**FACTORS AFFECTING THE EXTINCTION THRESHOLD AND
SCALE OF HABITAT INTERACTION IN
CERAMBYCID BEETLES**

by

Jeffrey D. Holland, B.Sc.(hon.)

A thesis submitted to

The Faculty of Graduate Studies and Research

In partial fulfillment of

The requirements for the degree of

Doctor of Philosophy

Department of Biology

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Habitat Interaction in Cerambycid Beetles**

Submitted by

Jeffrey D. Holland, B.Sc.(hon.)

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ABSTRACT

Studies of species-habitat relationships are often conducted at spatial scales that are much smaller than the scales at which the relationships are strongest. I expected that different species should respond to habitat at different spatial scales. I used focal point sampling and co-developed multi-scale software that permits the user to analyze species-habitat relations at multiple scales, to determine the spatial scale at which species respond to a habitat variable of interest. I used these methods to determine the spatial scales at which several species of wood-boring long-horned beetles (Cerambycidae) respond to forest cover. I found that different beetle species responded to forest habitat at different scales, from 20m to 1600m. I expect this technique and the accompanying software (FOCUS) to be useful for a wide range of studies to answer questions related to the large-scale responses of organisms to their environment.

I tested several predictions regarding what determines the characteristic scale of response to habitat. I found that larger species responded to forest cover at larger scales. I found no evidence that species that move outside of forest patches respond at larger scales than those species which do not move outside forest. I did not find evidence that species using more ephemeral larval habitat conditions responded at larger scales than species developing in more stable habitat conditions.

I determined the extinction threshold for 12 of the Cerambycid species. I also determined the maximum egg production of each species and whether they were likely to move outside of forest patches. I measured forest fragmentation around the trapping sites. I found a strong negative relationship between reproductive rate and the minimum habitat amount required for species presence. This relationship is obscured if the scale of

investigation is not appropriate for the study organisms. As well, species caught moving outside forest habitat had lower extinction thresholds than species not caught moving outside forest but this was not significant after accounting for reproductive rate. Fragmentation did not have an effect on the minimum habitat requirements. These relationships allow predictions of which species will be most at risk of local extinction because of habitat loss.

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Large fieldwork components of research always look great on paper, especially when the sample size is large. However, in the field each of those individual replicates can be a remote place where poison ivy, stinging nettle, sweltering heat, impassible vegetation, clouds of biting and stinging insects, and bears with a perverse interest in insect traps seem to conspire to erode the biologist's resolve. I have been lucky enough to work with many people who have faced these challenges with determination and optimism. The brunt of this abuse was carried by Larissa Parriag and Moshi Kotierk, both of whom provided cheerful help in the field even if I insisted on eating lunch while walking between sites, or running to make up lost time. Many other people helped in the field, especially Excedera St. Louis, Myra Burrell, David Ladd, Neil Charbonneau, Michelle Lee, Angela Brommitt, Rob Galdins, Megan Whitehead, and Dave Omond. Larissa Parriag, Moshi Kotierk and Excedera St. Louis also helped with many hours of beetle

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CHAPTER 1

GENERAL INTRODUCTION

1.1 UNDERSTANDING THE RELATIONSHIPS BETWEEN SPECIES AND THEIR HABITATS

Anthropogenic changes to natural landscapes have resulted in the loss of natural and semi-natural areas (Leemans and Zuidema 1995, Pearson *et al.* 1999) and a consequent loss of species diversity (Hanski *et al.* 1996, Hess 1996, Huxell and Hastings 1999, Britton *et al.* 2001). Since land-use changes are predicted to continue to affect species diversity, it is especially important to understand how populations react to habitat loss (With and King 1999). Such knowledge is necessary to help guide conservation efforts.

Because habitat loss is currently the leading cause of species extinction, research that allows prediction of the effects of habitat loss on different species should be of the highest priority. One important finding to come out of theoretical studies of habitat loss is the existence of an extinction threshold for some species. This threshold is the amount of habitat at which a further small incremental loss results in a much greater probability of extinction (Lande 1987). The identification of this threshold amount of habitat, as well as the characteristics that can be used to predict it for different species, are of obvious importance for conservation. Determining habitat amount thresholds could be especially important if the phenomenon of “extinction debt” (Tilman *et al.* 1994) is widespread. Extinction debt is the idea that there is a lag between the time that a species has become doomed to a deterministic decline to extinction and the moment when the species actually

becomes extinct. If extinction debt is a common phenomenon, some species may have already passed their critical threshold amount of habitat without any obvious decline in numbers. These considerations make the identification of general rules regarding what factors affect the extinction threshold an important aspect of ecological research. In this research, I test the effects of several variables on the extinction threshold of Cerambycid beetles to see if general trends occur.

