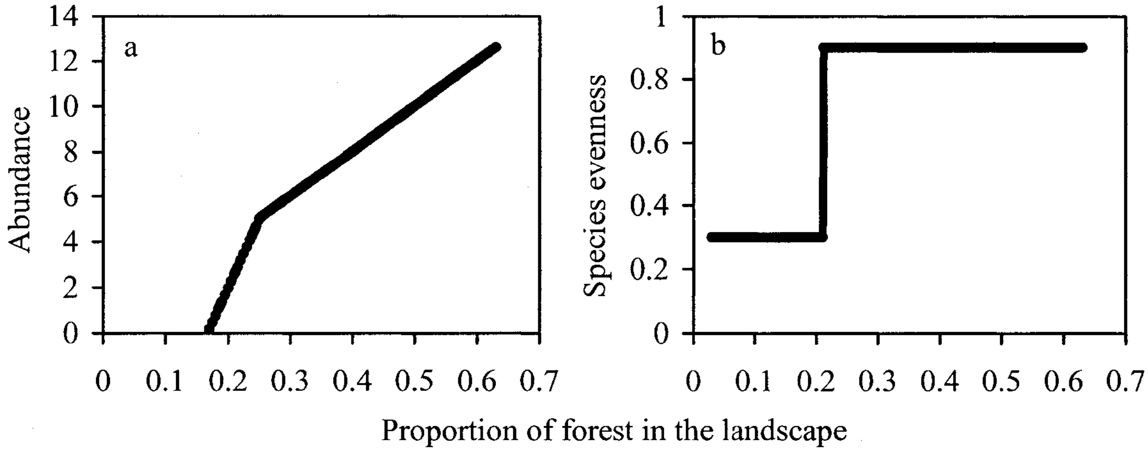

Fig. 4-1. Hypothetical continuous threshold (a) and discontinuous threshold (b) relationships with habitat proportion.

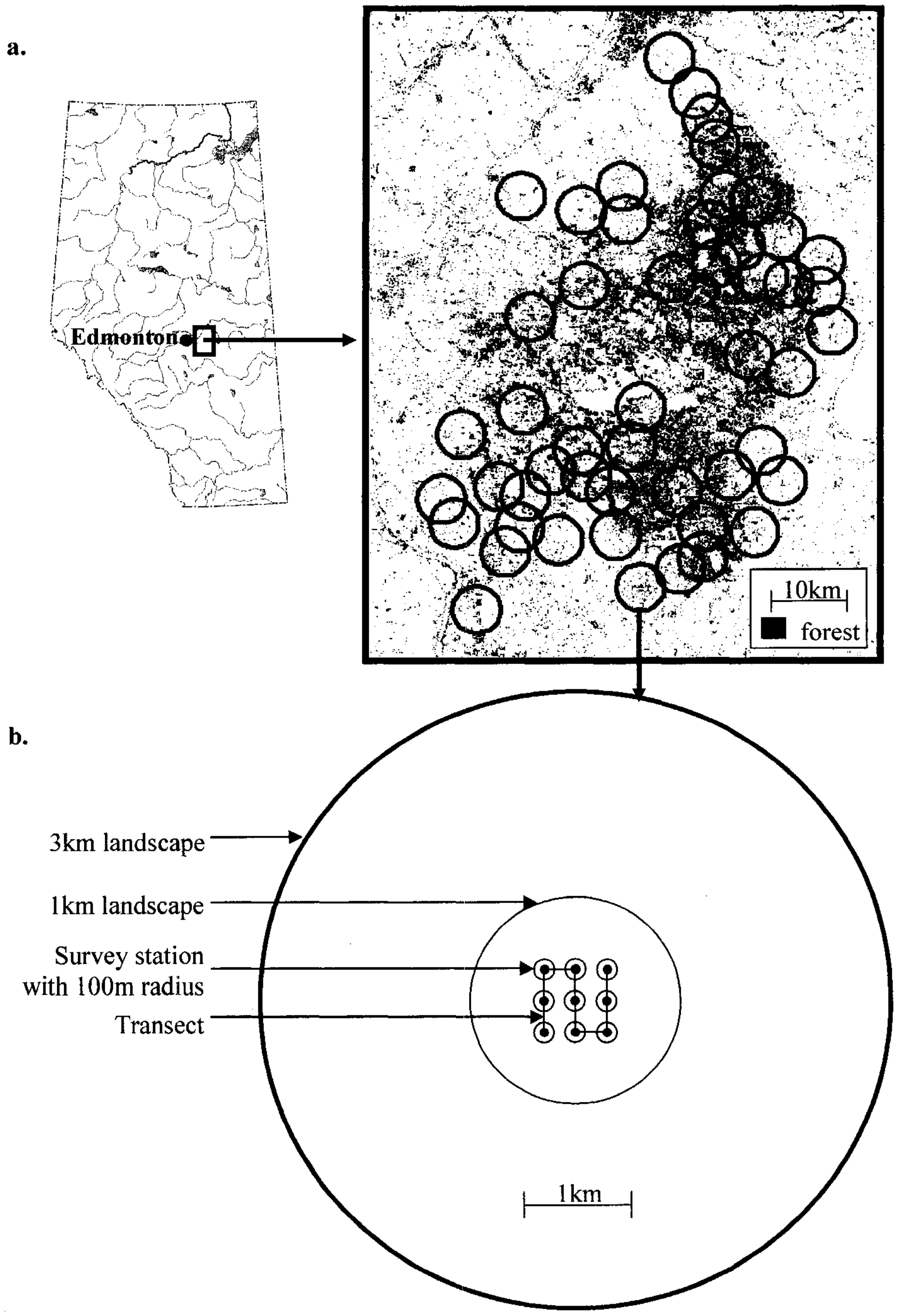

Fig. 4-2. a) Study area east of Edmonton, Alberta, showing all 3km radius landscapes; b) Schematic showing the lay out of survey stations and transects for one survey site, in relation to the 1km and the 3km radius.

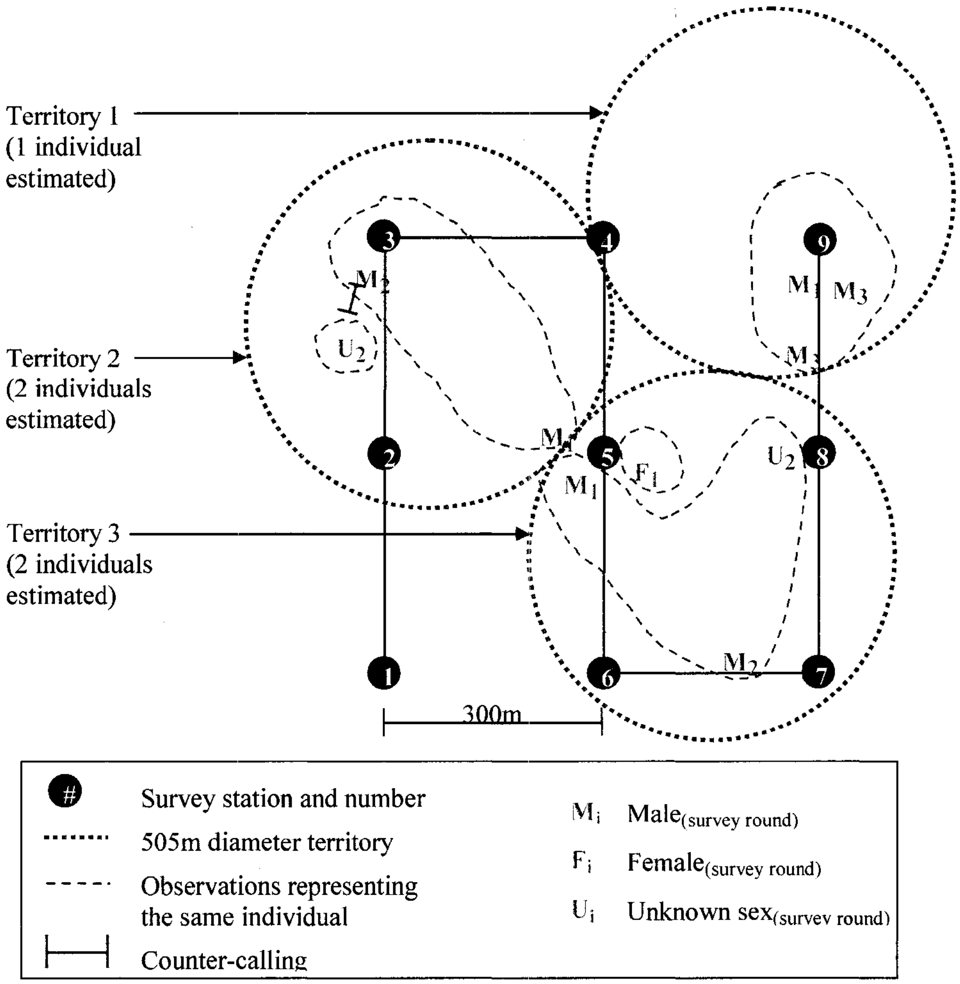

Fig. 4-3. Hypothetical example showing estimation of nuthatch or hairy woodpecker abundance for one year. In territory 1, three different observations of a male were counted as one individual, since they were <505m apart (less than the home range diameter of a hairy woodpecker or nuthatch), and not observed concurrently. In territory 2, three observations were made within 505m from one another, but two birds were heard counter-calling (i.e. at least two individuals present). In territory 3, both a male and a female were observed. The two observations of males near station 5 (one in territory 2 and one in territory 3) were different individuals, because they were seen at the same time. Alternative territory placements would not have reduced the minimum number of individuals estimated. For example, territory 1 could have included the unknown sex near point 8 and the male-female pair near point 5 (i.e. one more individual in territory 1 and one fewer in territory 3).

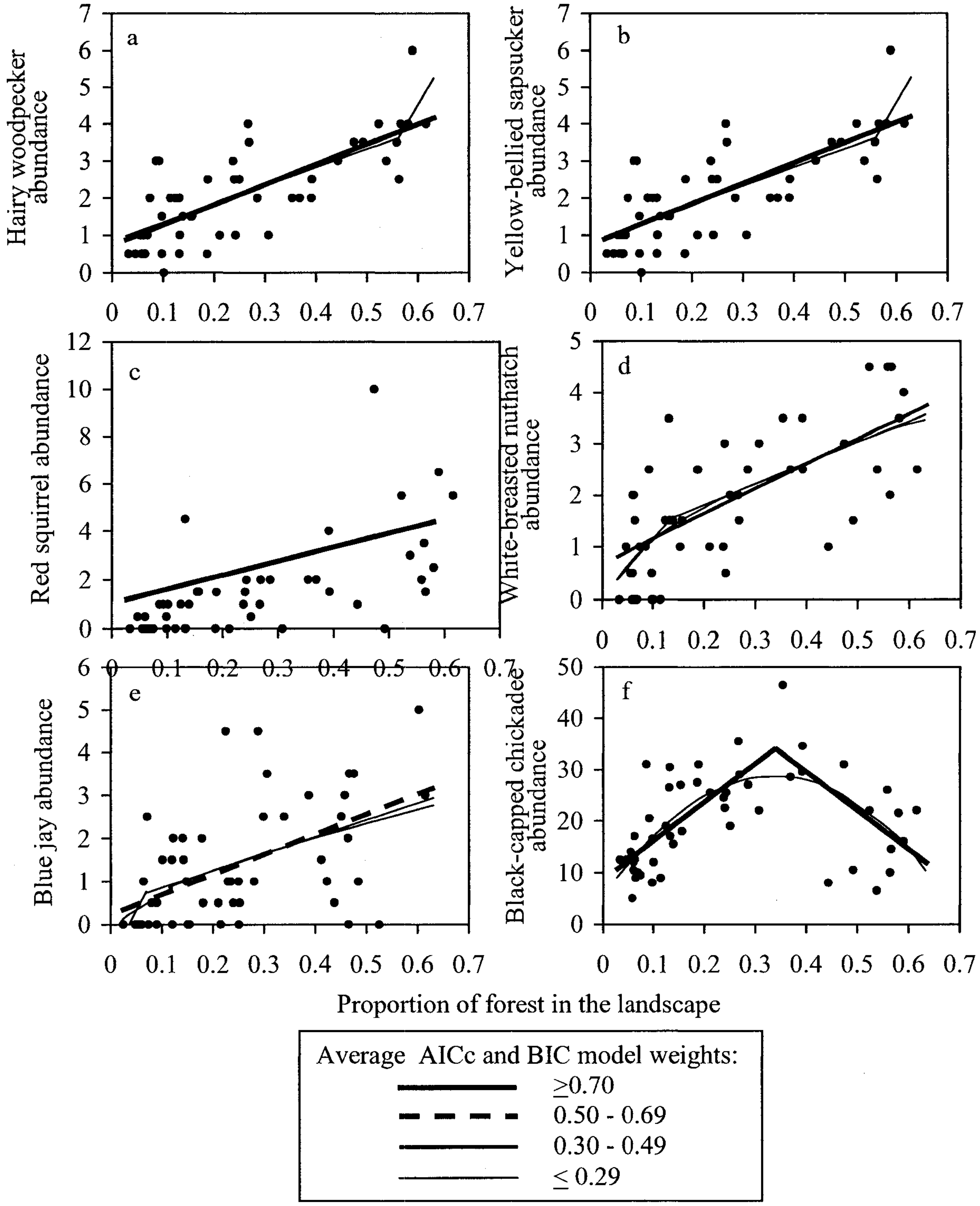

Fig. 4-4 a-f. Models included in the AICc or BIC confidence sets for the relationship between forest proportion and species' abundances or community indices. Average AICc / BIC weights for each model are reflected by the colour and weight of each regression line (see legend). Forest proportion was measured within 1km radius landscapes centred on each study site, except for the blue jay models, for which the best extent was a 3km radius (see next page

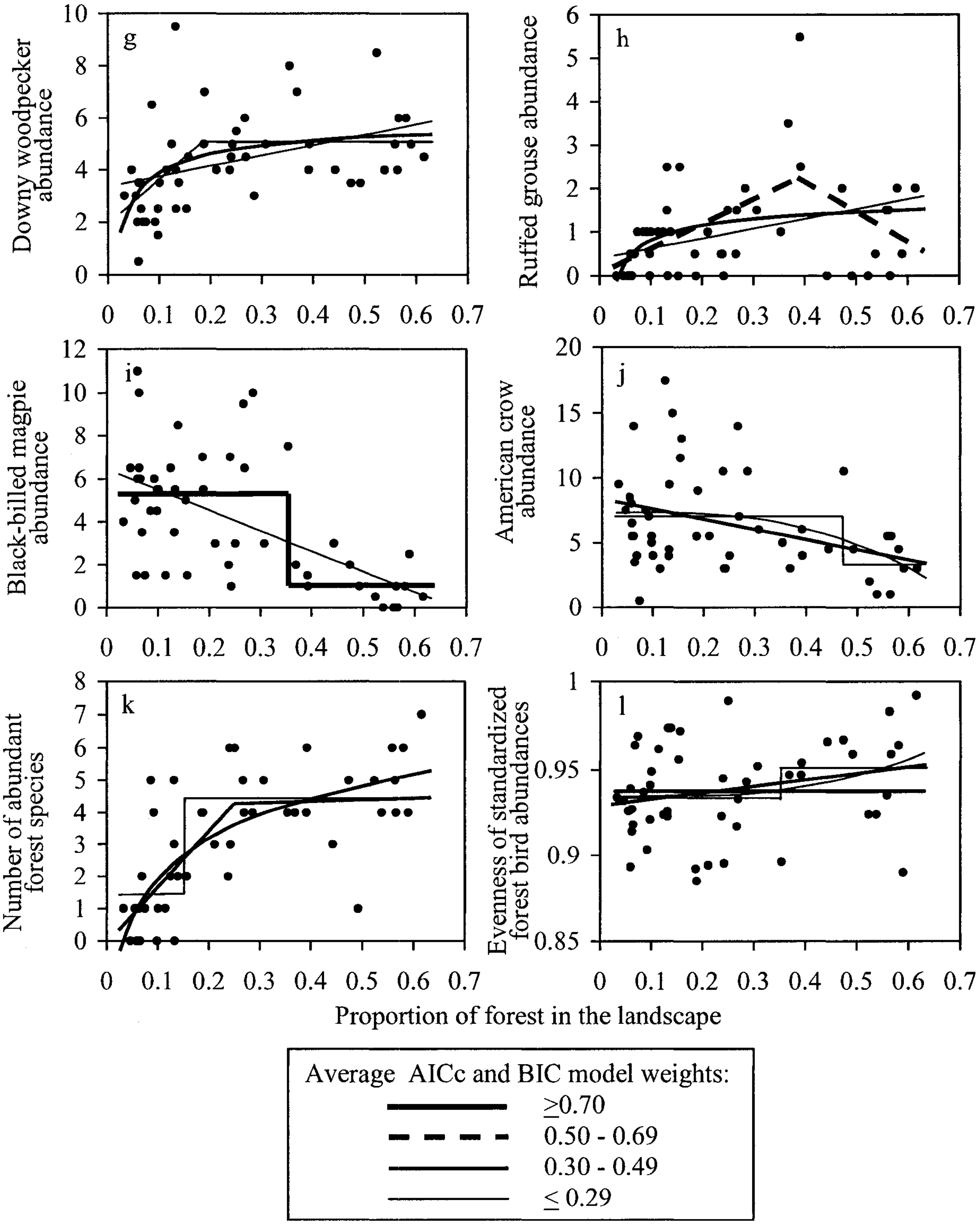

Fig. 4-4 g-l. See caption on previous page

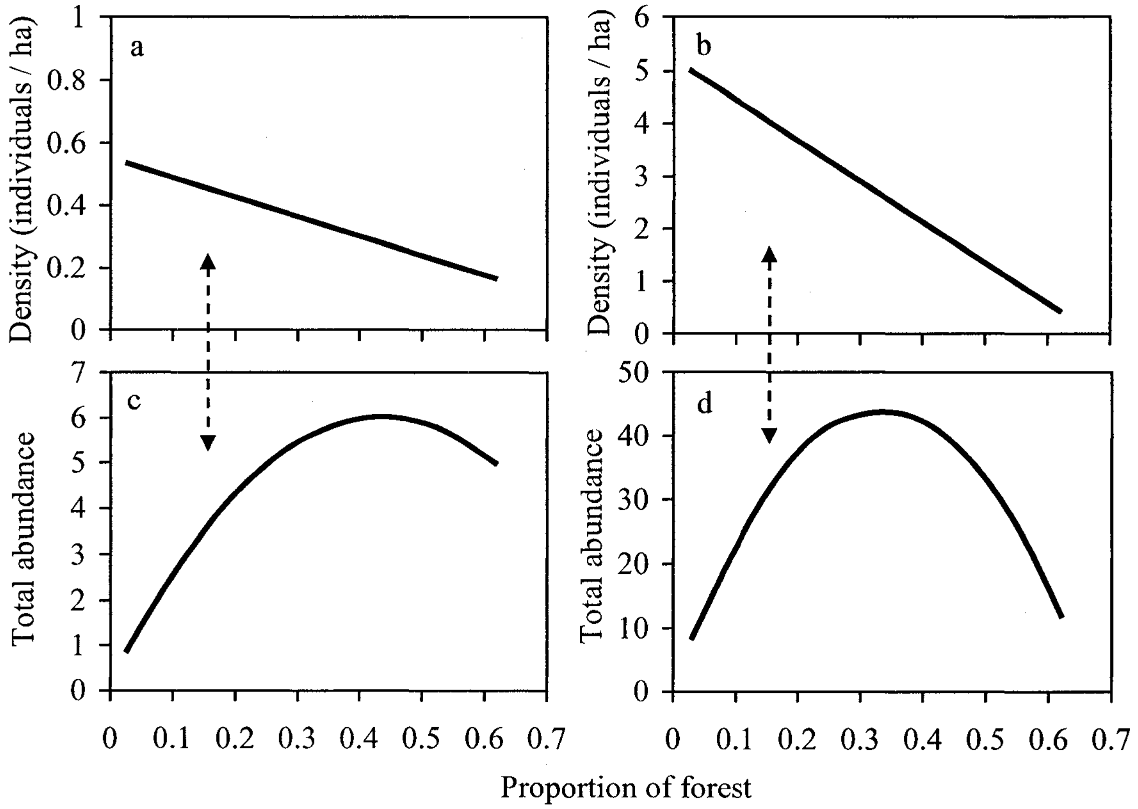

Fig. 4-5 a-c. Correspondence between hypothetical bird density vs. forest cover slopes and the shape of the relationship between bird abundance and forest cover. Abundance was calculated as density*forest proportion*50ha (the area actively sampled in each site during bird surveys, see methods). A. Moderate density vs. forest cover slope. B. Strong density vs. forest cover slope. C. Abundance vs. forest cover shape corresponding to the moderate density-forest cover slope. D. Abundance vs. forest cover shape corresponding to the strong densit y vs. forest cover slope.

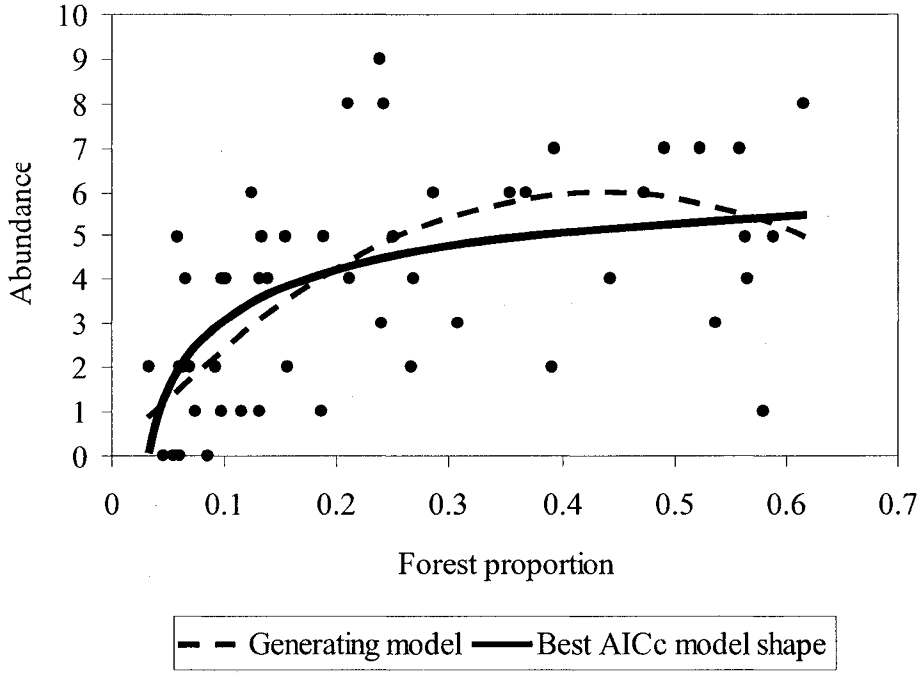

Fig. 4-6.. An example of Poisson abundance data generated around the abundance vs. forest cover shape shown in Fig. 4.5c. Although the generating model (dashed line) has a "hump", this is obscured by the variation in the data. Consequently, the best fitting model (according to AICc) is a simpler, degree-1 polynomial (solid line). This shape is similar to the best model for downy woodpeckers: a shallow decline preceding a more rapid decline below 10-20% forest.

References

Alfaro, M. E. & Huelsenbeck, J. P. 2006. Comparative performance of Bayesian and AIC-based measures of phylogenetic model uncertainty. *Systematic Biology* 55: 89-96.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73: 794-804.

Bibby, C. J. 1994. Recent past and future extinctions in birds. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 344: 35-40.

Bock, C. E. & Jones, Z. F. 2004. Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment* 2: 403-410.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S. & Hilton-Taylor, C. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16: 909-923.

Brooks, T. M., Pimm, S. L. & Collar, N. J. 1997. Deforestation predicts the number of threatened birds in insular Southeast Asia. *Conservation Biology* 11: 382-394.

Burnham, K. P. & Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261-304.

Dolby, A. S. & Grubb, T. C. Jr. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. *Condor* 408-412.

Dulvy, N. K. & Reynolds, J. D. 2003. Extinction vulnerability in marine populations. *Fish and Fisheries* 4: 25-64.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Flather, C. H. & Bevers, M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159: 40-56.

Herranz, J., Yanes, M. & Suárez, F. 2002. Does photo-monitoring affect nest predation? *Journal of Field Ornithology* 73: 97-101.

Herrera, C. M. 1978. On the breeding distribution pattern of European migrant birds: MacArthur's theme reexamined. *Auk* 95: 496-509.

Hurd, C. R. 1996. Interspecific attraction to the mobbing calls of black-capped chickadees (*Parus atricapillus*). *Behavioral Ecology and Sociobiology* 38: 287-292.

Jackson, J. A. & Ouellet, H. R. 2002. Downy woodpecker (*Picoides pubescens*). *In* The Birds of North America, No. 613 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Johnson, J. B. & Omland, K. S. 2004. Model selection in ecology and evolution . *Trends in Ecology and Evolution* 101-108.

Kilham, L. 1969. Reproductive behavior of hairy woodpeckers. III. Agonistic behaviour in relation to courtship and territory. *Wilson Bulletin* 81: 169-183.

Krebs, C. J. 1999. Ecological Methodology. Menlo Park, California: Addison-Wesley Educational Publishers, Inc.

Lahti, K., Orell, M., Rytkonen, S. & Koivula, K. 1998. Time and food dependence in willow tit winter survival. *Ecology* 2904-2916.

Lindenmayer, D. B., Fischer, J. & Cunningham, R. B. 2005. Native vegetation cover thresholds associated with species responses. *Biological Conservation* 124: 311-316.

Newton, I. 1994. Experiments on the limitation of bird breeding densities: A review . *Ibis* 136: 397-411.

Nilsson, S. G. 1987. Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *Journal of Animal Ecology* 56: 921-937.

Pravosudov, V. V. & Grubb, T. C. Jr. 1993. White-breasted nuthatch (*Sitta carolinensis*). The Birds of North America Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Qian, S. S., King, R. S. & Richardson, C. J. 2003. Two statistical methods for the detection of environmental thresholds. *Ecological Modelling* 166: 87-97.

Radford, J., Bennett, A. & MacRaild, L. 2004. How much habitat is enough? Planning for wildlife conservation in rural landscapes. Research booklet. http://www.deakin.edu.au/scitech/les/environment/staff/How%20much%20habitat%20is%20enough.pdf

Rodewald, A. D. & Yahner, R. H. 2001. Avian nesting success in forested landscapes: Influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* 118: 1018-1028.

Royston, P. & Altman, D. G. 1994. Regression using fractional polynomials of continuous covariates: parsimonious parametric modelling. *Applied Statistics* 43: 429-467.

Sherry, T. W. & Holmes, R. T. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.

Singh, J. S. 2002. The biodiversity crisis: a multifaceted review. *Current Science (Bangalore)* 82: 638-647.

Smith, S. M. Black-capped chickadee. 1993. *In* The Birds of North America, No. 39 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C: The American Ornithologists' Union.

StataCorp. 2005. Stata Statistical Software. Release 9. College Station, TX: StataCorp LP.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. & Waller, R. W. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306: 1783-1786.

Toms, J. D. & Lesperance, M. L. 2003. Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84: 2034-2041.

Trost, C. H. 1999. Black-billed magpie (*Pica pica*). *In* The Birds of North America, No. 389 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.

Verbeek, N. A. M. & Caffrey, C. 2002. American crow (*Corvus brachyrhynchos*). *In* The Birds of North America, No. 647 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

With, K. A. & King, A. W. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314-326.

Young, J. E., Sánchez-Azofeifa, G. A., Hannon, S. J. & Chapman, R. 2006. Trends in land cover change and isolation of protected areas at the interface of the southern boreal mixedwood and aspen parkland in Alberta, Canada. *Forest Ecology and Management* 230: 151-161.

Zanette, L. & Jenkins, B. 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. *The Auk* 117: 445-454.

Chapter 5: A review of the relative effects of habitat loss versus fragmentation: is it time to abandon the fragmentation bandwagon?

1. Introduction

The expansion of human activities across landscapes leads to major changes in the amount and spatial configuration of habitat, potentially the most important causes of species extinction (Bibby 1994, Singh 2002). There has been considerable debate over the relative ecological effects of these two phenomena (e.g. Fahrig 1997, Hiebeler 2000). *Habitat loss* refers to a reduction in the total amount of habitat in a landscape (Fahrig 1997). *Habitat fragmentation* is any change in spatial configuration that increases the number of habitat patches or increases the distance between them, independent of the total amount of habitat in the landscape (Fahrig 2003). In real landscapes, habitat loss and fragmentation tend to occur simultaneously, and are usually highly correlated (e.g. Bélisle et al. 2001, Villard et al. 1999). This makes it difficult to distinguish their independent ecological effects (Fahrig 1997), which may be profoundly different. Habitat loss may reduce population size and persistence by eliminating some vital resources, while fragmentation may do so via a number of mechanisms. These may include inhibition of dispersal among fragments, edge effects such as increased predation, or patch area effects that limit local population sizes (reviewed by Fahrig 2003). Positive effects of habitat fragmentation may also occur. For example, for a set amount of habitat, a greater number of patches would mean smaller inter-patch distances (less isolation), and some species may benefit from a greater density of edge habitats (Fahrig 2003).

Despite an enormous quantity of "fragmentation" literature, most studies have not explicitly accounted for concurrent habitat loss effects, or have equated habitat fragmentation with habitat loss (reviewed by Fahrig 2003). This has resulted in a relative paucity of evidence for the effects of fragmentation *per se* (Schmiegelow and Mönkkönen 2002, Fahrig 2003). The distinction between habitat loss versus fragmentation effects is important, since this will determine the most effective conservation strategies (Fahrig 1997, McGarigal and Cushman 2002). If fragmentation has a large negative effect over and above that due to habitat loss, then more aggregated configurations of habitat could effectively enhance the persistence of a population that has experienced habitat loss. However, if fragmentation has a very small effect relative to that of habitat loss, then habitat restoration would be a much more efficient conservation strategy.

1.1. Purpose and structure of review

The purpose of this review is to examine the evidence for the relative effects of habitat loss versus fragmentation on species' movement, prevalence, and persistence, and to explore possible reasons for any variation in the conclusions of different studies. There were two main criteria for the inclusion of a given study. First, the independent effects of habitat loss and fragmentation had to be distinguishable, either because these two variables were not highly correlated, or their correlation was removed statistically.

This eliminated most habitat loss/fragmentation studies. McGarigal and Cushman (2002) and Schmiegelow and Mönkkönen (2002) found a similar paucity of studies that distinguished between habitat loss and fragmentation. Second, habitat loss and fragmentation had to be measured at the landscape level, since this is the scale at which these phenomena occur (McGarigal and Cushman 2002). "Landscape" is defined loosely here, as a mosaic of habitat and non-habitat patches (or patches of varying quality) over an area large enough to be functionally relevant from a species-centred perspective (McGarigal and McComb 1995, Chust et al. 2004). Following the terminology of McGarigal and Cushman (2002), "landscape level" included a) "patch-landscape" studies, in which ecological responses within individual focal patches were measured and related to the landscape surrounding each patch, and b) "landscape" studies, in which ecological responses were measured within a mosaic of habitat patches and matrix.

A total of 31 studies were found that met both criteria. I will summarize these results, and suggests possible reasons for any differences in the conclusions among different studies. Potential sources of bias will also be considered, including how fragmentation was measured, the statistical approaches used, and the characteristics of the focal species. The review will conclude with a summary of major trends, conservation implications, and recommendations for future research.

2. Methods for comparing and summarizing results among and within studies

Fragmentation was quantified in different ways by different authors. Some used a set of metrics, each of which measured one particular aspect of fragmentation ("single-aspect" metrics). Essentially, these described: a) the amount of habitat-matrix edge; b) edge contrast between different habitat types; c) the amount of core (interior) habitat; d) the number and size of habitat patches; e) the shape of patches, often reflecting edge length relative to habitat area; or f) the distances or structural connectivity between patches, g) distance to a habitat-matrix edge, or h) variability in patch size, core area, or interpatch distances. Other studies used "overall" fragmentation metrics: a) principle components axes derived from several single-aspect metrics; or b) various indices of habitat aggregation (for the landscape as a whole, not patch averages), which probably correlate with several single-aspect metrics.

There was a similar variety in the methods used to quantify the relative effects of habitat loss and fragmentation. These included: a) the deviance explained by each habitat loss and fragmentation metric; b) standardized coefficients; c) the effect (change in the response variable) associated with variation in each metric, often indicated graphically; d) test statistics, p-values, or whether each metric was significant or not; e) number of species with significant responses to each metric; f) number of related response variables (e.g. movement pattern metrics) for which each metric was significant. I preferentially used deviance explained or standardized coefficients for comparing habitat loss and fragmentation effects (Table 5-1), if these were reported.

Some individual studies analyzed the data for more than one "case" (e.g. response variable, spatial extent, or range of habitat proportion), which sometimes yielded different results. Thus, in Table 5-1, results were recorded for each "case" rather than for each study as a whole. For each case, whether habitat amount or configuration had the larger effect was indicated with an upper-case bold "**X**" in the appropriate column. If an analysis used a set of single-aspect fragmentation metrics, their *combined* effect was compared to that of habitat loss as a single "case" where possible (e.g. total deviance explained, total number of species responding to fragmentation,) . This was intended to make the results of such analyses somewhat more comparable to those using "overall" fragmentation metrics. For interested readers, any cases representing combined fragmentation effects were broken down into the results for each individual single-aspects metrics, indicated with a lower case, non-bold "x" in Table 5-1.

3. Evidence for the relative effects of habitat amount versus configuration

3.1 Overview of results

The results of most analyses suggest that habitat amount had a larger effect on species movements, prevalence, and persistence than did habitat configuration (30 cases, Table 5-1). However, habitat configuration was occasionally equally or even more important (7 cases each). This variation suggests that the relative effects of habitat amount versus configuration may depend on ecological or experimental conditions. Indeed, there was considerable variation among studies in terms of which ecological response was measured, the characteristics and measurement of landscape attributes, and species characteristics. Below, I examine how these factors may have influenced the relative importance of habitat amount and configuration.

3.2. Potential sources of variation in the relative effects of habitat amount versus configuration

3.2.1. The response variable - movement, prevalence, or persistence

For all response types, habitat loss had a larger effect than did configuration in most cases, while habitat configuration had similar or larger effects only occasionally (movement: 6, 1, and 0 cases, respectively; prevalence: 19, 6, and 6 cases, respectively, persistence: 5, 0, and 1 case, respectively; Table 5-1). This similarity between these three response types is not surprising, given the interrelationships between movement, prevalence and persistence. An inability to move through the landscape may reduce population size (Cooper et al. 2002) and increase the chances of local or population extinctions (Fahrig 2001). Low population abundance is one of the most important determinant of population extinction risk (reviewed by McKinney 1997). Small populations may suffer low or even negative growth rates (Courchamp et al. 1999).

The way an ecological response is defined may influence our interpretation of the relative importance of habitat loss and fragmentation. Patch occupancy (the proportion *of remaining habitat* that is occupied) is a relative measure of abundance (Flather and Bevers 2002). Because patch occupancy is scaled to habitat amount, this should minimize the effect of habitat proportion, compared to when absolute measures of abundance are used. When Flather and Bevers (2002) re-analyzed their data using patch occupancy instead of population size as the response variable, the relative effect of fragmentation appeared larger (see Fig. 5 of Flather and Bevers 2002). Similarly, the relative effect of fragmentation was greater for population density (number of individuals per unit area of habitat) than for total population size in Henein et al.'s (1998) simulation (Table 5-1).

Flather and Bevers (2002) also found that while the effect of configuration on population abundance increased substantially at low levels of habitat, the effect on population persistence was small regardless of habitat amount. Flather and Bevers (2002) did not speculate on why this may have been. Their contrasting results may reflect a statistical effect of using a continuous (abundance) versus binary (persistence) response variable. The latter is a coarser measure of population response, and thus may be inherently less likely to reveal subtle fragmentation effects.

3.2.2. Characteristics and measurement of the landscape

A consistent finding among simulations is that as habitat cover decreases in the landscape, the effects of fragmentation become more important (e.g. for persistence: Henein et al. 1998, Schneider 2001, Flather and Bevers 2002, Jager et al. 2006, but see Fahrig 1997; for prevalence: Henein et al. 1998, Hill and Caswell 1999, With and King 1999, Flather and Bevers 2002, Jager et al. 2006; for movement: Ruckleshaus et al. 1997, Collingham and Huntley 2000, King and With 2002). Thus when habitat cover is low, fragmentation has the largest potential to compound the effects of habitat loss.

Based on a meta-analysis of empirical patch size and patch isolation studies, Andrén (1994) suggested that fragmentation effects become important below a 10-30% threshold level of habitat cover in the landscape. However, since patch size and isolation are correlated with landscape-level habitat loss, Andrén's results could instead reflect a stronger effect of habitat loss at low levels of habitat (Fahrig 2003). Relatively few empirical studies tested for a statistical interaction between habitat proportion and configuration. Where tested, these were usually either not significant, or were not consistent with a greater effect of fragmentation at low habitat cover (e.g. on prevalence: Guerry and Hunter 2002, Holland et al. 2005; on movement: McIntyre and Wiens 1999, With et al. 2002). Interactions consistent with a greater effect of fragmentation at low habitat cover are relatively rare (Trzcinski et al. 1999: occurrence of 1/31 species; Cumming and Schmiegelow 2001: occurrence of 8/34 species when habitat was defined as all mesic forest, but 0/34 species for old mesic or old deciduous; Betts et al. 2006: occurrence of 1/2 species).

The scale at which landscape attributes are measured may influence the outcome of the analysis. Two studies found that while habitat loss had a larger effect than configuration at the smallest extent (i.e. the radius most similar to the size of the survey site), habitat configuration had the largest effect at the largest extent (Langlois et al. 2001, Cooper and Walters 2002). Thus, habitat amount appeared to have mainly local effects, perhaps related to the carrying capacity of the survey sites. In contrast, habitat fragmentation appeared to be most important at broader scales, perhaps influencing the ability of the organisms to make long distance (e.g. dispersal) movements into the study site.

The relative effects of loss versus fragmentation can also depend on the way habitat is defined in relation to species perception of habitat. Cumming and Schmiegelow (2001) studied a suite of boreal birds, most of which were common in old aspen-dominated stands. The proportion of species responding to configuration (compared to habitat amount) increased as the definition of habitat was narrowed from all mesic forest to old deciduous forest (Cumming and Schmiegelow 2001). Fahrig (1997) noted that for forest "edge" species, loss of forest would overestimate actual habitat loss, since edge habitat density would increase as the proportion of forest decreased (Fahrig 1997). If "forest" was assumed to represent "habitat", this would reduce the apparent effect of "habitat loss". Consequently a larger relative effect of configuration (e.g. edge density) would be favored. Similarly, for forest interior species, forest loss would underestimate actual habitat loss (Fahrig 1997), hence overestimating the effects of *habitat* loss.

Finally, the type of anthropogenic disturbance in a landscape may influence organisms' responses to habitat loss or fragmentation (McGarigal and McComb 1995, Schmiegelow and Mönkkönen 2002). In agricultural landscapes, forest remnants are structurally isolated in a non-forest matrix that is probably inhospitable to many forest species. In contrast, regenerating forest in forestry systems is probably more hospitable and conducive to movement between preferred stand types than are agricultural fields. As well, habitat patterns are more temporally stable in agricultural systems (McGarigal and McComb 1995, Schmiegelow and Mönkkönen 2002). Fragmentation effects may be important only where habitat patches are stable relative to the generation time of the organism (Fahrig 1992). Thus, fragmentation may be expected to have more severe effects in an agricultural system (McGarigal and McComb 1995). There is some empirical support for this idea: edge-related bird nest predation is generally more prominent in agricultural than forestry systems (Chalfoun et al. 2002).

3.2.3. Species characteristics

Simulations predict that the relative effect of fragmentation should be greater for species with smaller dispersal distances (e.g. on movement: King and With 2002; on prevalence: With and King 1999, Wiegand et al. 2005) and for species unable to cross the matrix (King and With 2002). This makes intuitive sense: for less vagile species, successful dispersal to a new habitat pixel will depend more strongly on local habitat abundance (i.e. greater habitat clustering), compared to species capable of dispersing farther and / or crossing gaps between habitat patches. This effect may explain the surprising results of Hiebeler (2000), who found that habitat configuration strongly influenced patch occupancy, while habitat amount had no effect at all. In this simulation, propagules were sent from habitat pixels to one of the adjacent four pixels. If a propagule landed in a non-habitat cell, it died. Since fragmentation was defined by the probability that an adjacent pixel was also habitat, fragmentation alone determined the probability that a propagule landed in suitable habitat (Hiebeler 2000).

Direct empirical evidence for the effect of species' vagility on relative configuration effects is scarce. However, Guerry and Hunter (2002) noted that two of the three amphibian species responding to habitat configuration were the least vagile of the nine studied. These two species migrate seasonally between pond (breeding) and forest (wintering) habitats, and were more likely to be present in ponds that were directly adjacent to forest. Of the more vagile species with similar habitat requirements, none were influenced by pond-forest configuration (Guerry and Hunter 2002)

With and King (1999) also found that the relative effect of habitat configuration on patch occupancy was greater for simulated species with lower reproductive output, which had a larger effect than dispersal ability. Presumably, high reproductive rates helped to offset the effects of habitat fragmentation by increasing the chance that at least some propagules dispersed successfully. Species with greater reproductive rates may have a lower risk of extinction in general (reviewed in McKinney 1997, Henle et al. 2004)

3.3. Direction of habitat loss and fragmentation effects

While habitat loss effects were predominantly strong and negative, fragmentation had positive, negative, or no effect among the studies reviewed (Table 5-1; see also Bennett et al. 2006 for a review that includes community-level responses). Much of this variation comes from empirical studies; simulations primarily indicated negative fragmentation effects. This may reflect a tendency for simulation models to assume certain species or landscape characteristics that increase the negative effects of fragmentation, while real species and landscapes are more variable. For example, many species are capable of moving through the matrix, and some species move more quickly through landscapes as habitat loss and fragmentation increase (Matthysen et al. 1995, Diffendorfer et al. 1995). Some species may suffer from increased brood parasitism or predation at habitat edges (reviewed by Paton 1994, Batary and Baldi 2004), but this may be more strongly associated with agricultural than forested / forestry landscapes (reviewed by Chalfoun et al. 2002, Morrison and Hahn 2002, see also Bayne and Hobson 1997, Rodewald and Yahner 2001). Other species may benefit from more abundant food near habitat edges (Rodewald and Brittingham 2002) or nest resources (Aitken et al. 2002), and still others may be relatively unaffected by habitat edges.

However, when inter-patch distances or physical corridors were significant predictors of ecological response, the direction of the effect almost always indicated a negative fragmentation / isolation effect (on simulated abundance and persistence: Henein et al. 1998; on real species' occurrences: Villard et al. 1999 (3/3 species); Guerry and Hunter 2002 (2/2 species requiring the relevant habitat types), Westphal et al. 2003 (8/10 species, considering each species' best model only)). Both may play a role in the functional connectivity of a landscape (Tischendorf and Fahrig 2000). These metrics specifically attempt to describe the spatial arrangement of habitat patches *in relation to one another.* Others generally describe quantities, either absolute (e.g. total edge), average (mean patch size), or relative (e.g. habitat area to edge ratios). This, along with the consistently negative responses to inter-patch isolation, suggests that it might be useful to conceptually separate metrics of relative position from other, more quantitative metrics of structural fragmentation.

4. Potential sources of bias

4.1. Relative difficulty in defining habitat loss versus fragmentation

The greater difficulty in adequately measuring habitat fragmentation (compared to habitat loss) creates a potential bias against finding frequent or strong habitat fragmentation effects. That habitat loss should have a negative effect on populations is usually clear *a priori*, since habitat is defined by the observed requirements of a particular species. Habitat loss is easy to quantify, while fragmentation is qualitative in nature and more difficult to translate into a functionally relevant quantitative metric. For example, even for a set amount of habitat, the "mean nearest neighbour" distance between habitat patches in a landscape may fail to reflect the number and size of gaps a translocated bird may have to cross to return to its territory (Bélisle et al. 2001).

Further, the *range* of spatial configuration values that creates functional fragmentation is probably not well understood for many species. For example, while most black-capped chickadees are willing to cross forest gaps of 50m in response to conspecific mobbing calls, few are willing to cross 100-200m gaps (Desrochers and Hannon 1997, St. Clair et al. 1998, Bélisle and Desrochers 2002). Thus, one might expect that inter-patch distances less than 50m, or well above 200m, would have little effect on chickadee movement. However, the distance an organism is willing to cross may increase if there are large benefits to doing so, such as obtaining a rich food supply (Grubb and Doherty 1999), or securing a breeding territory. Thus, unless it is known that fragmentation has been measured within a reasonably large and species-relevant portion of the gradient, any statements about the "relative" effects of habitat loss versus fragmentation must be qualified as applying only within the sampled gradient. Given the complex and species-specific nature of fragmentation, this is unlikely to ever be achieved completely.

4.2. Statistical sources of bias

Unlike most simulation studies, in empirical studies habitat proportion and configuration were often highly correlated. This was frequently dealt with by regressing the configuration variables against habitat amount, and using the regression residuals as the measure(s) of configuration. However, if habitat amount and fragmentation are highly correlated, then comparing the effect of a raw measure of habitat amount with configuration residuals introduces a potential bias in favour of finding a larger effect of habitat proportion over configuration. This is because configuration residuals are less variable than the raw metrics (it is difficult to detect an effect of a variable that lacks variability), while habitat proportion retains its full variability. Second, the configuration residuals have had any statistical correlation with habitat amount removed, while the habitat amount metric remains correlated with the raw configuration metric. Thus, the effect of configuration residuals should be viewed as a conservative indication of configuration effects (Villard et al. 1999). See Villard et al. (1999), Drolet et al. (1999), and Cumming and Schmiegelow (2001) for additional discussion on this topic.

4.3. Focal species commonness

There is a tendency for empirical studies to focus on more common species (e.g. McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999) because of logistical and statistical constraints. However, the rarer species may be more at risk of declines due to habitat loss / fragmentation (Davies et al. 2000, Goodsell and Connell 2002, Henle et al. 2004) and of extinction in general (reviewed by McKinney 1997). I am not aware of any studies comparing the relative effects of habitat loss and fragmentation for rare versus common species.

5. Concluding remarks

5.1. Summary and conservation implications

Overall, habitat loss had large, negative effects on species' movement, prevalence, and persistence, while fragmentation effects were generally weaker and more variable in their direction. The relative strength of fragmentation effects may depend on the response variable, the characteristics and measurement of the landscape, and on species characteristics (summarized in Table 5-2). In particular, the relative influence of fragmentation may be greater for continuous (e.g. abundance) than binary (e.g. persistence) response variables; and for measures of population abundance that are scaled to habitat amount (e.g. patch occupancy or population density) than for absolute measures of abundance. The relative strength of fragmentation effects may also increase as a) the proportion of habitat in the landscape decreases, b) the spatial extent around the survey sites increase; and c) landscapes more closely resemble a binary habitat / nonhabitat system. In addition, if habitat is defined more broadly than species' perception of habitat, the relative effect of configuration may appear either larger (e.g. for edge species) or smaller (e.g. for interior species or habitat specialists). Finally, species with limited vagility and reproductive rates may have a greater relative sensitivity to fragmentation.

Is it time to abandon the fragmentation bandwagon? Perhaps not entirely, but the concept of fragmentation must not be allowed to overshadow that of habitat loss. From a strictly conservation point of view, more habitat is better, regardless of its configuration. From a practical perspective, however, human needs and desires often preclude this ideal. It is under low habitat conditions that simulations suggest fragmentation may have its largest effects over and above those of habitat loss, particularly for species with low vagility and reproductive output. However, this idea requires further empirical tests. Further, because the direction and strength of fragmentation effects appear to be species-dependent, generic approaches to fragmentation management are not appropriate. The most practical conservation approach may be to use a combination of "coarse-filter" and "fine-filter" strategies (Noss and Cooperrider 1994). For example, habitat preservation or restoration (e.g. in a park /reserve) would likely benefit many species, while management of habitat configuration could be geared towards species that experience strong, negative fragmentation effects. This might include efforts to reduce inter-patch distances in the landscape surrounding the reserve (since when inter-patch distances were significant, most species responded negatively). This may serve to enhance dispersal between the reserve and the surrounding habitat remnants.