Species-habitat research can lead to important guiding principals for conservation. The recent scrutiny that has been placed on the idea of habitat configuration helping to ameliorate habitat loss (e.g.: Fahrig 1999) has occurred because of such research. If habitat configuration can play a large role in species persistence then conservation efforts may be profitably aimed at optimizing the connectivity of the landscape. If, however, configuration effects are small compared to the amount of habitat, conservation resources will be better spent just retaining or restoring habitat (Harrison and Bruna 1999, Fahrig 2001).

1.2 THE IMPORTANCE OF APPROPRIATE SPATIAL SCALE

It has become increasingly evident in ecological research that the spatial scale of investigation can have a large impact on the results (Addicott *et al.* 1987, May 1994, Bellehumeur and Legendre 1998, Goodwin and Fahrig 1998, Schopf and Ivany 1998). Several studies have found that for a given species, certain predictors of species occurrence or success are important only at some spatial scales (e.g.: Bergin *et al.* 2000, Hecnar and M'Closkey 1997, Steffan-Dewenter *et al.* 2002). This implies that using an

inappropriate spatial scale would lead to some real species-habitat relationships being overlooked. Furthermore, different habitat predictors can be important at different spatial scales even for the same species (e.g.: Hovel 2003). Therefore, ecological studies must have a way to determine the spatial scale at which to measure variables in order to uncover the relationships being investigated.

An example of the confusion that can result from using inappropriate spatial scale is the common but often incorrect conclusion that the surveyed patches form a meta-population. In the original meta-population scheme of Levins (1969), sub-populations occasionally experience local extinction but these vacant patches are recolonized. Thus the larger population persists through a dynamic series of local extinctions and recolonizations. If the distance between replicate surveys is smaller than the daily movement distance of the organism, then it is probable that the species will be detected at some locations and not at others and that the locations at which the species is detected would likely change between different surveys. This could lead the researchers to erroneously conclude they are dealing with a meta-population (Harrison and Edwards 1994). As well, Harrison (1991) has stated that any time the factors causing population fluctuations operate at a smaller scale than the movement of the species, the system is properly viewed as a patchy population rather than a meta-population. Roslin and Koivunen (2001) found that some species of *Aphodius* dung beetles existed as patchy populations while others formed classic metapopulations. The population structure of the different species seemed to be related to the degree of habitat specialization and the movement of the species concerned. The ideal first step in determining whether a species is organized in a proper meta-population is the determination of the spatial scale of the

sub-populations, so that the occurrence of actual local extinctions and recolonizations can be assessed at the scale corresponding to the sub-population. Omitting the determination of the appropriate spatial scale in this example will most likely compromise the conclusions of the study.

It is not clear *a priori* how the appropriate spatial scales should be decided upon. However, because ecological relationships are strong at some spatial scales and not important at others, it seems reasonable to assume that their strength lessens as the spatial scale is shifted away (increased or decreased) from the scale at which some unknown causal relationship is operating. A plot of the strength of the ecological relationship against a range of spatial scales should show a unimodal relationship rather than simply “noise”. This provides a justification for one method of determining the spatial scale of importance that has been used recently: the statistical modeling of the relationship at multiple spatial scales to find the scale at which the model fit is maximized (e.g.: Findlay and Houlihan 1997, Pope *et al.* 2000). If model fit shows a smooth increase up to some scale followed by a smooth decrease then the above assumption is justified. If a plot of model fit across increasing spatial scale simply exhibits noise then this assumption is incorrect, and the use of model fit across a range of spatial scales may not be an appropriate method to determine the spatial scale of importance. Note that several spatial scales are required to determine the nature of the change in relationship strength with scale because even in a “noisy” relationship it is possible to randomly pick out a scale where the relationship is strong and one or two other scales where it is weak. I use the modeling of species abundance-habitat relationships across many spatial scales to find appropriate spatial scales at which to look for ecological relationships.