5.2. Future direction

A more complete understanding of the relative effects of habitat loss and fragmentation will require several issues to be addressed in future studies. First, the study design should allow the separation of the independent effects of habitat loss and fragmentation in the landscape. I found only 31 studies on species' movement, prevalence, or persistence that met this criterion. Where possible, researchers should select a set of landscapes for which habitat amount and configuration are not highly correlated. Using statistical methods to remove existing correlation from configuration metrics may create a bias against finding fragmentation effects.

Second, the spatial scale (i.e. extent and grain) of the landscape replicates should be potentially relevant to the species and response variable, and this rationale should be explicitly stated (McGarigal and Cushman 2002). Often, a multi-scale approach may be useful for exploring a range of scales, since the best scale(s) may not be known *a priori*; and the environment may be perceived at different scales by an organism, depending on the life-history stage (Orians and Wittenberger 1991, Levin 1992). Further, the scale at which fragmentation is measured will influence the value of fragmentation metrics (Saura 2004). For example, a coarse-grained map will not detect small patches and gaps, fine edge convolutions, or narrow strips such as fence-rows, which may be irrelevant for some species but important for others. GIS technology makes such multi-scaled approaches fairly easy to accomplish.

Third, the question of relative habitat loss versus fragmentation effects is inherently a management / conservation issue. Therefore, researchers should consider the conditions under which their results may have applied uses or theoretical relevance.: 1) When habitat cover is low, management actions may be most important, and fragmentation effects may be most pronounced (Andrén 1994, Fahrig 1998). Where sample sizes permit, it would be useful to compare the results obtained for a wide range of habitat cover to those obtained from a data subsample restricted to a lower range of habitat. 2) Certain response variables may be more relevant to management than others. Dispersal, reproduction and mortality themselves are of greater interest (McGarigal and Cushman 2002) than numeric responses such as presence or abundance, which may not always reflect local or current habitat quality (Van Horne 1983, Bock and Jones 2004). A major constraint to obtaining dispersal, reproductive or mortality data is the difficulty in obtaining such measures with a sufficient degree of replication at the landscape scale. However, GPS technology can be useful for tracking movement across landscapes (e.g. Linke et al. 2005), but can be costly. For birds, measures of reproductive success do not necessarily require detailed nest observations. Indices such as the presence or abundance of fledglings may suffice (Vickery et al. 1992, Weatherhead and Dufour 2000). These data are relatively simple to obtain for some species during landscape-level sampling (personal observation), but may be more difficult in dense habitats (Rangen et al. 2000). 3) There is also a need for future research to focus on the relative effects of habitat loss and fragmentation for less common species. Obtaining sufficient sample sizes for rare species will often require greater planning. For example, prior to landscape selection, areas where the species is more likely to occur could be identified using existing large-scale survey data (e.g. North American Breeding Bird Survey), or by applying predictive models to GIS images of potential study sites (e.g. Mitchell et al. 2001, Luoto et al. 2002).

Fourth, if the explicit purpose of a study is to compare the r*elative effects* of habitat loss versus fragmentation, it would be most informative to report comparable, statistical measures of importance (e.g. percent deviance explained, standardized coefficients) for each metric individually, and to show each metric's partial effect graphically. Although p-values (and thus test statistics) are correlated with effect size when sample sizes are the same, they do *not* indicate an absolute effect size (Vaske 2002). On their own, such statistics have limited utility in examining the importance of habitat amount and configuration.

Finally, to better understand the relative effects of habitat loss and fragmentation, we need a better understanding of what constitutes fragmentation for a given species. What aspects of fragmentation are important (e.g. patch size, edge effects, distance between patches) and over what range? For example, Fahrig (1998) found fragmentation to influence population survival only when distances between breeding patches were 1-3 times smaller than dispersal distances. Often, however, the range of structural fragmentation will be dictated by the study area, and / or a functional definition of fragmentation will be poorly understood for the focal species. For the time being many studies will be (and have been) exploratory, employing purely structurally-defined metrics of fragmentation. This may be unavoidable in some cases, but must be acknowledged in any discussion of the relative effects of habitat loss versus fragmentation.

Table 5-1. Summary of studies comparing the relative effect of habitat amount versus configuration

					Habitat amount effects			Configuration effects			Relative strength[H]		
Source[A]	Study type[B]	Response[C]	Taxon[D]	Landscape size	Habitat range (%)	Direction (if increase loss)[E]	Magnitude	Metrics (* = distance / isolation metric)[G]	Direction (if increase frag)[E]	Magnitude	Loss > config.	Loss ~ config.	Loss < config.
Ecological response = movement													
1	S	Disp. succ.	G	118 x 118 cells	2-24	N	Effect moderate (~70-95% success) to large (~30-90% success), depending on config.	PS	P	Effect small (none) to moderate (e.g. 30-65% success), depending on habitat amount	X		
2	S	Disp. succ.	B	76800 ha	n/a	N	Effect moderate (~0-7.5% success) to large (~0-55%), depending on config., sex, status.	AI	N	Effect small (none) to moderate (~25-50% success), depending on habitat amount, sex, status.	X		
3	S	Disp. succ.	G	128 x 128 cells	0.1-90	N	Effect small (~95-100% success) to large (~0-100% success), depending on config. & disperser type	AI	N	Effect small (~95-100% success) to large (~5-85% variance explained), depending on habitat amount & disperser type		X	
4	S	Mgr. rate	P	800 x 200 cells	1-90	N	Effect moderate (~16-30km/year) to large (~0-30 km/year), depending on config.	AI	P	Effect small (none) to large (~3-24 km/year), depending on habitat amount.	X		
5	E	Hom. succ.	B	range	14-98	N	G = 19.5	4 combined:	?, x	One metric sig., G=5.2	X		
							" "	NNCV *	?	G = 5.2	x		
							" "	NP	x	Not sig.	x		
							" "	TE/CA	x	Not sig.	x		
							" "	MNN *	x	Not sig.	x		
6	E	Patterns	I	5 x 5m	10-20	N, P	Sig. for 4-5 movement metrics (depending on config.)	AI	P	Sig. for 0-5 movement metrics, depending on habitat cover	X		
7	E	Patterns	I	16 x 16 m	10-80	N	Sig. for 1/5 movement metrics (15% variance explained)	AI	P	Sig. for 1/5 movement metrics (1% variance explained)	X		
Ecological response = prevalence													

Table 5-1. Summary of studies comparing the relative effect of habitat amount versus configuration

					Habitat amount effects			Configuration effects			Relative strength[H]		
Source[A]	Study type[B]	Response[C]	Taxon[D]	Landscape size	Habitat range (%)	Direction (if increase loss)[E]	Magnitude	Metrics (* = distance / isolation metric)[G]	Direction (if increase frag)[E]	Magnitude	Loss > config.	Loss ~ config.	Loss < config.
8	S	Abn.	M	15700 ha	50-99	N	Effect large (population size ~0-100), regardless of config.	NP	N	Effect small (no effect) to moderate (e.g. population size ~0-40), depending on habitat amount	X		
9	S	Abn.	M	27 x 27 cells	0-100	N	Effect moderate (populated cells 0 - 300) to large (0 - 650), depending on config.	NP	N	Effect small (populated cells ~0-10) to moderate (~0-250), depending on habitat amount	X		
10	S	Abn.	M	50 x 50 cells	10-25	N	68% variance explained	AI	N	12% variance explained	X		
11	S	Abn.	B	32 x 32 cells	10-90	N	97% variance explained	AI	N	<1% variance explained	X		
					10-50	N	30-52% variance explained	AI	N	6-10% variance explained	X		
					10-50	N	37-49% variance explained	4 combined:	N, P	33-39% variance explained		X	
							Stand. coefficient 0.82-0.92 depending on highest proportion of habitat included	LPE	N	Not sig. or stand. coefficient = -0.49, depending on highest proportion of habitat included	x		
							" "	TE	N	Not sig. or stand. coefficient = -0.83, depending on highest proportion of habitat included	x		
							" "	NP	P	Stand. coefficient 0.17-0.54 depending on highest proportion of habitat included	x		
							" "	LPS	N	Stand. coefficient = 0.26-1.08 depending on highest proportion of habitat included	x		
12	S	Abn.	M	64 x 64 cells	10-50	N	29% variance explained	2 combined:	N	47% variance explained			X
							" "	NP	N	3% variance explained	x		
							" "	CORQ *	N	44% variance explained			x

Table 5-1. Summary of studies comparing the relative effect of habitat amount versus configuration

					Habitat amount effects			Configuration effects			Relative strength[H]		
Source[A]	Study type[B]	Response[C]	Taxon[D]	Landscape size	Habitat range (%)	Direction (if increase loss)[E]	Magnitude	Metrics (* = distance / isolation metric)[G]	Direction (if increase frag)[E]	Magnitude	Loss > config.	Loss ~ config.	Loss < config.
12	S	Dens.	M	64 x 64 cells	10-50	N	4% variance explained	2 combined:	N	73% variance explained			X
							" "	NP	N	4% variance explained		x	
							" "	CORQ *	N	69% variance explained			x
13	S	Ptch occ.	G	256 x 256 cells	0-100	N	Effect always large (ptch occ. ~0-max for spp.) regardless of config.	AI	N	Effect small (none) to large (ptch occ. ~0 - near max. for spp.), depending on habitat proportion	X		
14	S	Ptch occ.	G	128 x 128 cells	10-100	N	Effect sometimes small (no effect); usually large (ptch occ. ~0-maximum for spp.), depending on config. & spp. characteristics	AI	N	Effect always small (none) when habitat cover high; often large otherwise (ptch occ. 0 - near maximum for spp.)	X		
15	S	Ptch occ.	G	180 x 180 cells	0-100	x	Effect small (no effect)	AI	N	Effect large (ptch occ. ~0 - 60%)			X
16	E	Abn.	B	25-400 ha	e.g. ~0-99 (young)	N, P	Sig. for 16/25 spp.	4 combined:	P, N	Sig. for 7/25 spp.	X		
							" "	TCA	P, N	Sig. for 4/25 spp.	x		
							" "	CWE	P, N	Sig. for 5/25 spp.	x		
							" "	NP	x	Not sig.	x		
							" "	MSI	x	Not sig.	x		
17	E	Abn.	B	250 - 300 ha	7-100	N	Average % variance explained / spp. = 21.88	25 combined:	P, N	Average % variance explained / spp. = 24.7		X	
							" "	CWED, ED, LCAS, MCA, MCAI, MECI, TECI	P	Average % variance explained / spp. = 1.12 - 4.53	x		
							" "	MPFD, MPS, TCAI	N	Average % variance explained / spp. = 2.12-2.29	x		

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Source[A]	Study type[B]	Response[C]	Taxon[D]	Landscape size	Habitat range (%)	Direction (if increase loss)[E]	Magnitude	Metrics (* = distance / isolation metric)[G]	Direction (if increase frag)[E]	Magnitude	Loss > config.	Loss ~ config.	Loss < config.
							" "	CACV, PSCV	?	Average % variance explained / spp. = 0.94-2.82	x		
							" "	15 others	x	Not sig.	x		
18	E	Pres.	B	28-1256 ha	~0-100	N	~18-30% variance explained	2 combined:	N, x	~0-12% variance explained	X		
							In best model for 2/2 spp.	PS	N, x	In best model for 1/2 spp.	x		
							" "	EDIST	x	Not in best model for either spp.	x		
19	E	Pres.	B	100 ha	2-90	N	Sig. for 3/14 spp. after partialling out effects of config.	2 combined:	x	Not sig. after partialling out effect of habitat amount	X		
							" "	TCA	x	Not sig. after partialling out effect of habitat amount	x		
							" "	TE	x	Not sig. after partialling out effect of habitat amount	x		
20	E	Pres.	A	314 ha	10-98	N	Sig. for 7/9 spp.	PFADJ *	N	Sig. for 3/9 spp.	X		
21	E	Pres.	I	615 ha	~0-95	N	Sig.	AI	x	Not sig.	X		
22	E	Pres.	B	28 ha	8-100	N	Sig.	TE	x	Not sig.	X		
23	E	Pres.	B	314 ha	?	N	Sig.	4 combined:	x	Not sig.	X		
							" "	ED	x	Not sig.	x		
							" "	MNN *	x	Not sig.	x		
							" "	MPS	x	Not sig.	x		
							" "	MSI	x	Not sig.	x		
24	E	Pres.	B	1000 ha	n/a	N	Sig. for 3/3 spp. (Chi squared = 7.71-27.17)	PCA	N	Sig. for 2/3 spp. (Chi squared = 5.05-7.44)	X		
25	E	Pres.	B	10000 ha	2-56	N	Sig. for 25/31 spp. (slopes[I] = 0.58-1.83)	PCA	N, P	Sig. for 6/31 spp. (slopes[I] = 0.52-1.11)	X		
26	E	Pres.	B	625 ha	3-67	N	Sig. for 8/15 spp. (slope[I] = 1.02	3 combined:	N, P	Sig. for 7/15 spp. (slopes[I] = 1.55		X	

Table 5-1. Summary of studies comparing the relative effect of habitat amount versus configuration

					Habitat amount effects			Configuration effects			Relative strength[H]		
Source[A]	Study type[B]	Response[C]	Taxon[D]	Landscape size	Habitat range (%)	Direction (if increase loss)[E]	Magnitude	Metrics (* = distance / isolation metric)[G]	Direction (if increase frag)[E]	Magnitude	Loss > config.	Loss ~ config.	Loss < config.
							- 15.58)			- 8.34)			
							" "	MNN *	N	Sig. for 3/15 spp.	x		
							" "	NP	P	Sig. for 2/15 spp.	x		
							" "	TE	N, P	Sig. for 3/15 spp.	x		
27	E	Pres.	B	1256-31400 ha	?	N, P	In the best model for 14/31 spp.	3 combined	N, P	In best model for 13/31 spp.		**X**	
							" "	LSI	P, N	In best model for 8/31 spp.	x		
							" "	MNN *	N, P	In best model for 7/31 spp.	x		
							" "	MPAR	N, P	In best model for 10/31 spp.	x		
28	E	Pres.	B	78.5 ha	?	N	Sig. for both years & for presence of >=2 individuals	PCA	?	Sig. for one year & for presence of >=2 individuals	**X**		
				1256 ha	5-55	N	Sig. for presence of >=2 individuals	PCA	x	Not sig.	**X**		
				6359 ha	6-34	x	Not sig.	PCA	N	Sig. for both years & for presence of >=2 individuals			**X**
29	E	Pres.	B	10000 ha	~1-75	N	4-10/34 spp. had good models that included habitat amount, depending on matrix terms & definition of habitat	PCA	?	5-15/34 spp. had good models including config., depending on matrix terms & habitat definition (always sig. for ≥ spp. than habitat amount)			**X**
30	E	Prop. with virus	M	314 ha	0-100	N, P	Effect moderate (~2-8%); Chi squared = 12.92, 15.48 (quadratic relationship)	AI	P	Effect moderate (~3-8%) but much scatter and one data point appears to have high leverage; Chi squared = 10.86	**X**		
				1256 ha	?	N, P	Chi squared = 5.6, 7.55 (quadratic relationship)	AI	P	Chi squared = 7.38		**X**	
				5025 ha	?	x	Not sig.	AI	P	Chi squared = 29.66			**X**

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					Habitat amount effects			Configuration effects			Relative strength[H]		
Source[A]	Study type[B]	Response[C]	Taxon[D]	Landscape size	Habitat range (%)	Direction (if increase loss)[E]	Magnitude	Metrics (* = distance / isolation metric)[G]	Direction (if increase frag)[E]	Magnitude	Loss > config.	Loss ~ config.	Loss < config.
Ecological response = persistence													
8	S	Prob.	M	15700 ha	50-99	N	Effect large (prob. ~0-100%), regardless of config.	NP	N	Effect small (no effect) to moderate (e.g. prob ~0-55%), depending on habitat amount	X		
11	S	Prob.	B	32 x 32 cells	10-90	N	Slope[I] = 25.4	AI	N	Slope[I] = 5.9	X		
					10-50	N	Slope[I] = 24.3	AI	N	Slope[I] = 5.7; relative contribution to classification accuracy greater than when habitat range = 10-90%	X		
31	S	Prob.	G	30 x 30 cells	0-100	N	Effect large (~0-100%)	AI	N	Effect small (~80-95%) to moderate (~30-75%), depending on habitat amount	X		
9	S	Time	M	27 x 27 cells	0-100	N	Effect moderate (~10-60 years) to large (~10-100 years), depending on config.	NP	N	Effect was small (no effect) to large (~0-100 years), depending on habitat amount	X		
12	S	Time	M	64 x 64 cells	10-50	N	4% variance explained	2 combined:	N	53% variance explained			X
							" "	NP	N	2% variance explained	x		
							" "	CORQ *	N	51% variance explained			x

A. **1** (Ruckleshaus et al. 2002), **2** (Schiegg et al. 2002), **3** (King & With 2002), **4** (Collingham & Huntley 2000), **5** (Bélisle et al. 2001), **6** (McIntyre & Wiens 1999), **7** (With et al. 2002), **8** (Jager et al. 2006), **9** (Schneider 2001), **10** (Wiegand et al. 2005), **11** (Flather & Bevers 2002), **12** (Henein et al. 1998), **13** (Hill & Caswell 1999), **14** (With & King 1999), **15** (Hiebeler 2000), **16** (Lichstein et al. 2002), **17** (McGarigal & McComb 1995), **18** (Betts et al. 2006), **19** (Drolet et al. 1999), **20** (Guerry & Hunter 2002), **21** (Holland et al. 2005), **22** (Imbeau & Desrochers 2002), 23 (Peery et al. 1999), **24** (Rosenberg et al. 1999), **25** (Trzcinski et al. 1999), **26** (Villard et al. 1999), **27** (Westphal et al. 2003), **28** (Cooper & Walters 2002), **29** (Cumming & Schmiegelow 2001), **30** (Langlois et al. 2001), **31** (Fahrig 1997).

Table 5-1. Summary of studies comparing the relative effect of habitat amount versus configuration

					Habitat amount effects			Configuration effects			Relative strength[H]		
Source[A]	Study type[B]	Response[C]	Taxon[D]	Landscape size	Habitat range (%)	Direction (if increase loss)[E]	Magnitude	Metrics (* = distance / isolation metric)[G]	Direction (if increase frag)[E]	Magnitude	Loss > config.	Loss ~ config.	Loss < config.

B. **S** (simulation), **E** (empirical)

C. **Abn.** (abundance), **Dens.** (density), **Disp. succ.** (dispersal success), **Hom. succ.** (homing success), **Migr. rate** (migration rate), **Pres.** (presence), **Prob.** (probability), **Ptch. occ.** (patch occupancy)

D. **B** (bird(s)), **I** (insect(s)), **G** (generic), **M** (mammal(s)), **P** (plant(s))

E. **N** (negative), **P** (positive), **x** (no significant effect), **?** (not clear)

F. **Config.** (configuration), **spp.** (species)

G. **AI** (an aggregation index), **CACV** (core area coefficient of variation), **CORQ** (corridor quality & presence), **CWE** (contrast weighted edge), **CWED** (contrast weighted edge density), **ED** (edge density), **EDIST** (distance to edge), **LCAS** (landscape core area similarity), **LPE** (largest patch edge), **LPS** (largest patch size), **LSI** (landscape shape index), **MCA** (mean core area size per patch), **MCAI** (average percent of a patch that is core), **MECI** (Mean patch edge contrast index), **MNN** (mean nearest neighbour), **MPAR** (mean perimeter area ratio), **MPFD** (mean patch fractal dimension), **MPS** (mean patch size), **MSI** (mean shape index), **NNCV** (nearest neighbour covariance), **NP** (number of patches), **PCA** (principle components analysis axis of several configuration indices), **PFADJ** (pond-forest adjacency), **PS** (patch size), **PSCV** (patch size coefficient of variation), **TCA** (total core area), **TCAI** (total core area index), **TE** (total edge), **TE/CA** (total edge / core area), **TECI** (total edge contrast index)

H. Bold upper-case "X" indicates result for each "case". A single study may represent more than one case if more than one response variable, scale, or range of %habitat was analyzed. If an analysis included a set of single-aspect configuration metrics (see text), their effect was combined as a single case. Where applicable, the results for combined configuration effects are broken down into the results / comparison for each single-aspect metric, indicated with an "x".

I. Slopes of habitat amount & configuration are comparable, since both metrics are either standardized or scaled similarly (e.g. 0-1).

Table 5-2. Factors that may influence the relative effect of habitat configuration compared to habitat amount

Greater relative effect	Smaller relative effect
Response variable	
Continuous (e.g. abundance)	Binary (e.g. persistence or presence)
Absolute measures of abundance (e.g. total population size)	Abundance measures that are relative to habitat amount (e.g. patch occupancy, population density)
Species characteristics	
Short dispersal distances	Long dispersal distances
Unable / unwilling to cross matrix	Able to move through / survive in matrix
Low reproductive rate	High reproductive rate
Landscape characteristics / measurement	
Low habitat proportion	Wide gradient or high habitat proportion
Landscapes measured at broad scale relative to sites where ecological response measured	Landscapes measured at scales similar to sampled site
"Binary" habitat / nonhabitat landscapes; inhospitable matrix (e.g. forest habitat in agricultural matrix)	"Mosaic" landscapes; matrix conducive to movement, survival (e.g. forest stands of varying species, age, or disturbance type)
Researcher's broad definition of habitat would overestimate functional habitat loss	Researcher's broad definition of habitat would underestimate functional habitat loss

References

Aitken, K., Wiebe, K. & Martin, K. 2002. Nest-site Reuse Patterns For A Cavity-nesting Bird Community In Interior British Columbia. *Auk* 119: 391-402.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.

Batary, P. & Baldi, A. 2004. Evidence of an edge effect on avian nest success. *Conservation Biology* 18: 389-400.

Bayne, E. M. & Hobson, K. A. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11: 1418-1429.

Bélisle, M. & Desrochers, A. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* 17: 219-231.

Bélisle, M., Desrochers, A. & Fortin, M.-J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82: 1893-1904.

Bennett, A. F., Radford, J. Q. & Haslem, A. 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation* 133: 250-264.

Betts, M. G., Forbes, G. J., Diamond, A. W. & Taylor, P. D. 2006. Independent effects of fragmentation on forest songbirds: an organism-based approach. *Ecological Applications* 16: 1076-1089.

Bibby, C. J. 1994. Recent past and future extinctions in birds. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 344: 35-40.

Bock, C. E. & Jones, Z. F. 2004. Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment* 2: 403-410.

Chalfoun, A. D., Thompson, F. R. & Ratnaswamy, M. J. 2002. Nest predators and fragmentation: A review and meta-analysis. *Conservation Biology* 16: 306-318.

Chust, G., Pretus, J. Ll., Ducrot, D. & Ventura, D. 2004. Scale dependency of insect assemblages in response to landscape pattern. *Landscape Ecology* 19: 41-57 .

Collingham, Y. C. & Huntley, B. 2000. Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications* 10: 131-144.

Cooper, C. B. & Walters, J. R. 2002. Independent effects of woodland loss and fragmentation on brown treecreeper distribution. *Biological Conservation* 105: 1-

10.

Cooper, C. B., Walters, J. R. & Priddy, J. 2002. Landscape patterns and dispersal success: simulated population dynamics in the brown treecreeper. *Ecological Applications* 12: 1576-1587.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. 1999. Inverse density dependence and the Allee effect . *Trends in Ecology & Evolution* 14: 405-410.

Cumming, S. G. & Schmiegelow, F. K. A. 2001. Effects of habitat abundance and configuration, and the forest matrix, on distributional patterns of boreal birds. Sustainable Forest Management Network working paper.

Davies, K. F., Margules, C. R. & Lawrence, J. F. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81: 1450-1461.

Desrochers, A. & Hannon, S. J. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11: 1204-1210.

Diffendorfer, J. E., Gaines, M. S. & Holt, R. D. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology* 76: 827-839.

Drolet, B., Desrochers, A. & Fortin, M.-J. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. *Condor* 101: 699-704 .

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* 41: 300-314.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603-610.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modeling* 105: 273-292.

Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100: 65-74.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Flather, C. H. & Bevers, M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159: 40-56.

Goodsell, P. J. & Connell, S. D. 2002. Can habitat loss be treated independently of habitat configuration? Implications for rare and common taxa in fragmented landscapes. *Marine Ecology Progress Series* 239.

Grubb, T. C. Jr. & Doherty, P. F. Jr. 1999. On home-range gap-crossing. *Auk* 116: 618-628.

Guerry, A. D. & Hunter, M. L. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology* 16: 745-754.

Henein, K., Wegner, J. & Merriam, G. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. *Oikos* 81: 168-186.

Henle, K., Davies, K. F., Kleyer, M., Margules, C. & Settele, J. 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* 13: 207-251.

Hiebeler, D. 2000. Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. *Ecology* 81: 1629-1641.

Hill, M. F. & Caswell, H. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecology Letters* 2: 121-127.

Holland, J. D., Fahrig, L. & Cappuccino, N. 2005. Fecundity determines the extinction threshold in a Canadian assemblage of longhorned beetles (Coleoptera: Cerambycidae). *Journal of Insect Conservation* 9: 109-119.

Imbeau, L. & Desrochers, A. 2002. Area sensitivity and edge avoidance: the case of the three-toed woodpecker (*Picoides tridactylus*) in a managed forest. *Forest Ecology and Management* 164: 249-256.

Jager, H. I., Carr, E. A. & Efroymson, R. A. 2006. Simulated effects of habitat loss and fragmentation on a solitary mustelid predator. *Ecological Modelling* 191: 416-430.

King, A. W. & With, K. A. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147: 23-39.

Langlois, J. P., Fahrig, L., Merriam, G. & Artsob, H. 2001. Landscape structure influences continental distribution of hantavirus in deer mice. *Landscape Ecology* 16: 255-266.

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.

Lichstein, J. W., Simons, T. R. & Franzreb, K. E. 2002. Landscape effects on breeding songbird abundance in managed forests. *Ecological Applications* 12: 836-857.

Linke, J., Franklin, S. E., Huettmann, F. & Stenhouse, G. B. 2005. Seismic cutlines, changing landscape metrics and grizzly bear landscape use in Alberta. *Landscape*

Ecology 20: 811-826.

Luoto, M., Toivonen, T. & Heikkinen, R. K. 2002. Prediction of total and rare plant species richness in agricultural landscapes from satellite images and topographic data. *Landscape Ecology* 17: 195-217.

Matthysen, E., Adriaensen, F. & Dhondt, A. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* 72: 375-381.

McGarigal, K. & Cushman, S. A. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* 12: 335-345.

McGarigal, K. & McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* 65: 236-260.

McIntyre, N. E. & Wiens, J. A. 1999. Interactions between habitat abundance and configuration: experimental validation of some predictions from percolation theory. *Oikos* 86: 129-137.

McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28: 495-516.

Mitchell, M., Lancia, R. & Gerwin, J. 2001. Using landscape-level data to predict the distribution of birds on a managed forest: Effects of scale. *Ecological Applications* 11: 1692-1708.

Morrison, M. L. & Hahn, D. C. 2002. Geographic variation in cowbird distribution, abundance, and parasitism. *Studies in Avian Biology* 25: 65-72.

Noss, R. F. & Cooperrider, A. Y. 1994. Saving nature's legacy: Protecting and restoring biodiversity. Washington, DC: Island Press.

Orians, G. H. & Wittenberger, J. F. 1991. Spatial and temporal scales in habitat selection. *The American Naturalist* 137: s29 - s49.

Paton, P. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8: 17-26.

Peery, M. Z., Gutierrez, R. J. & Seamans, M. E. 1999. Habitat composition and configuration around Mexican spotted owl nest and roost sites in the Tularosa Mountains, New Mexico. *Journal of Wildlife Management* 63: 36-43.

Rangen, S. A., Hobson, K. A. & Clark, R. G. 2000. A comparison of density and reproductive indices of songbirds in young and old boreal forest. *Wildlife Society Bulletin 2000* 28: 110-118.

Rodewald, A. D. & Yahner, R. H. 2001. Avian nesting success in forested landscapes: Influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* 118: 1018-1028.

Rodewald, P. G. & Brittingham, M. C. 2002. Habitat use and behavior of mixed species landbird flocks during fall migration. *Wilson Bulletin* 114: 87-98.

Rosenberg, K. V., Lowe, J. D. & Dhondt, A. A. 1999. Effects of forest fragmentation on breeding tanagers: a continental perspective. *Conservation Biology* 13: 568-583.

Ruckelshaus, M., Hartway, C. & Kareiva, P. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* 11: 1298-1306.

Saura, S. 2004. Effects of remote sensor spatial resolution and data aggregation on selected fragmentation indices. *Landscape Ecology* 19: 197-209 .

Schiegg, K., Walters, J. R. & . Priddy, J. A. 2002. The consequences of disrupted dispersal in fragmented red-cockaded woodpecker *Picoides borealis* populations. *Journal of Animal Ecology* 71: 710-721.

Schmiegelow, F. K. A. & Mönkkönen, M. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications* 12: 375-389.

Schneider, M. F. 2001. Habitat loss, fragmentation and predator impact: spatial implications for prey conservation. *Journal of Applied Ecology* 38: 720-735.

Singh, J. S. 2002. The biodiversity crisis: a multifaceted review. *Current Science (Bangalore)* 82: 638-647.

St. Clair, C. C., Belisle, M., Desrochers, A. & Hannon, S. 1998. Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology[online]* 2: 13.

Tischendorf, L. & Fahrig, L. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90: 7-19.

Trzcinski, M. K., Fahrig, L. & Merriam, G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* 9: 586-593.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.

Vaske, J. J. 2002. Communicating judgments about practical significance: effect size, confidence intervals and odds ratios. *Human Dimensions of Wildlife* 7: 287-300.

Vickery, P. D., Hunter, M. L. & Wells, J. V. 1992. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. *The Auk* 109:

697-705.

Villard, M.-A., Trzcinski, M. K. & Merriam, G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy . *Conservation Biology* 62: 774-783.

Weatherhead, P. J. & Dufour, K. W. 2000. Fledging success as an index of recruitment in Red-winged Blackbirds. *Auk* 117: 627-633.

Westphal, M. I., Field, S. A., Tyre, A. J., Paton, D. & Possingham, H. P. 2003. Effects of landscape pattern on bird species distribution in the Mt. Lofty Ranges, South Australia. *Landscape Ecology* 18: 413-426.

Wiegand, T., Revilla, E. & Moloney, K. A. 2005. Effects of habitat loss and fragmentation on population dynamics . *Conservation Biology* 19: 108-121.

With, K. A., Pavuk, D. M., Worchuck, J. L., Oates, R. K. & Fisher, J. L. 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications* 12: 52-65.

With, K. A. & King, A. W. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314-326.

Chapter 6: Relative effects of forest proportion versus configuration on bird abundance: importance of the habitat proportion gradient and spatial scale

1. Introduction

Habitat loss and fragmentation are among the major causes of declining wildlife populations worldwide (Bibby 1994, Singh 2002). Following European settlement in Canada, agricultural development has led to ongoing, extensive and permanent deforestation and forest fragmentation (Hobson et al. 2002, Bélanger and Grenier 2002). To manage forest wildlife we must be able to predict the independent effects of landscape-level habitat loss and fragmentation over a range of deforestation intensities.

Fragmentation is distinct from habitat loss (Fahrig 1997). While habitat loss changes the amount of habitat, fragmentation changes its spatial configuration. For example, fragmented habitat patches are smaller and more numerous, farther apart, and have more edge and less core area, compared with similar amounts of contiguous habitat. For birds, negative effects of fragmentation can include increased predation and brood parasitism (Donovan et al. 1997), harsher winter microclimate (Dolby and Grubb 1999), with concomitant reduced survival (Doherty and Grubb 2002) and body condition (Doherty and Grubb 2003), and decreased ability to move across the landscape (Bélisle et al. 2001, Bélisle and St. Clair 2001). Fragmentation may also have positive effects for some species, such as by increasing favored edge habitat (Bellamy et al. 1996). Although habitat loss and fragmentation tend to be correlated, distinguishing their separate ecological effects is important. This will help to determine where conservation efforts should focus (Fahrig 2001).

The effect of habitat configuration relative to habitat amount may depend on several factors. Theoretical evidence suggests that the spatial configuration of habitat is most important for organisms when total habitat cover is low (McLellan et al. 1986, Fahrig 1997, 1998, Collingham and Huntley 2000, Flather and Bevers 2002). The spatial scale (grain and extent) at which landscapes are measured may also influence the relative effects of habitat proportion and configuration. Configuration metrics are sensitive to grain size, with larger grains tending to yield less fragmented metrics (Saura 2004). Presumably, different species also perceive or respond to landscape pattern at different "grains". For example, a given landscape may be perceived as more or less fragmented, depending on species characteristics such as vagility (With and Crist 1995) or home range size. However, map grain size is often biologically arbitrary in landscape studies, probably because it is difficult to predict the grain size at which particular species perceive the landscape. As well, habitat loss and fragmentation may have different relative effects at different spatial extents. For example, the relative importance of fragmentation may increase during dispersal, which involves movement over large distances. Thus, its importance may increase at wider spatial extents (e.g. Langlois et al. 2001, Cooper and Walters 2002).

Of the vast number of "habitat fragmentation" studies, relatively few have distinguished the separate effects of habitat proportion versus configuration on species' abundance, occurrence, or diversity. Results have been mixed. A few have found configuration to have a larger effect than proportion (Cumming and Schmiegelow 2001), at least under certain conditions (e.g. larger spatial extent: Cooper and Walters 2002; species evenness but not richness: Cushman and McGarigal 2003). Others have suggested that both habitat proportion and configuration are important (e.g. Villard et al. 1999). The majority have indicated that habitat proportion has the greatest effect (McGarigal and McComb 1995, Peery et al. 1999, Trzcisnki et al. 1999, Rosenberg et al. 1999, Drolet et al. 1999, Imbeau and Desrochers 2002, Lichstein et al. 2002, Cushman and McGarigal 2004, Radford and Bennett 2004, Radford et al. 2005).

In most of these studies, the response variable was species' occurrence or richness (which is based on species' occurrences). Few measured species' abundance (McGarigal and McComb 1995, Lichstein et al. 2002, Cushman and McGarigal 2003), and none did so in an agricultural region. These factors may influence the apparent or actual importance of configuration. Specifically, Flather and Bevers (2002) found much larger relative configuration effects when using abundance rather than a binary response variable (persistence). As well, since agricultural areas generally have lower regional proportions of forest and a more inhospitable matrix than areas managed for forestry, larger configuration effects may occur in the former (McGarigal and McComb 1995). Thus, if the potential effects of configuration are large, the present study design (agricultural region, species' abundance or abundance based community indices as the dependents) should facilitate the detection of these effects. In addition, the effects of landscape habitat proportion and configuration may be more evident for residents than for migrants, because a) certain effects of habitat loss and fragmentation may occur mainly during the cold winter season (e.g. Dolby and Grubb 1999), and b) population limitation likely occurs in the winter (Nilsson 1987, Herrera 1978, Newton 1994, Sherry and Holmes1996, Lahti et al. 1998), both for resident birds (which are present year-round) and for migratory birds (which over-winter elsewhere).

I examined the abundance of forest birds (mainly residents) in an agricultural / boreal dry mixedwood region of Alberta. The main questions addressed were:

1) What are the relative effects of the proportion versus configuration of forest in the landscape on individual species (abundances) and on the community as a whole?
2) Are the relative effects of proportion versus configuration influenced by
    a) whether the range of forest proportion among landscapes is wide (e.g. 2-62%) or low (e.g. 2-30%)?
    b) the spatial scale (grain and extent) at which habitat proportion and configuration are measured?

2. Methods

2.1 Study area

The 75x55km study area was located 40km east of Edmonton, Alberta in an agricultural / boreal dry mixedwood system (see Chapter 4 for details). Fifty study sites (800x800m) were selected for bird surveys. The proportion of forest cover (PROP) ranged from about 2.5 to 62% in the 1km or 3km radius landscapes around the centre of each site. To allow the independent effects of forest amount versus fragmentation to be distinguished, these landscapes were selected to represent a wide range of fragmentation (based on subjective visual examination) for a given proportion of forest.

2.2. Habitat mapping and landscapes

A fine-resolution (5m), polychromatic (colour) image of the study region was created, by merging 1998 or 1999 Indian Remote Sensing (IRS) satellite images (5m, panchromatic) and Landsat (30m, polychromatic) images. The fine-resolution detail helped to visualize small features, and the colour information helped to distinguish habitat types. The merged image was hand digitized in ArcView 3.2 at an extent of 1:15000, to create a map that was classified by land-cover type. Only "forest" was used in statistical analyses; this included deciduous, coniferous, and occasional shrubby cover. This map was double checked using 1:20000 or 1:30000 air photos from 1998-2001. It was then converted to two raster maps, with 5m or 100m pixels.

Most forest metrics (see below) were measured from these two maps. Two distance metrics (see below) required another, more extensive map that was classified from 1998 Landsat images using an iterative k-means classification method, and then smoothed with a 3x3 majority filter (provided by J. Young from Young 2003). Before calculating the distance metrics, all different forest classes from this map were reclassified as "forest", and the map was converted to a patch theme.

2.3. Independent variables

In ArcView 3.2, the Spatial Statistics / Fragstats interface was used to measure forest proportion and all other available spatial metrics for forest at each scale. In addition, a clustering metric (CLUST) was calculated from two of these spatial statistics, two distance metrics (D100HA, D1000HA) were measured using the Nearest Features version 3.8a extension, and a fencerow density metric (DFENCE) was measured manually (see below). Most metrics were highly inter-correlated. A final set of seven metrics (Table 6-1) was chosen based on low inter-correlation and potential biological significance (see below).

These seven forest metrics (Table 6-1) can be divided into three general types:

1) proportion of forest in each landscape (PROP). This reflects habitat amount for most species, or heterogeneity of habitat composition for species using both forest and non-forest extensively).
2) configuration of forest:
a) Patch density (PD): A greater density of patches is associated with more numerous but on average smaller patches with less distance between them. This may reduce their suitability for species with larger home ranges, increase exposure to negative edge effects, or increase landscape connectivity. Patch edges are also associated with increased density of shrubby vegetation and arboreal arthropod density, which may benefit tree-foraging species.
b) Core area covariance (CORVAR): High core area covariance reflects a mix of large patches with a large total core area, and small or narrow patches with little or no core area. Low core area covariance would be found in landscapes with a more even

distribution of core area among patches. High core area covariance may be important for species that benefit from both core and edge habitats, or from both large (e.g. for home ranges) and numerous small patches (e.g. for movement).
c) Forest "clustering" (CLUST): Higher values of forest clustering reflect a higher ratio of core to edge area, relative to the maximum possible for the amount of forest in the landscape. All forest in a perfect square would yield the highest possible value, while numerous, narrow, or complex patches would yield low values.
d) Density of fencerows in unforested areas (DFENCE). For species with a limited ability to cross gaps, fencerows may facilitate movement across the landscape.
3) Distance to ≥100ha or ≥1000ha forest patches (D100HA and D1000HA), from the edge of the 3km radius landscape. This metric may reflect proximity to habitats that provide a large number of potential immigrants. These distance metrics involve components of both spatial configuration (distance) and forest quantity (patch size, and a probable correlation between distance and forest proportion surrounding the 3km landscape boundaries).

Finally, easting and northing (EAST, NORTH) were included in some models (see below). In this study, as in many landscape studies, it was not possible to control for every factor that may have varied over distances of tens of kilometers. For example, roads and subdivision density are higher in the east-central portion of the study area, which may influence the abundance of bird feeders or other human influences. Thus, easting and northing were included to control for potential environmental variation along geographical gradients. However, as geographical variation was not the focus of this study, significant effects of easting and northing will not be discussed. Details of models containing easting or northing for some species can be found in Appendices 6-1 and 6-2.

2.4. Choice of landscape scales for measurement of independent variables

I chose 2 spatial extents to measure independent variables: 1km and 3km radii from the centre of each study site. The local abundance of an organism may result from influences that are both "local" (e.g. reproduction, mortality, emigration, habitat carrying capacity) and / or "distant" (e.g. immigration from surrounding areas). For species with small average territory sizes and dispersal distances (e.g. black-capped chickadee, *Poecile atricapillus*: 1.5-5.3ha, references in Smith 1993; 1.1km, Weise and Meyer 1979), the 1km radius extent may encompass both local and distant landscape effects, but mainly local effects for species with large territories (e.g. hairy woodpecker, *Picoides villosus*: 500m width, Kilham 1969). The 3km extents may be more relevant for species with larger average dispersal distances (e.g. downy woodpecker, *Picoides pubescens*: ~3km, n=2, Jackson and Ouellet 2002; American crow, *Corvus brachyrhynchos:* 3.2km, McGowan 2001), if landscape structure influences dispersal ability.

Although the area I actively sampled in each site was contained within an 800m by 800m area, I chose a 1km radius as the smallest landscape size to accommodate species with larger territories. For example, a 20 ha white-breasted nuthatch territory would have a radius of about 505m.. A bird observed near the edge of its territory during bird surveys (see below) may thus be using portions of the landscape 905m away from the centre of the site. I did not measure forest cover in the 800 by 800m study sites. However, I did measure forest cover in 500m radius landscapes just large enough to encompass each site. Forest cover was highly correlated between the 500m and 1km radius scales (Pearson $r^2 = 0.92$). Thus, any statistical responses to % forest cover at the 1km extent may result from an effect of forest cover within the immediate study site.

I chose two grain sizes: 5m and 100m. The 5m grain was chosen because it reveals fine details such as fencerows and small wooded patches, which may be important for some species. For example, chickadees (St. Clair et al. 1998) and blue jays *Cyanocitta cristata* (Johnson and Adkisson 1985, but see Grubb and Doherty 1999) use fencerows as travel corridors. The 100m grain was expected to be more relevant for more vagile species. For example, two patches separated by less than 100m will often show up as one single patch (i.e. representing no functional fragmentation) at the 100m grain. While chickadees are often reluctant to cross gaps as large as 100m (Desrochers and Hannon 1997, St. Clair et al. 1998), the larger residents cross 100m gaps routinely (Grubb and Doherty 1999), and crows and black-billed magpies (*Pica hudsonia)* actively use open areas for foraging.

Hereafter, "scale" will refer to the particular combination of extent (1km or 3km) and grain (5m or 100m). It is important to note, however, that this set of scales is exploratory. The "best" measurement scale(s) to represent the scale(s) at which each species perceives its environment were and are usually not clearly apparent (Wiens 1989).

PROP, PD, CORVAR, CLUST, and DFENCE were "scale-variant", i.e. measured at more than one scale (DFENCE was measured at both extents but only the 5m grain, since fencerows were narrow and poorly represented at the 100m grain). For these metrics, two forest pixels belonged to the same patch if they were directly adjacent horizontally, vertically, or diagonally. The two distance metrics were measured outward from the 3km landscape boundaries, and so did not have a defined "extent". These metrics would have changed little (if at all) over the 5 - 100m range of grain sizes. Table 6-2 provides summary statistics for each metric. At all scales, each of the final metrics had Pearson correlation coefficients <0.6 with each other metric, with the exception of PD and CORVAR at the 1km / 5m scale (r=0.70). When forest cover was <30%, PD (1km/5m) also had higher correlations with CORVAR (1km, 3km / 5m; 0.69-0.72) and CLUST (1km/5m; -0.71).

2.5. Study species and survey methods

The species surveyed were: black-capped chickadee, white-breasted nuthatch (*Sitta carolinensis*), downy woodpecker, hairy woodpecker, ruffed grouse (*Bonasa umbellus*), black-billed magpie, blue jay, American crow, yellow-bellied sapsucker (*Sphyrapicus varius*), and red squirrels (*Tamiasciurus hudsonicus*). Excluding crows and magpies (which use both forest and non-forest extensively), these species will be grouped for convenience as "forest birds"or "forest species".

Survey methods are detailed in Chapter 3. Briefly, during each of four rounds between April and July (2002, 2003), birds and squirrels were counted along 2.4km of transects and 9 survey stations in each 800x800m site. Recordings of bird calls were broadcast at forested stations to increase detection rates.

For each species, the two-year average abundance was calculated (details Chapter 4). Two community level indices were also calculated for forest birds (details and rationale in Chapter 4): a) the number of species that were "abundant" (greater than the median values observed for each species), and b) the evenness of the standardized (0-1) species' abundances, based on the Shannon diversity index (index divided by the maximum possible index for the number of species in the sample).

2.6. Modelling the relative effects of habitat proportion versus configuration

All statistical analyses were performed using Intercooled Stata 9.2 (StataCorp 2005), unless otherwise noted. All regression models were estimated using the least-squares method, and were weighted if data were heteroscedastic (see Chapter 2 for details and discussion of this approach).

2.6.1. Single-scale models

To find the scale at which each of the five scale-variant metrics was most important for each species / community index, a set of four single-scale models was built using the scale-variant metrics only (one for each scale: 1km/5m, 3km/5m, 1km/100m, 3km/100m). Model building generally followed Hosmer and Lemeshow (2000). For each species / community index and scale, all five scale-variant metrics were entered into a forward stepwise regression ($\alpha = 0.15$ for entry, $\alpha = 0.2$ for removal). From the stepwise-selected model, variables with a likelihood ratio test p-value <0.05 were retained, and those with marginal significance ($p < 0.1$) were retained only if model r^2 fell more than 0.05 when that variable was dropped. Other variables were dropped, starting with the least significant. A multivariable fractional polynomial analysis was then performed to determine whether the remaining variables were best modelled as linear, degree-1 or degree-2 fractional polynomials. If any variables were transformed, the significance of all variables was re-assessed and non-significant variables were dropped, as above.

For each species / community index, the "best" scale for each metric was estimated as follows. Each variable in each of the single-scale models was dropped individually, and the change in model r^2 (Δr^2) was recorded. The scale of the model with the largest Δr^2 for a given metric was the "best" scale for that metric. If a metric was not included in a given model, its Δr^2 for that scale was zero.

2.6.2. Multi-scale models

For each species / community index, a multi-scale model was then built following the methods outlined above, except that the candidate variables for the stepwise procedure were a) any scale-variant metric that was included in one or more single-scale models (at its "best" scale), b) D100HA and D1000HA, and c) the easting and northing coordinates of the central survey station of each landscape (EAST and NORTH). As well, the significance of all two-way interactions between forest metrics were checked (likelihood ratio test, α=0.05), but none were significant.

This was usually the final multi-scale model. The influence of individual data points was then examined. Any data points (landscapes) that changed the coefficient for an independent by more than 2/sqrt(n) standard deviations was examined more closely (n = sample size). These points were (temporarily) dropped individually to determine whether the variable was still significant. If not, this indicated that the coefficient provided a poor fit to the data, and this was noted in the results. For the squirrel model, one strongly influential data point that changed the coefficient for PROP by >1 standard deviation was dropped permanently, and the model was refit (this did not affect the variables included in the model). This landscape had unusually high conifer density, which probably contributed to the very high squirrel numbers there. For one other species (downy woodpecker) one data point was very influential on the slope of PD, but there was no clear biological reason to drop this point.

The data were then checked for spatial autocorrelation by calculating Moran's I for the residuals of each multi-scale model, at neighbourhood distances of 0-10km, 10-25km, and 25-75km. The 10km neighbourhood was just large enough to encompass most landscapes' closest landscape neighbour, and the largest distance between any two landscapes was about 75 km. Spatial autocorrelation was not significant for any species or community metric (two-tailed, $\alpha=0.017$ to correct for multiple tests).

2.6.3. Single- and multi-scale models for landscapes with <30% forest

To examine whether the relative effects of forest proportion and configuration changed when forest cover was low, the single-scale and multi-scale modeling procedures (above) were repeated using only landscapes with PROP <0.3 ("low-forest" models). For the single-scale low-forest models, this resulted in a sample size of 34 landscapes for the 1km extent models, and 35 landscapes for the 3km extent models. The exact set of landscapes that had <30% forest depended somewhat on scale, so for the multi-scale models one scale had to be chosen to select the low forest landscapes. For each species / community index, the scale used to select the set of landscapes with <30% forest was either: a) the scale of the "most important" configuration metric - that with the largest Δr^2 among the four low-forest single-scale models, or b) the scale at which PROP explained the greatest proportion of model deviance, if no configuration metrics were significant in the single-scale models.