1.3 SAPROXYLIC CERAMBYCIDAE

The larvae of most long-horned beetles (Coleoptera: Cerambycidae) are xylophagous, feeding on wood. The species with larvae that feed within dead wood are important in the decomposition of wood in forested ecosystems (Safranyick and Moeck 1995, Gutowski 2002). Other species have larvae that feed within living trees (Hanks 1999), excavating galleries under the bark of host trees, often in the cambial region (Linsley 1954, Safranyick and Moeck 1995). These galleries cause long lasting, and sometimes fatal, damage to the host tree by severing the phloem and xylem (Barter 1957, Linsley 1954). Some live-tree borers may be considered serious pests because of the extreme nature of the damage they inflict (Linsley 1954), especially when introduced to new habitats where they are released from their usual predators and pathogens or host plant resistance is low (e.g.: Cavey *et al.* 1998). However, under most circumstances even the live-tree-feeding long-horned beetle species tend to be secondary agents, attacking trees already weakened by stress (Barter 1957, Berryman 1986, McCullough *et al.* 1998, Schowalter 1985, Wargo 1996). Nevertheless, long-horned beetles have recently achieved infamy in North America when several species, such as the Asian long-horned beetle and the brown spruce long-horn, have become established as well-known alien invasive species.

Most studies have focused on the role of long-horned beetles as forestry pests because of economic concerns (Gutowski 2002). This has overshadowed the important role in wood recycling (Berryman 1986) that most of the long-horned beetle species have in forested ecosystems. This role is largely unknown to most people because most species

are rarely seen; the larval stage responsible for the decomposition of wood is hidden within the wood and the adults are short lived (Safranyik and Moeck 1995), with adults of many species being nocturnal (Hanks 1999).

Some areas that have had large declines in the amount of forest habitat have experienced local extinctions of native long-horned beetle species (Speight 1989). Some countries have now included long-horned beetle species in lists of endangered species. The valley elderberry long-horned beetle, *Desmocerus californicus dimorphus* Fisher, is considered a threatened species in the United States (Collinge *et al.* 2001), and *Dorcadion fuliginator* (L.) (unusual in that the larvae feed on grass) is protected in Germany and Switzerland (Baur *et al.* 2002). Many long-horned beetle species are now recognized as being important indicators of forest “health” (Speight 1989). Both the conservation of long-horned beetles and their use as bioindicators will benefit from a greater knowledge of the nature and spatial scale of their relationship to forest habitat. Both conservation (Davies *et al.* 2000) and bioindicator efforts could benefit greatly from a better understanding of the factors that determine extinction in different species.

1.4 OBJECTIVES

The purpose of this study was to determine the effects of reproductive rate, emigration, and habitat fragmentation on the extinction threshold of saproxylic long-horned beetles using empirical data. I trapped long-horned beetles at 190 sites to determine abundance. I needed to find the appropriate spatial scale at which to measure the response variable, extinction threshold, so a large part of this study is devoted to

determining this spatial scale for each species of long-horned beetle (Chapter 2). The number of spatially independent areas decreases as the size of each area increases due to overlapping areas within which the habitat variables are measured. A challenge in determining the appropriate scale at which to examine species-habitat relationships was the development of a method to handle this problem while testing the strength of species-habitat relationships across a wide range of spatial scales. This step also allowed me to see if different species do in fact respond to forest habitat at different spatial scales. With an appropriate method for determining the spatial scale at which the different species respond to habitat, I tested several hypotheses regarding what causes different species to respond at different scales. Chapter 3 is a study that looks at the effect of body size, movement, and use of ephemeral habitat in determining the scale of response to habitat. Once I knew the spatial scale at which the different species responded to forest habitat I determined the extinction threshold amount of habitat for each species at the spatial scale appropriate for each species. I was then able to use these extinction threshold values as response variables (with each species as a data point) to test the effects of reproductive rate, emigration, and habitat fragmentation on the extinction threshold (Chapter 4).

CHAPTER 2

FOCUSING ON RELEVANT ECOLOGICAL SCALES

2.1 INTRODUCTION

It is becoming recognized that ecological attributes such as population abundance and species richness depend not only on patch characteristics but also on the characteristics of the landscape surrounding the patch, or the "patch context" (Åberg *et al.* 1995, Gascon *et al.* 1999, Saab 1999, Szacki 1999, Fahrig 2001). Focal patch studies are one approach to studying the effects of patch context. In such studies, the species abundance or richness data are collected in a number of patches or sites. The landscape predictor variables (e.g., habitat amount or fragmentation) are measured in areas that are centred on the patch or site locations (figure 2.1). Each patch and its associated landscape becomes a single data point in the data analysis (Brennan *et al.* 2002). In this way the influence of habitat variables measured at a large scale (in this paper "scale" refers to the area or radius within which habitat predictor variables are measured) on the species abundance or richness can be examined. For example, this approach has been used to study the effects of road density and forest amount on wetland species richness (Findlay and Houlihan 1997), landscape habitat diversity on alfalfa insect richness (Jonsen and Fahrig 1997), amount of forest on raccoon density (Pedlar *et al.* 1997), amount of wooded borders on alfalfa insect richness and density (Holland and Fahrig 2000), and amount of summer habitat and breeding pond density on leopard frog abundance (Pope *et al.* 2000).