2.6.4. Summary of model types

Thus, four types of models were built for each species / community index: a) a set of four single-scale, all-landscapes models; b) one (potentially) multi-scale, all-landscapes model; c) a set of four low-forest, single-scale models; and d) one (potentially) multi-scale, low-forest model. The single-scale models were used mainly to select the "best" candidate variables for the multi-scale models, and to examine the effect of scale on the relative importance of proportion versus configuration (see below). The multi-scale models were intended to reflect the most important predictor variables at their "best" scale. These were used to compare the overall relative effects of habitat proportion versus configuration (see below), over a wide and a low gradient of forest proportion.

2.7. Comparing the relative statistical effects of habitat loss versus fragmentation

As a measure of configuration effects relative to forest proportion effects, "relative configuration-Δr^2" was calculated for each model as follows: configuration-Δr^2 (the change in model r^2 when all configuration metrics were dropped), divided by configuration-Δr^2 plus PROP-Δr^2. Relative configuration-Δr^2 thus ranged from 0 to 1, and was < 0.5 when configuration explained less deviance than proportion. For each model type, only one relative configuration-Δr^2 was calculated for chickadees and fledgling chickadees, using their combined configuration- and PROP-Δr^2 values (since they don't represent independent species' responses). Again, the distance metrics were not considered as (pure) configuration effects, and were ignored in the calculation of relative configuration Δr^2, as were EAST and NORTH.

2.8. Testing the suitability of abundance as a dependent variable

The use of abundance as a measure of habitat loss or configuration "effects" implied that greater abundance was "better", reflecting greater landscape quality or persistance probability. This assumption may not hold under some conditions, such as if subdominant individuals are excluded from high quality habitats (Van Horne 1983), or if anthropogenic disturbance creates ecological traps (Bock and Jones 2004). Both empirical (Bock and Jones 2004) and simulation studies (Fahrig 1998, Flather and Bevers 2002) suggest that abundance is correlated with fitness or persistence, but less strongly in disturbed areas (Bock and Jones 2004). Although my study did not focus on gathering demographic data, for one species (black-capped chickadee), I was able to count fledglings during the fourth round of surveys. As an index of reproductive success I calculated the average ratio of fledgling to adult chickadees. This ratio was regressed against the average maximum chickadee abundance. A negative relationship between this ratio and adult abundance would mean that abundance was a poor indicator of landscape quality for chickadees. A neutral relationship would suggest that abundance is an unbiased indicator, and a positive relationship that abundance may underestimate the effects of habitat loss / fragmentation.

3. Results

The all-landscapes multi-scale models were used to address the broadest question: what are the relative effects of habitat proportion versus configuration? These models represent an "overall" picture, since the gradient of forest cover is wide and variables are included at their "best" scales only. Proportion of forest (PROP) had a larger effect than configuration on species' abundances (Table 6-3, left side). When averaged across species, the effects of configuration relative to forest proportion (relative configuration-Δr^2) was only 0.14, and forest proportion explained seven times as much variation as configuration (mean PROP-$\Delta r^2 = 0.30$; mean configuration-$\Delta r^2 = 0.04$). As well, forest proportion was included in the all-landscapes models for more species than were configuration metrics (10 versus 6). For all species, relative configuration-Δr^2 was < 0.5, indicating that forest proportion had a larger effect than configuration (Table 6-3). As well, for several species, one or more configuration metrics were poorly fit to the data, with significance being dependent on one data point (magpie, chickadee, jay, squirrel, downy woodpecker; Appendix 6-1).

The number of abundant species increased strongly with forest proportion, and fencerow density had a small positive effect on the evenness of standardized species' abundances (Table 6-3).

3.1. Effect of forest cover range on relative effects of proportion versus configuration

When only landscapes with <30% forest were included in the multi-scale models, PROP still had a larger effect on average than configuration (Table 6-3, right side). However, compared with the all-landscapes models, the relative effect of configuration increased at low forest cover. For example, the average (across species) relative configuration-Δr^2 increased from 0.14 to 0.44, and the average variation explained by forest proportion (PROP) was reduced from seven times to twice that of configuration (0.19 and 0.09, respectively). As well, there was less of a disparity between the number of species responding to forest proportion versus configuration (6 and 7, compared to 10 and 6, respectively), and relative configuration-Δr^2 exceeded 0.5 for more species (4) than when the forest proportion gradient was wide (0).

Species-specific results were variable, however. The effects of configuration relative to forest proportion (relative configuration-Δr^2) was greater in the low-forest than all-landscapes model for six species, unchanged for two species (zero for both models), and less for two species. However, for one of the latter species (downy woodpecker), the all-landscapes configuration effect was dependent on one outlier. Given this variability, a paired sign rank test comparing relative configuration Δr^2 for the all-landscapes versus low-forest models was only marginally significant ($p = 0.12$, n=10 species). At low forest cover, the only significant community level relationship was an increase in the number of abundant forest bird species with forest proportion (Table 6-3, right side).

3.2. Effect of spatial scale on relative effects of proportion versus configuration

To examine how spatial scale can influence the relative effects habitat proportion versus configuration, I compared the relative configuration-Δr^2 values among the single-scale models for each species (Table 6-4; model details in Appendices 6-3 and 6-4). For example, for several species configuration was significant only at certain scales, or relative configuration Δr^2 was larger at some scales than at others. This scale effect was quantified by calculating, for each species, the difference between the smallest and largest relative configuration Δr^2, depending on a) spatial extent (keeping grain constant), and b) grain (keeping extent constant). This difference could range from 0 (e.g. only proportion had an effect at any scale) to 1 (only proportion had an effect at one extent or grain, and only configuration at another extent or grain). Among the all-landscapes models (Table 6-4, left side), the differences in relative configuration Δr^2 ranged from a) 0 to 1 (mean 0.24, n=10), depending on extent, and b) 0 to 1 (mean 0.19, n=10 species), depending on grain. Among the low-forest models (Table 6-4, right side), the differences were also large, ranging from: a) 0 to 0.59 (mean 0.25, n=8) depending on extent, or b) 0 to 0.42 (mean 0.24, n=7) depending on grain. Given that configuration-Δr^2 only ranges from 0-1, a mean difference of 0.0.19-25 in this statistic (depending on extent or grain) is substantial. Thus, the scale of the landscape map has a large potential to influence a researcher's interpretation of relative configuration versus proportion effects.

An examination of the multi-scale model details (Appendices 6-1 and 6-2) is also informative, since only the most important scales and variables are included. For most species and for the number of abundant forest birds, PROP was modelled at the 1km extent, although PROP was modelled at both extents for jays (1km: low-forest; 3km: all-landscapes) and downy woodpeckers (1km: all-landscapes; 3km: low-forest model). In contrast, the best extent for configuration metrics was species-specific: 3km (chickadee, squirrel, forest bird evenness), 1km (crow, downy and hairy woodpeckers) or both extents (magpie and jay, depending on the model / configuration metric). Configuration metrics were best modelled at a) the 100m grain (except DFENCE) for bird species using non-forest extensively (crows, magpies), or b) the 5m grain for forest birds (chickadees, jays, sapsuckers, downy and hairy woodpeckers). The "best" grain for PROP is not meaningful, since PROP was highly correlated between grains.

3.3. Direction of forest proportion, configuration, and distance effects

To determine whether each forest metric had a positive or negative effect, the coefficients of the multi-scale models were examined (all-landscapes: Appendix 6-1; low-forest: Appendix 6-2). The direction of the effect of several forest metrics was consistent among forest species, but often different from species using non-forest extensively. For example, the abundance of all forest species increased with forest proportion, while crows and magpies responded negatively. Forest species' abundance increased with patch density (chickadee, jay, downy and hairy woodpecker) and forest clustering (chickadee, squirrel, hairy woodpecker), while magpies decreased. Abundance decreased with increasing distance to large patches (D100HA, D1000HA) for three forest species (chickadee, squirrel, ruffed grouse), while crow abundance increased. Responses to fencerow density and core area covariance did not follow the forest species / open species dichotomy. Both magpies and sapsuckers increased with fencerow density, as did forest bird evenness. Crows and jays increased with core area covariance, while squirrels decreased.

3.4. Suitability of abundance as a dependent variable

The ratio of fledgling to adult chickadees tended to increase with the average maximum number of adults ($p<0.05$), though deviance explained was low ($r^2=0.08$; Fig. 6-1). This suggests that a decrease in chickadee abundance may somewhat underestimate the effects of unfavorable landscape changes.

4. Discussion

4.1. Effect of forest gradient on relative effects of proportion versus configuration

When all landscapes (~2.5-62% forest) were included in the models, the abundance of all ten species responded to forest proportion. Fewer responded to configuration (crows, magpies, chickadees, jays, squirrels, downy woodpecker), and in several cases the configuration coefficient provided a poor fit to the data. Averaged over all ten species, forest proportion explained seven times more variation in species' abundance than did configuration. Further, even for species responding to configuration, forest proportion explained more variance. Similarly, forest proportion had a large effect on the number of abundant forest birds, while configuration had a small effect on forest bird evenness. These results support previous empirical work that has primarily indicated a larger relative effect of habitat loss over configuration, on species and community responses (e.g. Villard et al. 1999). The majority have indicated that habitat proportion has the greatest effect (McGarigal and McComb 1995, Peery et al. 1999, Trzcisnki et al. 1999, Rosenberg et al. 1999, Drolet et al. 1999, Imbeau and Desrochers 2002, Lichstein et al. 2002, Cushman and McGarigal 2004, Radford and Bennett 2004, Radford et al. 2005, but see Villard 1999, Cumming and Schmiegelow 2001).

From a conservation perspective, it is probably more relevant to focus on landscapes with low habitat cover, since maintaining very high proportions of habitat is often not a management option. When forest cover was <30%, forest proportion explained on average only twice the variation in species' abundance as did configuration. This was because the *relative* effect of configuration increased for several species in landscapes with less than 30% forest cover (jay, squirrel, hairy woodpecker, sapsucker, crow, magpie). This is consistent with simulations suggesting that fragmentation effects should be greatest when the proportion of habitat is low (e.g. McLellan et al. 1986, Fahrig 1997, 1998, Collingham and Huntley 2000, Flather and Bevers 2002). Previous empirical studies have also suggested that patch size and / or isolation effects on population density were greater when there was a low proportion of habitat in the landscape surrounding the patch (reviewed by Fahrig 2003). However, these patch-level metrics are both correlated with landscape habitat proportion. Because these relationships were not controlled for, these studies could be interpreted as indicating stronger effects of habitat loss (rather than configuration) when habitat proportion was low (Fahrig 2003).

In contrast to the general trend of greater fragmentation effects at low forest cover, two species (chickadee, downy woodpecker) responded to configuration over the wider gradient of forest cover (~2-62%), but not at all when forest cover was <30%. For the downy woodpecker, the significance of the configuration effect was entirely dependent on one outlier, suggesting a weak or spurious effect. However, for chickadees, the implication is that configuration appeared to have a stronger effect at moderately high than at low proportions of forest. Simulations suggest that fragmentation effects become important at lower levels of habitat loss for species with lower vagility (e.g. Henein et al. 1998, King and With 2002). Since natal dispersal distances (Sutherland et al. 2000) and home range gap crossing distances (Grubb and Doherty 1999) increase with body size, chickadees (the smallest species) may be less vagile than the larger species. It may be that for these small birds, relatively little forest loss was required for fragmentation effects to come into play, and that when forest loss was advanced (i.e. <30% remaining), the functional level of fragmentation was very high for all landscapes (i.e. little or no functional gradient, and hence no effect of configuration). This would be consistent with the suggestion of Turcotte and Desrochers (2005) that dispersing chickadees in landscapes with advanced forest loss and fragmentation may be "gap-locked", unable to cross large areas of non-forest to find new habitat.

4.2. Effect of spatial scale on relative effects of forest proportion versus configuration

The relative statistical effects of habitat proportion versus configuration depended strongly on the extent and grain of the landscape map. For several species (e.g. crow, magpie, chickadee, blue jay, hairy woodpecker), configuration had no effect at certain scales, but a moderate or large relative effect (relative configuration-Δr^2) at other scales. This highlights the importance of exploring different measurement scales when attempting to quantify configuration using purely structural metrics, particularly when little is known about which scales are likely to be most relevant for a species. For example, a researcher employing a single-scale approach might have chosen the larger extent and grain for larger species such as jays or hairy woodpeckers, or the smaller scale (1km, 5m) for chickadees, based on dispersal and gap crossing distances. However, for several species this approach would have failed to reveal configuration effects.

My results also suggest that the finer details of forest configuration may be important for forest birds, since configuration metrics were only included at the 5m grain in the multi-scale models. In contrast, crows and magpies responded most strongly to configuration at the 100m grain (except to fencerow density, which was only measured at the 5m grain). Configuration metrics from the 5m grain maps generally indicate greater fragmentation (e.g. more patches) than metrics from the coarser map. This suggests that forest birds perceive the forest cover as more fragmented than birds that use the non-forest matrix extensively.

For most species, habitat proportion was more important at the 1km than the 3km extent. The smaller extent corresponded most closely to the area of the survey sites (see Fig. 4-2b of Chapter 4). This suggests that forest proportion has mainly "local" effects (e.g. by influencing local carrying capacity). In contrast, the best extent for configuration was species-specific. The 3km extent would suggest that configuration had "distant" effects, perhaps through its influence on landscape connectivity and thus the ability of dispersers to reach the study sites. For example, chickadee abundance increased with greater patch density at the 3km extent. A larger number of patches is associated with smaller inter-patch distances. This may have enhanced landscape connectivity for chickadees, which are reluctant to cross large gaps (e.g. Desrochers and Hannon 1997, St. Clair et al. 1998). The 1km extent would suggest more local configuration effects. Small forest patches and forest edges can have a greater density of arboreal arthropods (Jokimäki et al. 1998, Major et al. 2003, but see Song 1998), and may thus provide good quality foraging habitat. This may explain, for example, the greater abundance of hairy woodpeckers in 1km landscapes with greater patch density.

4.3. Management implications of species' and community responses to forest metrics

The abundance of all forest species increased with the proportion of forest in the landscape, while crow and magpie abundance decreased. Similarly, the direction of the responses to most forest configuration and distance metrics differed between forest species and birds using both forest and non-forest. For example, some forest species' abundances increased with patch density (chickadee, jay, downy, hairy woodpecker) and forest clustering (chickadee, squirrel, hairy woodpecker), and decreased with increasing distance to the nearest $\geq$1000ha patch (chickadee, ruffed grouse). In contrast, magpie abundance decreased with patch density and forest clustering, and crows increased with distance to the nearest 100ha patch.

Several forest species had stronger configuration effects when the proportion of forest was <30% (sapsucker, hairy woodpecker, squirrel, blue jay). This suggests that when habitat loss is extensive, favorable configurations may compensate for habitat loss to some degree. However, the fact that configuration explained only 8-22% of the variation in abundance for these species suggests that manipulation of configuration may be of limited use as a practical management strategy.

Further, management is more likely to be applied at a community than a species-specific level. Within the forest birds, responses to configuration and distance metrics were species-specific, in terms of which metrics and / or scales were most important. Reflecting this, configuration had very little effect on measures of the forest-bird community as a whole. Evenness of the standardized forest-bird species' abundances increased somewhat with fencerow density, suggesting that certain species (e.g. sapsucker) became relatively more rare than other species when fencerow density was low. However, this was a small effect, explaining only 8% of the variance in species' evenness.. After fencerow density was accounted for, forest proportion had no significant effect on species evenness. In contrast, the number of species that were "abundant" (i.e. above their 50th percentile for abundance) depended strongly on forest proportion, whether the gradient of forest cover was wide ($\Delta r^2 = 0.59$) or low ($\Delta r^2 = 0.50$). The number of abundant species present also increased with closer proximity to large forested patches, though this effect was relatively small. Therefore, the only broad recommendation that can be made for the management of forest birds is that a larger proportion of forest should increase the abundance of forest birds in the local landscape.

4.4. Suitability of abundance as the response variable

The ratio of fledgling to adult chickadees increased significantly with the average maximum abundance of adult chickadees. However, the relationship was weak, with only 8% of the variance in the reproductive index explained by the adult abundance. Thus, abundance may have slightly underestimated the "effects" of habitat loss / fragmentation. Specifically, not only did habitat loss reduce chickadee abundance, but lower abundance was associated with lower reproductive success. Even this coarse level of reproductive information was lacking for other species, for which very few fledglings were identified. This represents one limitation of landscape-level studies: detailed information from each landscape is often sacrificed in favor of increasing sample sizes (e.g. McGarigal and McComb 1995, Villard et al. 1999). Thus, the effects of habitat loss and fragmentation on species' abundance should be taken as minimum ecological effects, which may be further compounded by reductions in fitness.

4.5. Limitations for comparing relative effects of habitat proportion and configuration

In my study, "forest" was used as a substitute for "habitat". Cumming and Schmiegelow (2001) found that as their definition of habitat was narrowed (with respect to stand age and tree species), relatively more boreal bird species responded to configuration than to proportion. Thus, my results may have been different had I defined habitat more narrowly. For example, in some study areas downy woodpeckers are most abundant in stands that include smaller trees and lower canopies (references in Jackson and Ouellet 2002), while hairy woodpeckers prefer mature forests (references in Jackson et al. 2002). However, the forest cover in my study area was relatively homogenous compared to Cumming and Schmiegelow's (2001) study area. The latter was more diverse in stand type and age due to industrial harvesting, which was largely absent in my study area.

The habitat configuration metrics I selected may have failed to represent aspects of habitat spatial pattern that were important for some species. Many other configuration metrics, not included in the multivariate analyses, varied strongly with forest proportion. Because their independent effects were not distinguished from those of habitat proportion, it is possible that forest proportion "effects" included a configuration effect. However, the metrics I selected represented several different aspects of configuration with potential biological significance. Patch density represented fragmentation *per se*, forest clustering represented the relative amounts of edge and core areas, core area covariance reflected variability in patch size and shape, and fencerow density reflected potential travel corridors. Presumably, a species that was very sensitive to patch size, edge, or isolation would have responded relatively strongly to one or more of these metrics.

Finally, while the range of forest proportion sampled (~2.5-62%) could reasonably be assumed a priori to represent a strong functional gradient of habitat proportion (or habitat heterogeneity) for most study species, this was less clear for each of the configuration metrics analyzed. Fahrig (1998) found that fragmentation did not influence species persistence unless the distance between breeding patches was 1-3 times less than dispersal distances. While Fahrig's (1998) breeding patches do not directly correspond to my forest patches (many of which were individually too small to support a population or even a single territory), her results can be generalized: a species will not respond strongly to a structural fragmentation gradient if it is either too low (all/most landscapes functionally unfragmented) *or* too high (all/most landscapes very functionally fragmented). However, because forest fragmentation increases with agricultural activity (Young et al. 2006), which is long-standing and widespread in the present study area, the highest levels of structural fragmentation observed here are probably close to the maximum that is likely to occur in an agricultural region. If so, the effects of much greater fragmentation would not be of practical relevance for management. On the other hand, structurally unfragmented landscapes were not well-represented at low forest cover in my study (see Fig. 4-2a of Chapter 4), nor in other studies in agricultural regions (e.g. Fig. 1 of Villard et al. 1999, Fig. 3 of Trzcisnki et al.

1999). Potentially, a gradient that included very low fragmentation could reveal stronger effects than those observed in the present and other studies, with a corresponding potential to manage for negative fragmentation effects. The most direct way to address this would be to manipulate fragmentation experimentally, which would be extremely difficult on a landscape scale. A more indirect approach would be to examine the univariate relationship between a species' abundance and forest proportion. If fragmentation has large negative effects over and above those due to forest loss, species' abundances should reach zero well before forest proportion reaches zero. As shown in Chapter 4, this was not the case for any of the study species, suggesting that the results of the present study do not underestimate negative fragmentation effects.

Table 6-1. Forest proportion and configuration metrics

Metric	Description	Calculation
PROP	Proportion of forest cover	(Total forest area) / (total landscape area)
PD	Patch density	(# forest patches) / (total landscape area)
CORVAR	Core area variability	(core area standard deviation among patches) / (mean core area per patch)*100
CLUST	Forest clustering	(core area : edge area[A]) / (max[B] core area : edge area) Residuals from regression on PROP.
DFENCE	Fencerow density	(Total fencerow length) / (total non-forest area)
D100HA	Distance to 100 ha patch	Shortest distance to >=100ha patch from 3km radius boundary[C]
D1000HA	Distance to nearest 1000 ha patch	Shortest distance to >=1000 ha patch from 3km radius boundary[C]

A. Core and edge areas based on 50m or 100m edge area buffer (for 5m and 100m grains, respectively)
B. Maximum ratio based on forest in a perfect square
C Non-zero distances only, unless nearest four patches had distance of zero

Table 6-2. Summary statistics for landscape metrics, by scale

Metric	Extent / grain	Mean	SD	Min	Max
PROP	1km / 5m	0.247	0.1844	0.033	0.616
	1km / 100m	0.247	0.1871	0.038	0.627
	3km / 5m	0.240	0.1571	0.025	0.603
	3km / 100m	0.240	0.1581	0.027	0.608
PD (#/ha)	1km / 5m	0.091	0.0431	0.019	0.205
	1km / 100m	0.027	0.0142	0.003	0.068
	3km / 5m	0.075	0.0275	0.024	0.144
	3km / 100m	0.020	0.0082	0.006	0.038
CORVAR	1km / 5m	365.5	108.5	175.6	700.0
	1km / 100m	158.9	119.4	0	447.2
	3km / 5m	626.2	178.5	353.0	1322.0
	3km / 100m	484.4	170.2	0	922.0
CLUST	1km / 5m	0.0052	0.05342	-0.0607	0.1814
	1km / 100m	0.0028	0.06680	-0.0722	0.2907
	3km / 5m	0.0003	0.00639	-0.0095	0.0142
	3km / 100m	0.0008	0.00878	-0.01917	0.0278
DFENCE (m/ha)	1km / 5m	11.35	8.196	0	36.37
	3km / 5m	8.77	4.547	0	18.79
D100HA (m)		1650	1501.8	0	6231
D1000HA (m)		6872	4981.9	520	18392

Table 6-3. Absolute and relative proportions of deviance explained by forest proportion versus configuration, in the all-landscapes and low-forest multi-scale models. See Appendices 6-1 and 6-2 for model details.

	All-landscapes models			Low-forest models			
Response variable	PROP-Δr^2 [A]	Configuration-Δr^2 [B]	Relative configuration-Δr^2 [C]	PROP-Δr^2 [A]	Configuration-Δr^2 [B]	Relative configuration-Δr^2 [C]	Change in relative configuration-Δr^2 when forest <30% [D]
Species' abundance:							
American crow	0.23	0.07	0.23	0.00	0.14	1.00	+
Black-billed magpie	0.13	0.04	0.24	0.00	0.20	1.00	+
Black-capped chickadee	0.32	0.09	0.21	0.54	0.00	0.00	-
Blue jay	0.31	0.09	0.25	0.12	0.17	0.59	+
Red squirrel	0.37	0.05	0.14	0.09	0.08	0.45	+
Ruffed grouse	0.14	0.07	0.00	0.17	0.00	0.00	=
Downy woodpecker	0.25	0.10	0.30	0.14	0.00	0.00	-
Hairy woodpecker	0.58	0.00	0.00	0.29	0.14	0.32	+
White-breasted nuthatch	0.50	0.00	0.00	0.51	0.00	0.00	=
Yellow-bellied sapsucker	0.19	0.00	0.00	0.00	0.22	1.00	+
Species' average	0.30	0.04	0.14	0.19	0.09	0.44	
Forest bird community [E]:							
# "abundant" species	0.59	0.00	0.00	0.50	0.00	0.00	=
Species evenness	0.00	0.08	1.00	0.00	0.00	0.00	n/a

A. PROP-Δr^2 = change in model r^2 when forest proportion dropped from model

B. configuration-Δr^2 = change in model r^2 when all configuration metrics dropped from model

C. relative configuration-Δr^2 = configuration-Δr^2 / (configuration-Δr^2 + PROP-Δr^2). Equal to 0 when only forest proportion is significant, 1 when only configuration is significant, and 0.5 when model r^2 changes by the same amount whether the proportion or configuration metrics were dropped from the model.

D. + (increased); - (decreased), = (no change), n/a (cannot be calculated since neither PROP nor configuration had an effect in one of the models)

E. Chickadee, jay, grouse, downy and hairy woodpeckers, nuthatch, sapsucker

Table 6-4. Absolute and relative proportions of deviance explained by forest proportion versus configuration, in the all-landscapes and low-forest single-scale models. See Appendices 6-3 and 6-4 for model details.

		All-landscapes			Low-forest		
Species	Extent (km), grain (m)	PROP-Δr^2 [A]	Configuration-Δr^2 [A]	Relative configuration -Δr^2 [A]	PROP-Δr^2 [A]	Configuration -Δr^2 [A]	Relative configuration -Δr^2 [A,B]
American crow	1, 5	0.19	0.00	0.00	0.00	0.00	n/a
	1, 100	0.23	0.07	0.23	0.00	0.11	1.00
	3, 5	0.00	0.09	1.00	0.00	0.00	n/a
	3, 100	0.09	0.00	0.00	0.00	0.00	n/a
Black-billed magpie	1, 5	0.21	0.05	0.19	0.00	0.00	n/a
	1, 100	0.48	0.00	0.00	0.00	0.20	1.00
	3, 5	0.16	0.06	0.27	0.00	0.00	n/a
	3, 100	0.34	0.00	0.00	0.00	0.17	1.00
Black-capped chickadee	1, 5	0.46	0.00	0.00	0.43	0.00	0.00
	1, 100	0.45	0.00	0.00	0.43	0.00	0.00
	3, 5	0.12	0.32	0.72	0.35	0.00	0.00
	3, 100	0.28	0.11	0.28	0.39	0.06	0.14
Blue jay	1, 5	0.21	0.00	0.00	0.12	0.08	0.40
	1, 100	0.25	0.00	0.00	0.28	0.00	0.00
	3, 5	0.25	0.06	0.19	0.16	0.00	0.00
	3, 100	0.29	0.00	0.00	0.18	0.00	0.00
Red squirrel	1, 5	0.38	0.00	0.00	0.21	0.10	0.31
	1, 100	0.37	0.00	0.00	0.20	0.00	0.00
	3, 5	0.27	0.07	0.20	0.00	0.00	n/a
	3, 100	0.30	0.06	0.16	0.08	0.11	0.59
Ruffed grouse	1, 5	0.16	0.00	0.00	0.17	0.00	0.00
	1, 100	0.16	0.00	0.00	0.16	0.00	0.00
	3, 5	0.13	0.00	0.00	0.08	0.00	0.00
	3, 100	0.13	0.00	0.00	0.08	0.00	0.00
Downy woodpecker	1, 5	0.16	0.13	0.45	0.18	0.00	0.00
	1, 100	0.23	0.09	0.28	0.09	0.07	0.42
	3, 5	0.18	0.07	0.27	0.20	0.00	0.00
	3, 100	0.22	0.07	0.25	0.19	0.00	0.00
Hairy woodpecker	1, 5	0.59	0.00	0.00	0.29	0.14	0.32
	1, 100	0.58	0.00	0.00	0.30	0.00	0.00
	3, 5	0.52	0.00	0.00	0.18	0.00	0.00
	3, 100	0.52	0.00	0.00	0.18	0.00	0.00
White-breasted nuthatch	1, 5	0.49	0.00	0.00	0.21	0.00	0.00
	1, 100	0.50	0.00	0.00	0.20	0.00	0.00
	3, 5	0.37	0.00	0.00	0.10	0.00	0.00
	3, 100	0.36	0.00	0.00	0.09	0.00	0.00
Yellow-bellied sapsucker	1, 5	0.21	0.00	0.00	0.00	0.14	1.00
	1, 100	0.19	0.00	0.00	0.00	0.00	n/a
	3, 5	0.17	0.00	0.00	0.00	0.00	n/a
	3, 100	0.16	0.00	0.00	0.08	0.09	0.54
# abundant forest bird species	1, 5	0.55	0.00	0.00	0.50	0.00	0.00
	1, 100	0.57	0.00	0.00	0.50	0.00	0.00
	3, 5	0.32	0.00	0.00	0.25	0.00	0.00
	3, 100	0.32	0.00	0.00	0.25	0.00	0.00

Table 6-4. Absolute and relative proportions of deviance explained by forest proportion versus configuration, in the all-landscapes and low-forest single-scale models. See Appendices 6-3 and 6-4 for model details.

		All-landscapes			Low-forest		
Species	Extent (km), grain (m)	PROP-Δr^2 [A]	Configuration-Δr^2 [A]	Relative configuration -Δr^2 [A]	PROP-Δr^2 [A]	Configuration -Δr^2 [A]	Relative configuration -Δr^2 [A,B]
Forest bird evenness	1, 5	0.06	0.00	0.00	0.00	0.00	n/a
	1, 100	0.05	0.00	0.00	0.00	0.00	n/a
	3, 5	0.00	0.08	1.00	0.00	0.00	n/a
	3, 100	0.00	0.00	0.00	0.00	0.00	n/a

A. Calculated as in Table 6-3

B. n/a (cannot be calculated because neither proportion nor configuration was significant)

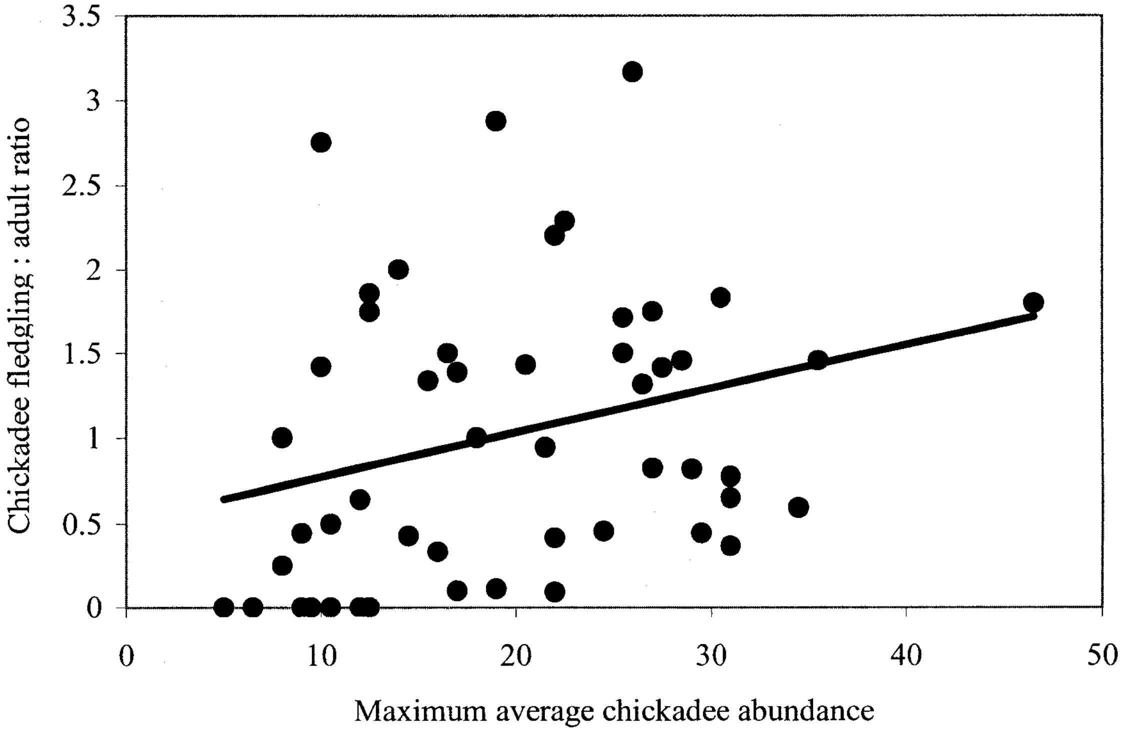


Fig. 6-1. Relationship between estimated chickadee abundance (average maximum over 2 years) and the ratio of juveniles to adults observed in round 4 (average over 2 years).

References

Bélanger, L. & Grenier, M. 2002. Agriculture intensification and forest fragmentation in the St. Lawrence valley, Québec, Canada. *Landscape Ecology* 17: 495-507.

Bélisle, M. & St. Clair, C. C. 2001. Cumulative effects of barriers on the movements of forest birds. *Conservation Ecology* 5: 9.

Bélisle, M., Desrochers, A. & Fortin, M.-J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82: 1893-1904.

Bellamy, P., Hinsley, S. & Newton, I. 1996. Factors influencing bird species numbers in small woods in south-east England. *Journal of Applied Ecology* 33: 249-262.

Bibby, C. J. 1994. Recent past and future extinctions in birds. *Philosophical Transactions of the Royal Society of London, Biological Sciences* 344: 35-40.

Bock, C. E. & Jones, Z. F. 2004. Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment* 2: 403-410.

Collingham, Y. C. & Huntley, B. 2000. Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications* 10: 131-144.

Cooper, C. B. & Walters, J. R. 2002. Independent effects of woodland loss and fragmentation on brown treecreeper distribution. *Biological Conservation* 105: 1-10.

Cumming, S. G. & Schmiegelow, F. K. A. 2001. Effects of habitat abundance and configuration, and the forest matrix, on distributional patterns of boreal birds. Sustainable Forest Management Network working paper.

Cushman, S. A. & McGarigal, K. 2003. Landscape level patterns of avian diversity in the Oregon Coast Range. *Ecological Monographs* 73: 259-281.

Cushman, S. A. & McGarigal, K. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* 14: 1090-1105.

Desrochers, A. & Hannon, S. J. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11: 1204-1210.

Doherty, P. F. & Grubb, T. C. Jr. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. *Ecology* 83: 844-857.

Doherty, P. F. Jr. & Grubb, T. C. Jr. 2003. Relationship of nutritional condition of permanent-resident woodland birds with woodlot area, supplemental food, and snow cover. *Auk* 120: 331-336.

Dolby, A. S. & Grubb, T. C. Jr. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bark-foraging birds. *Condor* 408-412.

Donovan, T. M., Jones, P. W., Annand, E. M. & Thompson, F. R. I. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78: 2064-2075.

Drolet, B., Desrochers, A. & Fortin, M.-J. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. *Condor* 101: 699-704 .

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603-610.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modeling* 105: 273-292.

Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100: 65-74.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487-515.

Flather, C. H. & Bevers, M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159: 40-56.

Grubb, T. C. Jr. & Doherty, P. F. Jr. 1999. On home-range gap-crossing. *Auk* 116: 618-628.

Henein, K., Wegner, J. & Merriam, G. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. *Oikos* 81: 168-186.

Herrera, C. M. 1978. On the breeding distribution pattern of European migrant birds: MacArthur's theme reexamined. *Auk* 95: 496-509.

Hobson, K., Bayne, E. & Van Wilgenburg, S. 2002. Large-Scale Conversion of Forest to Agriculture in the Boreal Plains of Saskatchewan. *Conservation Biology* 16: 1530-1541.

Hosmer, D. W. & Lemeshow, S. 2000. Applied Logistic Regression, 2nd Edition. United States of America: John Wiley & Sons, Inc.

Hurd, C. R. 1996. Interspecific attraction to the mobbing calls of black-capped chickadees (*Parus atricapillus*). *Behavioral Ecology and Sociobiology* 38: 287-292.

Imbeau, L. & Desrochers, A. 2002. Area sensitivity and edge avoidance: the case of the three-toed woodpecker (*Picoides tridactylus*) in a managed forest. *Forest*

Ecology and Management 164: 249-256.

Jackson, J. A. & Ouellet, H. R. 2002. Downy woodpecker (*Picoides pubescens*). *In* The Birds of North America, No. 613 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Jackson, J. A., Ouellet, H. R. & Jackson, B. J. S. 2002. Hairy woodpecker (*Picoides villosus*). *In* The Birds of North America, No. 702 (A. Poole and F. Gill, eds.). The Birds of North America., Inc., Philadelphia, PA.

Johnson, C. W. & Adkisson 1985. Dispersal of beech nuts by blue jays in fragmented landscapes. *American Midland Naturalist* 113: 319-321.

Jokimäki, J., Huhta, E., Itaemies, J. & Rahko, P. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Canadian Journal of Forest Research* 28: 1068-1072.

Kilham, L. 1969. Reproductive behavior of hairy woodpeckers. III. Agonistic behaviour in relation to courtship and territory. *Wilson Bulletin* 81: 169-183.

King, A. W. & With, K. A. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147: 23-39.

Krebs, C. J. 1999. Ecological Methodology. Menlo Park, California: Addison-Wesley Educational Publishers, Inc.

Lahti, K., Orell, M., Rytkonen, S. & Koivula, K. 1998. Time and food dependence in willow tit winter survival. *Ecology* 2904-2916.

Langlois, J. P., Fahrig, L., Merriam, G. & Artsob, H. 2001. Landscape structure influences continental distribution of hantavirus in deer mice. *Landscape Ecology* 16: 255-266.

Lichstein, J. W., Simons, T. R. & Franzreb, K. E. 2002. Landscape effects on breeding songbird abundance in managed forests. *Ecological Applications* 12: 836-857.

Major, R., Christie, F., Gowing, G., Cassis, G. & Reid, C. 2003. The effect of habitat configuration on arboreal insects in fragmented woodlands of south-eastern Australia. *Biological Conservation* 113: 35-48.

McGarigal, K. & McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* 65: 236-260.

McGowan, K. J. 2001. Demographic and behavioral comparisons of surburban and rural American Crows. Avian Ecology and Conservation in an Urbanizing World (pp. 365-381). Norwell, MA: Kluwer Academic Publishers.

McLellan, C. H., Dobson, A. P., Wilcove, D. S. & Lynch, J. F. 1986. Effects of forest fragmentation on new and old world bird communities: empirical observations and theoretical implications. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates (pp. 305-313). Madison, Wisconsin: University of Wisconsin Press.

Newton, I. 1994. Experiments on the limitation of bird breeding densities: A review . *Ibis* 136: 397-411.

Nilsson, S. G. 1987. Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *Journal of Animal Ecology* 56: 921-937.

Peery, M. Z., Gutierrez, R. J. & Seamans, M. E. 1999. Habitat composition and configuration around Mexican spotted owl nest and roost sites in the Tularosa Mountains, New Mexico. *Journal of Wildlife Management* 63: 36-43.

Pravosudov, V. V. & Grubb, T. C. Jr. 1993. White-breasted nuthatch (*Sitta carolinensis*). *In* The Birds of North America, No. 54 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Radford, J. Q. & Bennett, A. F. 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia . *Biological Conservation* 117: 375-391.

Radford, J. Q., Bennett, A. F. & Cheers, G. J. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124: 317-337.

Rosenberg, K. V., Lowe, J. D. & Dhondt, A. A. 1999. Effects of forest fragmentation on breeding tanagers: a continental perspective. *Conservation Biology* 13: 568-583.

Saura, S. 2004. Effects of remote sensor spatial resolution and data aggregation on selected fragmentation indices. *Landscape Ecology* 19: 197-209 .

Sherry, T. W. & Holmes, R. T. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.

Singh, J. S. 2002. The biodiversity crisis: a multifaceted review. *Current Science (Bangalore)* 82: 638-647.

Smith, S. M. Black-capped chickadee. 1993. *In* The Birds of North America, No. 39 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C: The American Ornithologists' Union.

Song, S. J. 1998. Effects of natural and anthropogenic forest edge on songbirds breeding in the boreal mixed-wood forest of northern Alberta. Dissertation, University of Alberta.

St. Clair, C. C., Belisle, M., Desrochers, A. & Hannon, S. 1998. Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology[online]* 2: 13.

StataCorp. 2005. Stata Statistical Software. Release 9. College Station, TX: StataCorp LP.

Sutherland, G. D., Harestad, A. S., Price, K. & Lertzman, K. P. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4.

Trost, C. H. 1999. Black-billed magpie (*Pica pica*). *In* The Birds of North America, No. 389 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Trzcinski, M. K., Fahrig, L. & Merriam, G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* 9: 586-593.

Turcotte, Y. & Desrochers, A. 2005. Landscape-dependent distribution of northern forest birds in winter. *Ecography* 28: 129-140.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47: 893-901.

Verbeek, N. A. M. & Caffrey, C. 2002. American crow (*Corvus brachyrhynchos*). *In* The Birds of North America, No. 647 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Villard, M.-A., Trzcinski, M. K. & Merriam, G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy . *Conservation Biology* 62: 774-783.

Weise, C. M. & Meyer, J. R. 1979. Juvenile dispersal and development of site fidelity in the black-capped chickadee. *The Auk* 96: 40-55.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

With, K. A. & Crist, T. O. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76: 2446-2459.

Young, J. E. 2003. Land-use and land-cover change in a highly fragmented boreal forest: the Beaverhills case study. Dissertation, University of Alberta.

Young, J. E., Sánchez-Azofeifa, G. A., Hannon, S. J. & Chapman, R. 2006. Trends in land cover change and isolation of protected areas at the interface of the southern boreal mixedwood and aspen parkland in Alberta, Canada. *Forest Ecology and Management* 230: 151-161.

Chapter 7: Thesis summary

1. Shape of the relationship between habitat loss and ecological responses

1.1. Literature review

Critical threshold responses to habitat amount are expected to occur when fragmentation effects compound those of habitat loss, when the amount of habitat drops below a critical level (Andrén 1994, Flather and Bevers 2002). Critical thresholds could also result from Allee effects that lead to negative growth at low habitat levels (Amarasekare 1998), or from time lags which initially mask the full effects of habitat loss (Schrott et al. 2005, Carlson 2000). Simulations suggest that threshold values should be higher for landscapes with greater fragmentation and temporal variability, lower matrix quality or slower rates of habitat loss (e.g. With et al. 1999, Wimberly 2000, Fahrig 2001, Schrott et al. 2005). Less vagile species are also predicted to have higher thresholds, unless high levels of mortality in the matrix makes dispersal among habitat patches too risky. In addition, species with low reproductive rates and greater sensitivity to fragmentation (e.g. negative edge or patch area effects) are predicted to exhibit higher thresholds (Fahrig 2001, Schrott et al. 2005). I found in my review that empirical thresholds tended to fall within Andrén's (1994) predicted 10-30% habitat, but not without exception, and linear relationships were common.

1.2. Comparison of statistical methods for determining shape of relationship

Relatively few of the threshold studies I reviewed used statistical methods to estimate the presence or value of thresholds, and instead relied on visual estimates. I compared two threshold models, piecewise regression and changepoint analysis (Toms and Lesperance 2003, Qian et al. 2003). The former was an unbiased estimator of "continuous thresholds" (e.g. Fig. 3-1a from Chapter 3), and the latter of "discontinuous thresholds" (e.g. Fig. 3-1b from Chapter 3). However, piecewise regression tended to over- or underestimate discontinuous thresholds (if the true threshold was low or high on the habitat proportion gradient, respectively). In contrast, changepoint analysis tended to underestimate continuous thresholds. Thus, if only one threshold model is estimated, careful consideration should be given to the type of threshold that is theoretically expected or which is clearly apparent in the data. If several shapes could plausibly describe an ecological response to habitat proportion, multimodel selection methods (Burnham and Anderson 2004, Johnson and Omlan 2004) are useful for exploring the evidence for each. AICc was somewhat biased towards overfitting (choosing more complex shapes than the true shape), while BIC had a small bias towards underfitting. Thus, an examination of both AICc and BIC results together can be more informative than relying on either method alone, if their respective biases are kept in mind.

1.3. Shape of relationship between forest cover and forest bird and mammal responses

I used the statistical methods described above to examine the shape of the relationship between the abundance of each study species and the proportion of forest in the landscape. Most species responded linearly to forest proportion, suggesting that fragmentation did not compound the effects of forest loss when forest cover was low. A few species exhibited nonlinear responses to a gradient of forest cover. However, these relationships were not consistent with a large negative effect of fragmentation below the threshold. Downy woodpeckers declined little until below a threshold of about 10-20% forest. Black-capped chickadee abundance increased as forest cover decreased from 62 - 34% forest. These relationships suggest that, for these edge-preferring species (Smith 1993, Jackson and Ouellet 2002), positive fragmentation effects may have compensated for (downy woodpeckers) or exceeded (chickadees) the negative effects of moderate habitat loss. Reflecting the nonlinear declines of these two species, the number of forest species that were abundant in a landscape decreased moderately until below a threshold of about 25% forest, below which declines became steeper. In contrast, forest bird evenness decreased only slightly with forest loss, suggesting that the relative abundance of these species did not change much in relation to one another. Magpie abundance decreased abruptly above a discontinuous threshold of 35% forest. In the segment below the threshold, any increases in forest cover may have been balanced by a corresponding loss of foraging habitat (agricultural land) for this generalist. Above the threshold, foraging habitat quality may have declined abruptly, due to an abrupt shift in the composition of unforested habitats towards nonagricultural openings.

2. Relative effects of habitat amount and spatial configuration

2.1. Literature review

A review of the relative effects of habitat amount versus habitat spatial configuration suggested that habitat amount had a larger effect than configuration on population responses to landscape structure. However, these relative effects may depend on a variety of factors, several of which are consistent with the critical thresholds hypothesis. For example, several simulations suggested the relative effect of configuration increased at lower levels of habitat (e.g. Flather and Bevers 2002). As well, low species vagility and reproductive rates were predicted to increase species' sensitivity to habitat fragmentation (With and King 1999), just as these traits increased the predicted critical threshold value (suggesting sensitivity to fragmentation over a broader range of habitat cover). Other factors found to influence the relative effect of configuration related to choices made by the researcher. For example, relative configuration effects tended be greater for continuous (e.g. abundance) than binary (e.g. persistence) response variables, and for relative measures of abundance scaled to habitat amount (e.g. density or patch occupancy, the proportion of remaining habitat occupied) than for absolute measures of abundance (Flather and Bevers 2002). In addition, defining habitat more broadly than species' perceptions of habitat may either increase the relative effect of configuration (e.g. for edge species) or to decrease it (e.g. for interior species or habitat specialists; Fahrig 1997, Cumming and Schmiegelow 2001). In two multi-scale studies, the relative effect of configuration was scale-dependent, being greatest at extents that were broad relative to the area in which the ecological response was measured. For these study organisms, this may suggest an important role of fragmentation during dispersal from the surrounding landscape into the study area (Langlois et al. 2001, Cooper and Walters 2002).

2.2. Relative effects of forest amount and configuration for forest birds and mammals

My empirical research suggested that the relative effect of forest amount and configuration on the abundance of forest breeding birds and mammals (mainly residents) depended on the spatial extent and grain of the landscape. However, at each metric's best scale, the abundance of all species was more strongly influenced by forest amount (2-62%) than configuration. For several species the relative effect of configuration increased when forest cover was <30% (hairy woodpecker, blue jay, yellow-bellied sapsucker, red squirrel, American crow, black-billed magpie), consistent with simulation predictions (e.g. Flather and Bevers 2002). As mentioned above, these relatively larger configuration effects did not translate into threshold declines in response to forest loss, for any of the four forest species in this list. This probably reflects the small absolute effect of configuration for all species. Contrary to simulation predictions, two species (downy woodpecker, black-capped chickadee) appeared to be influenced most strongly by forest configuration when the amount of habitat was moderate to high. Among the forest birds, responses to fragmentation were species-specific in terms of which of four configuration metrics were significant, the direction of their effects, and their best scale. In contrast, all forest birds responded negatively to forest loss, most at the smaller (1km) rather than the larger (3km) extent. This was reflected by a large effect of forest amount, and a very small effect of configuration, on forest bird community-level responses.

3. Conservation implications

The presence and value of critical threshold responses to habitat amount was predicted and observed empirically to vary among species and landscapes. Thus, basing management decisions on a generic or average threshold value (e.g. 10-30%) is inappropriate. Further study is required to determine whether empirical threshold values can be accurately predicted from species and landscape characteristics. Thresholds for many ecological responses, such as population abundance or species richness, may not accurately reflect the amount of habitat required for long term persistence. Therefore, threshold relationships should be interpreted cautiously when guiding management decisions. For example, a threshold for richness reflects the amount of habitat by which several species have declined to zero; a higher target level of habitat would clearly be required to protect all species (Radford et al. 2005). Similarly, a threshold for the abundance of a single species may be an inadequate target, if the population has already declined substantially by the threshold amount of habitat. Further, a threshold response may not always indicate greater sensitivity than species responding linearly to habitat loss. Among the forest birds and mammals studied, species with linear responses to forest loss were arguably more sensitive than those with threshold responses. For two forest birds, these thresholds reflected the fact that declines did not occur at all until forest loss was advanced.