In addition to these focal patch studies, there are probably hundreds of existing datasets in which researchers have studied effects of local or patch habitat variables on population abundance or species richness in a number of patches. Can these data sets be re-analyzed to study the effects of landscape context on population abundance or species richness? Given the relative ease of obtaining remotely-sensed large-scale habitat data, these data sets seem to represent a mine of potential information on effects of landscape context. The main problem with this is that in such studies the patches or sites are often rather closely spaced. This leads to spatial non-independence of the data points because the landscape areas overlap (radius of the area around the sampling site considered is greater than half the distance between some of the sampling locations; figure 2.1), possibly leading to pseudo-replication. This constrains the number of data points that can be used for examining the relationship between species abundance/richness and the measures of landscape context. Nevertheless, because the collection of field data is time consuming and expensive, it would be beneficial if there were a way to use this sort of data to examine questions related to the larger scale landscape context. The first objective of this paper is to present a randomization method and computer program (Focus: <http://www.carleton.ca/lands-ecol/>) that permits analysis of effects of landscape context in this situation.

Multi-species landscape-scale studies are often conducted at a single spatial scale for all the species (ex: McGarigal and McComb 1995, Trzinski *et al.* 1999, Holland and Fahrig 2000). However, it is likely that different species (e.g.: Roland and Taylor 1997) and guilds (e.g.: Steffan-Dewenter *et al.* 2002) respond to their environments at different scales, and that these scales are probably related to the movement ranges of the

organisms (Addicott *et al.* 1987, Wiens and Milne 1989, Wiens *et al.* 1993, Cale and Hobbs 1994, Vos *et al.* 2001, Dungan *et al.* 2002). Often little or nothing is known about the scales at which a species responds to structural characteristics of its environment and this may greatly limit the effectiveness of study designs. One method of estimating the appropriate scale is to model the relationship at a number of scales and determine where the fit of the model is best (e.g., Findlay and Houlihan 1997, Elliot *et al.* 1998, Pope *et al.* 2000, Savignac *et al.* 2000). The second objective of this chapter is to use this approach and the "Focus" program to test the hypothesis that different species of dead-hardwood boring beetles in the family Cerambycidae (Coleoptera) respond to their habitat at different scales. I refer to the scale at which different species respond to the amount of habitat as the characteristic scale of response to habitat amount.

2.2 METHODS

2.2.1 THE FOCUS PROGRAM

Three matrices are the basic inputs to the Focus program: response variable measure (e.g., species abundance/richness) at the each site, a matrix of between-site geometric distances, and a matrix of the predictor variable measurements at various increasing scales around the sites. At each spatial scale, Focus conducts multiple simple linear regressions of the ecological response on the landscape predictor. Each regression at each scale involves a different set of independent and randomly chosen data points. The program selects spatially independent sites for the regressions as follows: 1. It randomly selects a site n_i from the entire set of N sites. 2. It selects a second site n_j that

satisfies the constraint of spatial independence C . For the case considered here, C is a measure of geometric distance where $C > 2r$. In other words areas within which the predictor variable is measured may not overlap. 3. It continues to randomly select sites until the constraint C can no longer be met, or until a predetermined number of sites are selected. 4. It fits a regression to the selected points. In this study, the abundance of a beetle species was regressed on the proportion of forest cover. The program records the following regression statistics: R^2 , r , MSE, N . 5. It then repeats steps 1-4 for X different sets of spatially independent sites, to develop a distribution of regression model fit and/or effect size. 6. Finally, it repeats steps 1-5 for each spatial scale. The output of the program run is the mean and standard error of the regression statistics (R^2 , r , MSE, N) at each scale.

In principle, the constraint C and the pattern of site selection (here it is random) could take many different forms. For example, instead of a geometric distance, the constraint C could be defined in such a way that sites must not be significantly spatially auto-correlated to be included in a final set. The pattern of site selection could follow a grid-based or stratified random design. We expect that researchers will adapt the program to suit their particular applications.