Most simulation and empirical work suggests that overall, the amount of habitat is more important than its spatial configuration. However, active management of habitat for species' persistence is most critical in landscapes where habitat cover is low or declining. Under these conditions, the relative effect of habitat spatial configuration may increase, a prediction supported by my empirical results for forest birds and red squirrels. This suggests that manipulating the degree of fragmentation in landscapes with low habitat cover may enhance species' persistence. However, while most simulations suggest that reducing fragmentation should enhance species abundance or persistence, real organisms are variable in terms of the direction of fragmentation effects. Indeed, several of the forest species studied in my empirical work responded positively to more fragmented configurations. Thus, no general recommendations can be made for the management of habitat configuration that will benefit all species requiring that habitat type. In contrast, most species are likely to benefit from a greater amount of habitat, regardless of its spatial configuration. The most efficient conservation strategy would be to focus on habitat preservation or restoration. Where necessary, this approach could be combined with species-specific management of habitat configuration for sensitive or endangered species that experience strong, negative fragmentation effects.

References

Amarasekare, P. 1998. Allee effects in metapopulation dynamics. *American Naturalist* 152: 298-302.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.

Burnham, K. P. & Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261-304.

Carlson, A. 2000. The effect of habitat loss on a deciduous forest specialist species: the white-backed woodpecker (*Dendrocopos leucotos*). *Forest Ecology and Management* 131: 215-221.

Cooper, C. B. & Walters, J. R. 2002. Independent effects of woodland loss and fragmentation on brown treecreeper distribution. *Biological Conservation* 105: 1-10.

Cumming, S. G. & Schmiegelow, F. K. A. Effects of habitat abundance and configuration, and the forest matrix, on distributional patterns of boreal birds. 2001.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603-610.

Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100: 65-74.

Flather, C. H. & Bevers, M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159: 40-56.

Jackson, J. A. & Ouellet, H. R. 2002. Downy woodpecker (*Picoides pubescens*). *In* The Birds of North America, No. 613 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Johnson, J. B. & Omland, K. S. 2004. Model selection in ecology and evolution . *Trends in Ecology and Evolution* 101-108.

Langlois, J. P., Fahrig, L., Merriam, G. & Artsob, H. 2001. Landscape structure influences continental distribution of hantavirus in deer mice. *Landscape Ecology* 16: 255-266.

Qian, S. S., King, R. S. & Richardson, C. J. 2003. Two statistical methods for the detection of environmental thresholds. *Ecological Modelling* 166: 87-97.

Radford, J. Q., Bennett, A. F. & Cheers, G. J. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124: 317-337.

Schrott, G. R., With, K. A. & King, A. W. 2005. On the importance of landscape history for assessing extinction risk. *Ecological Applications* 15: 493-506.

Smith, S. M. Black-capped chickadee. 1993. *In* The Birds of North America, No. 39 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C: The American Ornithologists' Union.

Toms, J. D. & Lesperance, M. L. 2003. Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84: 2034-2041.

Wimberly, M. C. 2006. Species dynamics in disturbed landscapes: when does a shifting habitat mosaic enhance connectivity? *Landscape Ecology* 21: 35-46.

With, K. A., Cadaret, S. J. & Davis, C. 1999. Movement responses to patch structure in experimental fractal landscapes. *Ecology* 80: 1340-1353.

With, K. A. & King, A. W. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314-326.

Appendices

Appendix 3-1. Program to calculate a piecewise threshold using weighted least-squares regression, where independent variable is a proportion.

To use this program in Stata, save script below as an ado file named pw_thresh_min in the appropriate folder. In the command box or a do file, type:

pw_thresh_min y x obs minobs weight

where y is the name of the dependent, x is the name of the independent (must be on 0-1 scale), obs is the number of observations in the data set, minobs is the minimum number of data points to fall at/below or above the threshold, and weight is the name of the weighting variable (type 1 if no weights are desired).

The threshold estimate will be listed on the screen, and a new variable called pwthresh will also be generated, containing this value.

```
cap program drop pw_thresh_min
program pw_thresh_min
version 9
args y x  obs minobs weight

//1) SORT BY X:
        sort `x'

//2) GENERATE A VARIABLE LISTING ALL POTENTIAL THRESHOLD
VALUES
// AT 1% INTERVALS, AS PROPORTIONS (0-1 SCALE):
        if _N < 100 set obs 100
        range thresh_pw 0.01 1 100

//3) GENERATE TEMP VARIABLE FOR RECORDING THE LOG LIKELIHOOD
//WHEN THE PIECEWISE MODEL IS RUN AT EACH POTENTIAL THRESHOLD
//VALUE
        tempvar ll_pw
        generate `ll_pw'=.

//4)  RUN A SERIES OF PIECEWISE MODELS, TRYING THRESHOLDS
//AT ~ ALL VALUES OF THRESH_PW (AS LONG AS THERE ARE AT LEAST
// MINOBS DATAPOINTS BOTH AT/BELOW THE THRESHOLD AND ABOVE
// THE THRESHOLD

        //4a) FIRST MUST FIND LOWEST AND HIGHEST THRESHOLD VALUES
        // SATISFYING THE MINOBS CONSTRAINT:
```

```
                //GENERATE X VALUES, ROUNDED UP TO NEAREST %,
                //CONVERT TO 0-100 SCALE (forvalues REQUIRES INTEGERS,
                //STEP 4B):
                tempvar rndx rndx_minusx rndupx
                gen `rndx' = round(`x', 0.01) if `x'~=.
                gen `rndx_minusx' = `rndx' - `x' if `x'~=.
                gen `rndupx' = `rndx' if `x'~=.
                replace `rndupx' = `rndupx'+0.01 if `rndx_minusx'<0 & `x'~=.
                replace `rndupx' = `rndupx' * 100 if `x'~=.

                //LOWEST, HIGHEST POSSIBLE THRESHOLD VALUE * 100
                tempvar low_t high_t
                gen  `low_t' = `rndupx'[`minobs'] if `x' ~=.
                gen  `high_t' = `rndupx'[`obs' - `minobs'] if `x' ~=.
                local low_t = `low_t'
                local high_t = `high_t'

        //4b)  RUN A SERIES OF PIECEWISE MODELS, ONE FOR EACH
        // POTENTIAL THRESHOLD (i) AND RECORD LOG LIKELIHOOD
        // FOR EACH i:
        forvalues i = `low_t'/`high_t' {
                generate tterm = `x'-`i'/100 if `x' ~=.
                replace tterm = 0 if tterm<0 & `x' ~=.
                regress `y' `x' tterm [aweight=`weight'] if `x' ~=.
                replace `ll_pw' = e(ll) in `i'
                drop tterm
        }

//5) FIND THE THRESHOLD VALUE(S) (THRESH_PW) THAT RESULTS IN THE
//MODEL(S) WITH THE LEAST NEGATIVE LOG LIKELIHOOD VALUE
        tempvar maxll_pw tmp_t tmppwthresh
        egen `maxll_pw' = max(`ll_pw')
        generate `tmp_t' = thresh_pw if `maxll_pw'==`ll_pw' & `ll_pw'~=.
        egen `tmppwthresh' = max(`tmp_t')
        gen pwthresh = `tmppwthresh' if `x' ~=.
        drop thresh_pw

//6) LIST THRESHOLD VALUE
        list pwthresh if _n==1

end
```

Appendix 3-2a. Program to estimate a change-point threshold for Poisson data

To use this program in Stata, save the script below as an ado file named ncpa_Poisson_min in the appropriate folder. In the command box or do file, type:

```
ncpa_Poisson_min y x obs minobs
```

where y, x, obs, and minobs are as defined in Appendix 3-1, except that x is not restricted to being on the 0-1 scale.

The threshold estimate will be listed on the screen, and a new variable called changepoint will also be generated, containing this value.

```
capture program drop ncpa_Poisson_min
program define ncpa_Poisson_min
version 9

//1) DEFINE ARGUMENTS: DEPENDENT, INDEPENDENT, #OBSERVATIONS;
SORT BY INDEPENDENT
        args y x obs minobs
        sort `x'

//1b) SET THE MAX OBSERVATION AT WHICH TO CONSIDER A THRESHOLD,
        local high_n = `obs'-`minobs'

//2) MAKE TEMP VARIABLE WITH OBSERVATION #S
        tempvar id
        qui generate `id'=_n if `x'~=.

//3) CALCULATE THE TOTAL DEVIANCE OF THE DEPENDENT:

        //MEAN VALUE OF DEPENDENT:
        tempvar meany_t
        qui egen `meany_t' = total(`y') if `x'~=.
        qui replace `meany_t' = `meany_t'/`obs' if `x'~=.

        //DEVIANCE RESIDUALS FOR ALL OBSERVATIONS:
        tempvar dr_t
        qui generate `dr_t' = 2*`meany_t'  if `y'==0 & `x'~=.
        qui replace `dr_t' = 2*(`y'*ln(`y'/`meany_t') - (`y'- `meany_t')) if `y'>0 & `x'~=.

        //TOTAL DEVIANCE FOR ALL OBSERVATIONS:
        tempvar dev_t
        qui egen `dev_t' = total(`dr_t') if `x'~=.

//4a) CALCULATE DEVIANCE OF EACH SUBGROUP OF THE DEPENDENT <=i
```

```
//(I.E. AT/BELOW EACH POTENTIAL THRESHOLD VALUE OF X)

        //CALCULATE MEAN VALUE OF DEPENDENT FOR ALL SUBGROUPS
        //<=i
        tempvar meany_1
        qui generate `meany_1' = sum(`y')/_n  if `x'~=.

        //MAKE TEMP VARIABLE FOR DEVIANCE RESIDUALS, AND FOR THE
        //SUM OF THE DEVIANCE RESIDUALS FOR SUBGROUPS <=i
        tempvar dr_1
        qui generate `dr_1' =.
        tempvar sumdr_1
        qui generate `sumdr_1'=.

        //CALCULATE THE DEVIANCE FOR EACH SUBGROUP (<=i) OF THE
        //DEPENDENT (I.E. SUM OF ALL THE DEVIANCE RESIDUALS FOR
        //EACH SUBGROUP)
        tempvar dev_1
        qui generate `dev_1'=.
        forvalues i = `minobs'/`high_n' {
                qui replace `dr_1' = 2*`meany_1'[`i'] if `id' <=`i'
                qui replace `dr_1' = 2*(`y'*ln(`y'/`meany_1'[`i']) - (`y'- `meany_1'[`i'])) ///

                        if `y'>0 & `id' <=`i'
                qui replace `sumdr_1'= sum(`dr_1') if `id' <=`i'
                qui replace `dev_1' = `sumdr_1' in `i'
        }

//4b) CALCULATE DEVIANCE OF EACH SUBGROUP OF INDEPENDENT >i
//(I.E. FOR EACH SUBGROUP ABOVE EACH POTENTIAL THRESHOLD)

        //CALCULATE MEAN VALUE OF DEPENDENT FOR ALL SUBGROUPS >i
        tempvar sumy meany_2
        qui generate `sumy' = sum(`y') if `id'<=`obs'
        qui replace `sumy' = 0 if `sumy'==.
        qui generate `meany_2' = (`sumy'[`obs']-`sumy') / (`obs' - _n) if _n<=`obs'

        //MAKE TEMP VARIABLE FOR DEVIANCE RESIDUALS, AND FOR SUM
        //OF DEVIANCE RESIDUALS, FOR SUBGROUPS >i.
        tempvar dr_2
        qui generate `dr_2' =.
        tempvar sumdr_2
        qui generate `sumdr_2'=.

        //CALCULATE TOTAL DEVIANCE FOR EACH SUBGROUP OF THE
        //DEPENDENT >i
```

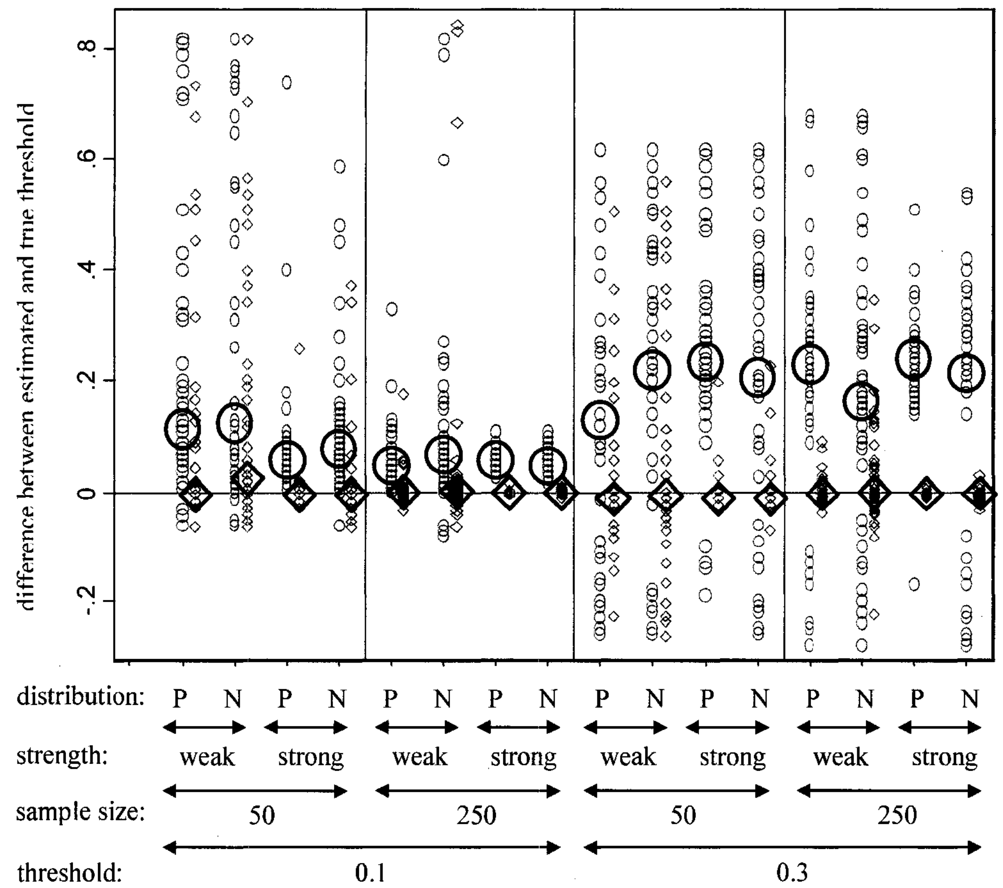
```
        tempvar dev_2
        generate `dev_2'=.
        forvalues i = `minobs'/`high_n' {
                qui replace `dr_2' = 2*`meany_2'[`i'] if `id' >= `i' & `id'<_N
                qui replace `dr_2' = 2*(`y'[_n+1]*ln(`y'[_n+1]/`meany_2'[`i']) ///
                 - (`y'[_n+1]- `meany_2'[`i'])) if `y'[_n+1]>0 & `id' >= `i' & `id'<_N
                qui replace `sumdr_2'= sum(`dr_2') if `id' >=`i'  & `id'<=`obs'
                qui replace `dev_2' = `sumdr_2'[`high_n'] in `i' if `id'<=`obs'
        }

//5) CALCULATE THE CHANGEPOINT VALUE OF THE INDEPENDENT

        //5a) CALCULATE, FOR EACH POTENTIAL CHANGE-POINT (i), THE
        //DEVIANCE OF GROUP-1 (<=i) PLUS DEVIANCE OF GROUP-2 (>i)
        tempvar dev_1plus2
        qui generate `dev_1plus2' = `dev_1' + `dev_2'

        //5b) FIND THE CHANGE-POINT VALUE OF X: THAT WHICH YIELDS
        //THE SMALLEST TOTAL DEVIANCE FOR GROUP1 + GROUP2
        tempvar   min_dev_1plus2   tempcp
        qui egen `min_dev_1plus2' = min(`dev_1plus2')
        qui generate `tempcp' = `x' if `dev_1plus2' == `min_dev_1plus2'
        qui egen changepoint = max(`tempcp')

        //5c) LIST THE CHANGE-POINT VALUE
        list changepoint  if `dev_1plus2' == `min_dev_1plus2'

end
```

Appendix 3-2b. Partial program to calculate change-point threshold for negative binomial data. Steps 1, 2, and 5 are the same as for Appendix 3-2a.

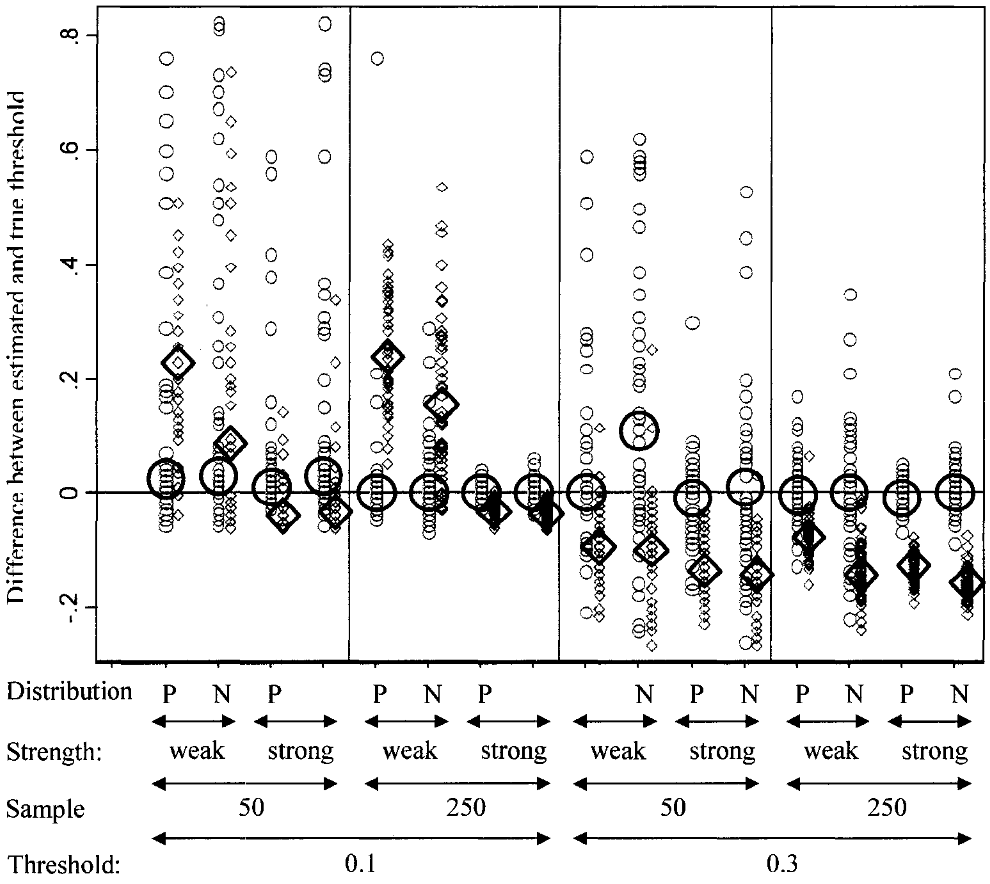
To use this program in Stata, follow the instructions as for Appendix 3-2a, except that the ado file and command name are ncpa_negbin_min.

```
capture program drop ncpa_negbin_min
program define ncpa_negbin_min
version 9

//***SUBSTITUTE STEPS 1-2 FROM ncpa_Poisson_min

//3) CALCULATE THE TOTAL DEVIANCE OF THE DEPENDENT:

        //OBTAIN OVERDISPERSION FACTOR (k)
        quietly nbreg `y'
        tempvar k
        qui generate `k' = e(alpha)

        //CALCULATE MEAN VALUE OF DEPENDENT:
        tempvar meany_t
        qui egen `meany_t' = total(`y') if `x'~=.
        qui replace `meany_t' = `meany_t'/`obs' if `x'~=.

        //CALCULATE DEVIANCE RESIDUALS FOR ALL OBSERVATIONS
        tempvar dr_t
        qui generate `dr_t'= 2*ln(1+`k'*`meany_t')/`k'  if `y'==0 & `x'~=.
        qui replace `dr_t' = 2*`y'*ln(`y'/`meany_t') ///
                - 2*((1+`k'*`y')/`k')*ln((1+`k'*`y')/(1+`k'*`meany_t')) if `y'>0 & `x'~=.

        //CALCULATE TOTAL DEVIANCE FOR ALL OBSERVATIONS:
        tempvar dev_t
        qui egen `dev_t' = total(`dr_t') if `x'~=.

//4a) CALCULATE DEVIANCE OF EACH SUBGROUP OF DEPENDENT <=i
        //CALCULATE MEAN VALUE OF DEPENDENT FOR ALL SUBGROUPS
        //<=i
        tempvar meany_1
        qui generate `meany_1' = sum(`y')/_n if `x'~=.

        //MAKE TEMP VARIABLE FOR DEVIANCE RESIDUALS, AND FOR THE
        //SUM OF THE DEVIANCE RESIDUALS FOR SUBGROUPS <=i
        tempvar dr_1
        qui generate `dr_1' =.
        tempvar sumdr_1
        qui generate `sumdr_1'=.
```

```
    //CALCULATE THE DEVIANCE FOR EACH SUBGROUP (<=i) OF THE
    //DEPENDENT (I.E. SUM OF ALL THE DEVIANCE RESIDUALS FOR
    //EACH SUBGROUP)
    tempvar dev_1
    qui generate `dev_1' =.
    forvalues i = `minobs'/`high_n' {
        qui replace `dr_1' = 2*ln(1+`k'*`meany_1'[`i'])/`k'  if `id'<=`i' & `y'==0
        qui replace `dr_1' = 2*`y'*ln(`y'/`meany_1'[`i']) ///
            - 2*((1+`k'*`y')/`k')*ln((1+`k'*`y')/(1+`k'*`meany_1'[`i'])) ///
            if `y'>0 & `id'<=`i'
        qui replace `sumdr_1'= sum(`dr_1') if `id' <=`i'
        qui replace `dev_1'  = `sumdr_1' in `i'
    }

//4b) CALCULATE DEVIANCE OF EACH SUBGROUP OF INDEPENDENT >i
//(I.E. FOR EACH SUBGROUP ABOVE EACH POTENTIAL THRESHOLD)

    //CALCULATE MEAN VALUE OF DEPENDENT FOR ALL SUBGROUPS >i
    tempvar sumy meany_2
    qui generate `sumy' = sum(`y') if `id'<=`obs'
    qui replace `sumy' = 0 if `sumy'==.
    qui generate `meany_2' = (`sumy'[`obs']-`sumy') / (`obs' - _n) if _n<=`obs'

    //MAKE TEMP VARIABLE FOR DEVIANCE RESIDUALS, AND FOR SUM
    //OF DEVIANCE RESIDUALS, FOR SUBGROUPS >i.
    tempvar dr_2
    qui generate `dr_2' =.
    tempvar sumdr_2
    qui generate `sumdr_2'=.

    //CALCULATE TOTAL DEVIANCE FOR EACH SUBGROUP  >i
    tempvar dev_2
    qui generate `dev_2'=.
    forvalues i = `minobs'/`high_n' {
        qui replace `dr_2' = 2*ln(1+`k'*`meany_2'[`i'])/`k' ///
            if `y'[_n+1]==0 & `id' >=`i' & `id'<_N
        qui replace `dr_2' = 2*`y'[_n+1]*ln(`y'[_n+1]/`meany_2'[`i']) ///
            - 2*((1+`k'*`y'[_n+1])/`k')*ln((1+`k'*`y'[_n+1]) ///
            /(1+`k'*`meany_2'[`i']))  if `y'[_n+1]>0 & `id' >=`i' & `id' <_N
        qui replace `sumdr_2'= sum(`dr_2') if `id' >=`i' & `id' <=`obs'
        qui replace `dev_2' = `sumdr_2'[`high_n'] in `i' if `id'<=`obs'
        }

//***SUBSTITUTE STEP 5  FROM POISSON VERSION
end
```



Appendix 3-3a. Distance of change-point (red) and piecewise (blue) threshold estimates from the "true" discontinuous threshold value, for different data types (P = Poisson, N = negative binomial). Circles (median piecewise estimates); diamonds (median change-point estimates). Horizontal line (0) represents an exact match between the true and estimated threshold, positive values are over-estimates, negative values are under-estimates.



Appendix 3-3b. Distance of change-point (red diamonds) and piecewise (blue circles) threshold estimates from the "true" continuous threshold value, for different data types (P = Poisson, N = negative binomial). Circles (median piecewise estimates); diamonds (median change-point estimates). Horizontal line (0) represents an exact match between the true and estimated threshold, positive values are over-estimates, negative values are under-estimates.

Appendix 3-4. Proportions of data sets correctly and misidentified by the best AICc and best BIC model, by sample size, distribution, and true shape. Bold indicates correct identification; non-bold indicates misidentification.

SS[1]	Distribution	True shape[2]	# data sets	AICc best model[2]					BIC best model[2]				
				N	L	DT	FP	CT	N	L	DT	FP	CT
50	Negative binomial	N	200	**0.72**	0.02	0.20	0.02	0.04	**0.96**	0.00	0.04	0.00	0.00
		L	400	0.13	**0.52**	0.24	0.03	0.08	0.19	**0.62**	0.16	0.01	0.02
		DT	800	0.21	0.09	**0.56**	0.05	0.10	0.33	0.14	**0.45**	0.05	0.05
		FP	400	0.01	0.06	0.23	**0.42**	0.28	0.03	0.20	0.27	**0.39**	0.11
		CT	800	0.00	0.24	0.17	0.22	**0.38**	0.03	0.36	0.16	0.25	**0.22**
	Poisson	N	200	**0.64**	0.06	0.24	0.02	0.04	**0.88**	0.02	0.08	0.00	0.02
		L	400	0.00	**0.66**	0.17	0.06	0.11	0.02	**0.79**	0.13	0.01	0.05
		DT	800	0.04	0.08	**0.73**	0.03	0.13	0.15	0.11	**0.66**	0.03	0.07
		FP	400	0.00	0.04	0.08	**0.49**	0.39	0.00	0.04	0.10	**0.60**	0.26
		CT	800	0.00	0.07	0.03	0.28	**0.63**	0.00	0.13	0.04	0.36	**0.48**
250	Negative binomial	N	200	**0.52**	0.02	0.40	0.02	0.04	**0.92**	0.00	0.08	0.00	0.00
		L	400	0.00	**0.58**	0.19	0.06	0.17	0.01	**0.88**	0.07	0.00	0.04
		DT	800	0.00	0.02	**0.91**	0.04	0.04	0.08	0.06	**0.84**	0.03	0.01
		FP	400	0.00	0.00	0.02	**0.43**	0.55	0.00	0.00	0.04	**0.65**	0.31
		CT	800	0.00	0.02	0.01	0.13	**0.85**	0.00	0.08	0.03	0.36	**0.54**
	Poisson	N	200	**0.50**	0.00	0.40	0.04	0.06	**0.98**	0.00	0.00	0.02	0.00
		L	400	0.00	**0.76**	0.02	0.03	0.19	0.00	**0.96**	0.02	0.01	0.01
		DT	800	0.00	0.01	**0.97**	0.01	0.02	0.00	0.03	**0.97**	0.01	0.01
		FP	400	0.00	0.00	0.00	**0.56**	0.44	0.00	0.00	0.00	**0.63**	0.37
		CT	800	0.00	0.01	0.00	0.06	**0.94**	0.00	0.01	0.00	0.17	**0.82**

1. SS = sample size

2. N = null; L = linear; DT = discontinuous threshold; FP = fractional polynomial; CT = continuous threshold

Appendix 6-1. Details of the all-landscapes multi-scale models

Species	Extent (km), grain (m)	Independent[A]	Coefficient	S.E.	T	Standardized coefficient	Δr^2	Model r^2
American crow	1, 100	PROP	-8.22	2.16	-3.81	-0.49	0.23	0.26
	1, 100	CORVAR	4.33e-03	4.33e-03	2.08	0.27	0.07	
		constant	7.03	1.00	7.04			
Black-billed magpie	1, 100	PROP	-6.66	1.91	-3.49	-0.49	0.13	0.52
	3, 5	DFENCE#	0.16	8.23e-02	1.97	0.28	0.04	
		constant	4.30	1.18	3.66		0.00	
Black-capped chickadee	1, 5	PROP^-0.5	-4.68*	0.78	-6.01	-0.64	0.32	0.61
	3, 5	PD	111.69	34.44	3.24	0.36	0.09	
	3, 5	CLUST#	323.08	154.16	2.10	0.22	0.04	
		D1000HA	-4.08e-04	1.86e-04	-2.20	-0.25	0.04	
		EAST	-3.50e-04	7.21e-05	-4.85	-0.59	0.21	
		constant	155.11	28.13	5.51			
Blue jay	3, 100	PROP	5.04	1.00	5.02	0.58	0.31	0.43
	3, 5	CORVAR#	2.10e-03	7.35e-04	2.86	0.33	0.10	
		EAST	-2.39e-05	1.02e-05	-2.34	-0.28	0.07	
		constant	7.58	3.60	2.11			
Red squirrel	1, 5	PROP	5.86	1.07	5.49	0.61	0.37	0.43
	3, 5	CLUST#	47.63	21.11	2.26	0.25	0.06	
		constant	-9.42e-02	0.19	-0.49			
Ruffed grouse	1, 100	PROP	2.27	0.70	3.23	0.39	0.15	0.33
		D1000HA	-5.26e-05	2.20e-05	-2.39	-0.29	0.08	
		NORTH	-1.57e-05	5.62e-06	-2.79	-0.34	0.11	
		constant	93.53	33.30	2.81			
Downy woodpecker	1, 100	PROP	5.04	1.22	4.13	0.52	0.25	0.32
	1, 5	PD#	14.67	5.37	2.73	0.35	0.11	
		EAST	-3.68e-05	1.75e-05	-2.11	-0.28	0.07	
		constant	15.26	6.25	2.44			
Hairy woodpecker	1, 5	PROP	5.44	0.65	8.35	0.77	0.59	0.59
		constant	0.71	0.20	3.53			
White-breasted nuthatch	1, 100	PROP	4.91	0.70	7.05	0.71	0.51	0.51
		constant	0.62	0.21	2.88			
Yellow-bellied sapsucker	1, 5	PROP	5.90	1.67	3.53	0.45	0.21	0.21
		constant	0.98	0.33	2.93			
# abundant forest bird species	1,5	PROP	9.16	1.06	8.68	-0.29	0.59	0.65
		D100HA	3.68e-4	1.28e-4	-2.88	0.82	0.06	
		D1000HA	9.16e-5	4.22e-5	-2.17	-0.27	0.04	
		EAST	-4.42e-5	1.52e-5	-2.90	-0.22	0.07	
		constant	18.23		3.23			
Forest bird evenness	3,5	DFENCE	1.75e-3	8.38e-4	-2.09	-0.29	0.08	0.08
		constant	0.95	8.26e-2	115.4			

A. Abbreviations for independents as in Table 6-1
\# Significance dependent on one influential data point
* Chickadees increased with PROP; slope was negative because power was negative

Appendix 6-2. Details of the low-forest multi-scale models

Species	Extent (km), grain (m)	Independent[A]	Coefficient	S.E.	T	Standardized coefficient	Δr^2	Model r^2
American crow	1, 100	CORVAR	1.14e-02	4.90e-03	2.33	0.39	0.14	0.18
		D100HA[#]	2.19e-04	1.37e-04	1.60	0.27	0.07	
		constant	4.43	1.37	3.23			
Black-billed magpie	1, 100	PD	-74.31	29.80	-2.49	-0.42	0.15	0.28
	1, 100	CLUST	-13.93	6.42	-2.17	-0.38	0.11	
		NORTH[#]	4.19e-05	2.25e-05	1.87	0.31	0.08	
		constant	-240.67	133.09	-1.81			
Black-capped chickadee	1, 5	PROP	80.59	11.41	7.06	0.75	0.57	0.64
		EAST	-1.17e-04	6.51e-05	-2.70	-0.29	0.08	
		constant	72.49	23.92	3.03			
Blue jay	1, 100	PROP	6.37	2.46	2.59	0.37	0.12	0.48
	1, 5	PD[#]	10.84	3.50	3.10	0.50	0.17	
		EAST	-2.58e-05	9.89e-06	-2.61	-0.39	0.12	
		constant	8.64	3.52	2.46			
Red squirrel	1, 5	PROP	3.52	1.71	2.06	0.32	0.09	0.31
	3, 100	CORVAR	-1.38e-03	7.45e-04	-1.86	-0.28	0.08	
		D100HA	-1.19e-04	1.11e-04	-1.70	-0.27	0.06	
		constant	1.22	0.53	2.30			
Ruffed grouse	1, 5	PROP	3.85	1.50	2.56	0.41	0.17	0.17
		constant	0.17	0.21	0.82			
Downy woodpecker	3, 5	PROP	8.20	3.33	2.46	0.38	0.14	0.29
		NORTH	-3.06e-05	1.40e-05	-2.18	-0.34	0.11	
		constant	184.03	83.12	2.21			
Hairy woodpecker	1, 5	PROP	7.75	1.90	4.07	0.59	0.29	0.47
	1, 5	PD	9.42	4.12	2.29	0.44	0.09	
	1, 5	CLUST	8.86	3.22	2.75	0.52	0.13	
		constant	-0.46	0.45	-1.02			
White-breasted nuthatch	1, 5	PROP	4.91	1.99	2.93	0.71	0.51	0.51
		constant	0.62	0.31	1.55			
Yellow-bellied sapsucker	1, 5	DFENCE	0.10	3.38e-02	2.99	0.47	0.22	0.22
		constant	0.40	0.47	0.84			
# abundant forest bird species	1, 100	PROP	17.73	3.15	5.63	0.71	0.50	0.50
		constant	-0.16	0.48	-0.32	0.75		
Forest bird evenness		constant	1.13	2.94e-2	38.2			0.00

A. Abbreviations for independents as in Table 6-1

Significance dependent on one influential data point

Appendix 6-3. Details of all-landscapes single-scale models

Species	Extent (km), grain (m)	Independent[A]	Coefficient	S.E.	T	Standardized coefficient	Δr^2	Model r^2
American crow	1, 5	PROP	-7.82	2.36	-3.31	-0.43	0.19	0.19
		constant	8.33	0.88	9.46			
	1, 100	PROP	-8.22	2.16	-3.81	-0.49	0.23	0.26
		CORVAR	8.99e-03	4.33e-03	2.08	0.27	0.07	
		constant	7.03	1.00	7.04			
	3, 5	DFENCE	0.25	0.12	2.21	0.30	0.09	0.09
		constant	4.19	1.14	3.68			
	3, 100	PROP	-7.09	3.32	-2.13	-0.29	0.09	0.09
		constant	8.12	0.95	8.53			
Black-billed magpie	1, 5	PROP	-7.58	1.62	-4.68	-0.55	0.21	0.54
		DFENCE	8.96e-02	3.98e-02	2.25	0.27	0.05	
		constant	4.92	0.87	5.67			
	1, 100	PROP	-9.28	1.41	-6.59	-0.69	0.48	0.48
		constant	6.35	0.56	11.3			
	3, 5	PROP	-8.96	2.35	-3.81	-0.49	0.16	0.50
		DFENCE	0.16	7.15e-02	2.30	0.30	0.06	
		constant	4.83	1.20	4.03			
	3, 100	PROP	-11.9	1.98	-6.01	-0.66	0.34	0.43
		constant	7.04	0.69	10.2			
Black-capped chickadee	1, 5	PROP	139.6	23.2	6.01	2.68	0.46	0.46
		PROP^2	-208.0	39.0	-5.34	-2.38		
		constant	4.93	2.18	2.26			
	1, 100	PROP	126.0	22.1	5.71	2.33	0.45	0.45
		PROP^2	-182.8	37.5	-4.88	-1.99		
		constant	6.11	1.99	3.07			
	3, 5	PROP	20.2	6.67	3.03	0.35	0.12	0.41
		PD	199.2	43.5	4.58	0.61	0.28	
		CLUST	473.4	190.9	2.48	0.32	0.08	
		CORVAR	-1.55e-02	6.38e-03	-2.43	-0.32	0.08	
		constant	9.51	4.48	2.12			
	3, 100	PROP^-0.5	-3.92	0.87	-4.50	-0.53	0.28	0.37
		PD	306.3	142.0	2.16	0.27	0.06	
		CORVAR	-1.48e-02	6.16e-03	-2.40	-0.30	0.08	
		constant	30.6	4.27	7.17			
Blue jay	1, 5	PROP	3.59	1.00	3.58	0.46	0.21	0.21
		constant	0.42	0.25	1.67			
	1, 100	PROP	3.95	0.98	4.05	0.50	0.25	0.25
		constant	0.32	0.22	1.43			
	3, 5	PROP	4.43	1.04	4.25	0.51	0.25	0.34
		CORVAR	1.56e-03	7.50e-04	2.09	0.25	0.06	
		constant	-0.74	0.50	-1.49			
	3, 100	PROP	4.73	1.06	4.47	0.54	0.29	0.29
		constant	0.17	0.23	0.74			
Red squirrel	1, 5	PROP	6.73	1.25	5.38	0.61	0.38	0.37
		constant	-0.16	0.23	-0.69			
	1, 100	PROP	6.66	1.25	5.34	0.60	0.37	0.36
		constant	-0.13	0.21	-0.59			
	3, 5	PROP	6.44	1.41	4.57	0.52	0.27	0.34

Appendix 6-3. Details of all-landscapes single-scale models

Species	Extent (km), grain (m)	Independent^A	Coefficient	S.E.	T	Standardized coefficient	Δr^2	Model r^2
		CLUST	61.57	26.82	2.30	0.26	0.07	
		constant	-0.12	0.27	-0.46			
	3, 100	PROP	6.60	1.41	4.69	0.53	0.30	0.34
		CORVAR	-1.77e-03	8.78e-04	-2.02	-0.24	0.06	
		constant	0.75	0.52	1.46			
Ruffed grouse	1, 5	PROP	2.25	0.75	2.98	0.40	0.16	0.16
		constant	0.35	0.17	2.05			
	1, 100	PROP	2.29	0.77	2.99	0.40	0.16	0.16
		constant	0.36	0.17	2.04			
	3, 5	PROP	2.56	0.96	2.68	0.36	0.13	0.13
		constant	0.37	0.20	1.83			
	3, 100	PROP	2.51	0.95	2.64	0.36	0.13	0.13
		constant	0.38	0.20	1.88			
Downy woodpecker	1, 5	PROP	3.94	1.21	3.25	0.40	0.16	0.31
		PD	21.2	7.15	2.96	0.51	0.13	
		CORVAR	-5.94e-03	2.87e-03	-2.07	-0.36	0.06	
		constant	3.53	0.89	3.98			
	1, 100	PROP	4.73	1.22	3.87	0.49	0.23	0.27
		PD	39.1	16.04	2.44	0.31	0.09	
		constant	2.03	0.62	3.29			
	3, 5	PROP	4.94	1.49	3.32	0.43	0.18	0.22
		PD	17.0	8.51	2.00	0.26	0.07	
		constant	1.79	0.81	2.21			
	3, 100	PROP	6.53	1.78	3.68	0.57	0.22	0.22
		PD	71.9	34.26	2.10	0.33	0.07	
		constant	1.24	1.02	1.22			
Hairy woodpecker	1, 5	PROP	5.44	0.65	8.35	0.77	0.59	0.59
		constant	0.71	0.20	3.53			
	1, 100	PROP	5.32	0.65	8.22	0.76	0.58	0.58
		constant	0.74	0.20	3.69			
	3, 5	PROP	5.99	0.83	7.23	0.72	0.52	0.52
		constant	0.61	0.24	2.58			
	3, 100	PROP	5.93	0.82	7.20	0.72	0.52	0.52
		constant	0.63	0.24	2.65			
White-breasted nuthatch	1, 5	PROP	4.91	0.72	6.85	0.70	0.49	0.49
		constant	0.62	0.22	2.79			
	1, 100	PROP	4.91	0.70	7.05	0.71	0.50	0.50
		constant	0.62	0.21	2.88			
	3, 5	PROP	4.96	0.94	5.26	0.60	0.37	0.37
		constant	0.64	0.27	2.37			
	3, 100	PROP	4.87	0.94	5.18	0.60	0.36	0.36
		constant	0.66	0.27	2.45			
Yellow-bellied sapsucker	1, 5	PROP	5.90	1.67	3.53	0.45	0.21	0.21
		constant	0.98	0.33	2.93			
	1, 100	PROP	5.80	1.73	3.35	0.44	0.19	0.19
		constant	0.99	0.35	2.86			
	3, 5	PROP	6.20	2.01	3.08	0.41	0.17	0.17
		constant	0.96	0.42	2.30			

Appendix 6-3. Details of all-landscapes single-scale models

Species	Extent (km), grain (m)	Independent[A]	Coefficient	S.E.	T	Standardized coefficient	Δr^2	Model r^2
	3, 100	PROP	6.11	2.02	3.03	0.40	0.16	0.16
		constant	0.98	0.42	2.35			
# abundant forest bird species	1, 5	ln(PROP)	1.84	0.24	7.70	0.74	0.55	0.55
		constant	6.11	0.45	13.45			
	1, 100	ln(PROP)	1.83	0.23	7.91	0.75	0.57	0.57
		constant	6.11	0.44	13.78			
	3, 5	PROP	7.49	1.56	4.79	0.57	0.32	0.32
		constant	1.16	0.45	2.59			
	3, 100	PROP	7.41	1.56	4.76	0.57	0.32	0.32
		constant	1.18	0.45	2.65			
Forest bird evenness	1, 5	PROP	3.60e-2	2.09e-2	1.72	0.24	0.00	0.06
		constant						
	1, 100	PROP	3.45e-2	2.07e-2	1.67	0.23	0.00	0.05
		constant						
	3, 5	DFENCE	1.75e-3	8.38e-3	-2.09	-0.29	0.00	0.08
		constant						
	3, 100	constant	0.94	3.90e-3	240.5			0.00

A. Abbreviations for independents as in Table 6-1.

Appendix 6-4. Details of low-forest single-scale models

Species	Extent (km), grain (m)	Independent^A	Coefficient	S.E.	T	Standardized coefficient	Δr^2	Model r^2
American crow	1, 5	constant	7.41	0.69	10.8		0.00	0.00
	1, 100	CORVAR	9.65e-3	4.89e-3	1.97	0.33	0.11	0.11
		constant	6.04	0.96	6.32			
	3, 5	constant	7.43	0.66	11.3			0
	3, 100	constant	7.43	0.66	11.3			0
Black-billed magpie	1, 5	constant	5.22	0.45	11.6			0
	1, 100	PD	-81.3	30.7	-2.65	-0.46	0.18	0.20
		CLUST	-10.8	6.44	-1.68	-0.29	0.07	0.20
		constant	7.65	1.00	7.63			
	3, 5	constant	5.34	0.43	12.4	n/a	n/a	n/a
	3, 100	PD	-164.0	62.8	-2.61	-0.41	0.17	0.17
		constant	9.25	1.55	5.98			
Black-capped chickadee	1, 5	PROP	76.8	13.3	5.75	0.71	0.51	0.51
		constant	8.50	2.06	4.12			
	1, 100	PROP	77.0	13.4	5.73	0.71	0.51	0.51
		constant	8.63	2.05	4.21			
	3, 5	PROP	73.9	14.75	5.01	0.66	0.43	0.43
		constant	8.18	1.99	4.10			
	3, 100	PROP	79.8	14.28	5.59	0.71	0.48	0.50
		CORVAR	1.07e-2	5.20e-3	-2.05	-0.26	0.07	0.50
		constant	12.8	2.94	4.34			
Blue jay	1, 5	PROP	6.47	2.79	2.32	0.37	0.12	0.32
		PD	6.92	3.63	1.90	0.30	0.08	0.32
		constant	-0.49	0.39	-1.25			
	1, 100	PROP	9.02	2.54	3.55	0.53	0.28	0.28
		constant	-0.16	0.31	-0.51			
	3, 5	PROP	5.85	2.30	2.54	0.40	0.16	0.16
		constant	7.35e-2	0.31	0.24			
	3, 100	PROP	5.99	2.26	2.65	0.42	0.18	0.18
		constant	5.19e-2	0.30	0.17			
Red squirrel	1, 5	PROP	5.79	1.86	3.11	0.46	0.21	0.32
		CORVAR	-2.48e-3	1.19e-3	-2.09	-0.31	0.10	0.32
		constant	0.90	0.54	1.67			
	1, 100	PROP	5.60	2.00	2.80	0.44	0.20	0.20
		constant	3.96e-3	0.31	0.01			
	3, 5	constant	0.73	0.16	4.54			0
	3, 100	PROP	3.28	1.92	1.70	0.28	0.08	0.16
		CORVAR	0.40	0.25	-2.05	-0.34	0.11	0.16
		constant	1.09	0.50	2.20			
Ruffed grouse	1, 5	PROP	3.85	1.50	2.56	0.41	0.17	0.17
		constant	0.17	0.21	0.82			
	1, 100	PROP	3.85	1.54	2.50	0.40	0.16	0.16
		constant	0.18	0.20	0.88			
	3, 5	PROP	3.85	1.50	2.56	0.28	0.08	0.08
		constant	0.17	0.21	0.82			
	3, 100	PROP	2.38	1.45	1.64	0.27	0.08	0.08
		constant	0.40	0.25	1.61			
Downy woodpecker	1, 5	PROP	9.83	3.70	2.66	0.43	0.18	0.18

Appendix 6-4. Details of low-forest single-scale models

Species	Extent (km), grain (m)	Independent[A]	Coefficient	S.E.	T	Standardized coefficient	Δr^2	Model r^2
		constant	2.48	0.57	4.34			
	1, 100	PROP	7.64	3.88	1.97	0.33	0.09	0.26
		PD	33.3	19.7	1.69	0.28	0.07	0.26
		constant	1.81	0.67	2.72			
	3, 5	PROP	10.2	3.60	2.84	0.44	0.20	0.20
		constant	2.38	0.62	3.86			
	3, 100	PROP	10.1	3.64	2.79	0.44	0.19	0.19
		constant	2.40	0.62	3.89			
Hairy woodpecker	1, 5	PROP	7.75	1.90	4.07	0.59	0.29	0.47
		PD	8.86	3.22	2.75	0.52	0.09	0.47
		CLUST	9.42	4.12	2.29	0.44	0.13	0.47
		constant	-0.46	0.45	-1.02			
	1, 100	PROP	7.29	1.97	3.70	0.55	0.30	0.30
		constant	0.56	0.30	1.86			
	3, 5	PROP	5.24	1.93	2.72	0.43	0.18	0.18
		constant	0.48	0.33	2.26			
	3, 100	PROP	5.28	1.94	2.72	0.43		0.18
		constant	0.75	0.33	2.26			
White-breasted nuthatch	1, 5	PROP	5.83	1.99	2.93	0.46	0.21	0.21
		constant	0.48	0.31	1.55			
	1, 100	PROP	5.67	2.01	2.82	0.45	0.20	0.20
		constant	0.51	0.31	1.66			
	3, 5	PROP	4.12	2.13	1.94	0.32	0.10	0.10
		constant	0.77	0.37	2.12			
	3, 100	PROP	3.99	2.16	1.85	0.31	0.09	0.09
		constant	0.80	0.37	2.18			
Yellow-bellied sapsucker	1, 5	DFENCE	7.83e-2	3.43e-2	2.28	0.37	0.14	0.14
		constant	0.61	0.48	1.28			
	1, 100	constant	1.67	0.24	7.08			0
	3, 5	constant	1.66	0.27	6.18			0
	3, 100	PROP	6.23	3.63	1.72	0.28	0.08	0.15
		CORVAR	-2.47e-3	1.32e-3	-1.87	-0.31	0.09	0.15
		constant	2.17	0.77	2.82			
# abundant forest bird species	1, 5	PROP	17.61	3.14	5.61	0.70	0.50	0.50
		const	-0.18	0.49	-0.36			
	1, 100	PROP	17.73	3.15	5.63	0.71	0.50	0.50
		const	-0.16	0.48	-0.32			
	3, 5	PROP	12.04	3.62	3.32	0.50	0.25	0.25
		const	0.49	0.62	0.79			
	3, 100	PROP	12.08	3.65	3.31	0.50	0.25	0.25
		const	0.50	0.62	0.80			
Forest bird evenness	1, 5	const	0.93	0.00	205.3	0.00	0.00	n/a
	1, 100	const	0.93	0.00	205.3	0.00	0.00	n/a
	3, 5	const	0.93	0.00	210.3	0.00	0.00	n/a
	3, 100	const	0.93	0.00	210.3	0.00	0.00	n/a

A. Abbreviations for independents as in Table 6-1