The procedure has several advantages over randomly selecting a single set of independent sites: (1) by doing several regressions, site selection is not affected by the particular point that is selected first, (2) sites at different scales are not nested, because the subsets in any regression at a smaller scale may be quite different than the subsets used at larger scales, and (3) it maximizes the data available. Even though at a large spatial scale the sample size of each individual regression may be very small, the

randomization method allows for multiple estimates of the regression (using different sets of data points), thus increasing the power of the analysis.

Focus also allows the user to test two assumptions that apply to the overall analysis of re-sampling the data to find the scale of best model fit: (1) functional stability at different scales, and (2) representative sampling. A test for functional stability is necessary because Focus uses linear regression at all scales whereas the relationship between the organism and the habitat variable may be non-linear at some scales. This would cause the measures of model fit to decrease at these scales independently of the real relationship. Focus tests for such a non-linear trend by using forward stepwise multiple regression to attempt to fit second-order and third-order polynomial terms (of the landscape predictor) to the model. The model is considered to be significantly improved by the addition of these higher order terms if the fit is improved at the $\alpha=0.05$ level. This analysis is carried out on a number (determined by the user) of the chosen data sets that are used in the regressions at each scale.

A test to ensure representative sampling is necessary because if the number of regressions chosen is too small, then the resulting distribution of regression statistics may not adequately represent the entire data set. If the variability in the data is not adequately represented by the sets of independent points that have been selected, then re-running the same analysis could lead to very different measures of model fit reported at the different scales. The representative sampling test checks that the number of iterations used is sufficient, by re-running the analysis (including the data point selection process) 10 times at the smallest scale included, and displays the mean and variance of the resulting MSE distribution, as well as the mean and standard error of the coefficient. If these values are

stable across the 10 analyses, then the number of iterations used is sufficient and the results are representative of the data set. This assumption is tested at the smallest scale because for many datasets it is at this scale that the number of possible ways to sample the data is greatest. A subset of the possible points can be chosen many ways because the constraint of spatial independence is least limiting in terms of which other points may be included. For the hypothetical set of points in figure 2.2, for example, at the smaller scale shown there are 28 ways that six of the points could be chosen while maintaining spatial independence (figure 2.2H). At the larger scale there are only six possible independent sets of points (figure 2.2B-G).

2.2.2 CHARACTERISTIC SCALES OF WOOD-BORING BEETLE RESPONSE TO HABITAT AMOUNT

Most long-horned beetles (Coleoptera: Cerambycidae) have larvae that develop within the wood of living or dead trees or shrubs. Species with larvae that develop within dead woody material are much less host-specific than species whose larvae develop within living or very recently dead trees (Linsley 1954), probably because the trees' defensive chemicals are not as important (Kletecka 1996). In a study that considered 3 different scales, Økland *et al.* (1996) found that long-horned beetles responded to environmental habitat variables at scales of at least 1km². Schiegg (2000) found that saproxylic beetles responded to the spatial connectedness of dead wood pieces at the 150m scale in a study that considered 50m-200m scales.

I used the Focus program to determine the scales at which different species of dead-hardwood boring beetles respond to amount of forest cover in the landscape. The beetles

were sampled as part of an extensive study on the response of wood-boring beetles to ice storm damage in the Ottawa, Canada area. Beetles were trapped across an extensive area (approx. 80km by 40km) with the sampling points clustered in 19 1km² areas with 10 sampling points each (figure 2.3). This means that the number of spatially independent points decreased rapidly as the radius of the area considered increased up to about ½ km (figure 2.4). I used only polyphagous species, whose larvae develop in a variety of dead tree species. I also only used beetle species that do not appear to show a preference for any particular tree species (Linsley 1962a, 1962b, 1963, 1964, Linsley and Chemsak 1972, 1976, Yanega 1996) to ensure that the proportion of forest would be a fair approximation of the proportion of breeding habitat in the landscape. The response variable for each species was the number of individuals caught at each site, summed over the two years. I only used species that were caught in at least five of the sampling locations during the two years. I deposited voucher specimens of all long-horned beetle species in the Carleton University insect collection.

To detect the characteristic scale at which the beetle species respond to forest habitat, for each species I used Focus to estimate the fit of simple linear regressions of beetle abundance on the proportion of forest in the landscapes around the beetle sampling sites. The proportion of forest was measured at multiple scales: radii of 20m to 200m in 20m increments, 400m to 2000m in 200m increments, and 3000m to 7000m in 1000m increments. I used digital topographical maps (National Capital Commission 1999) in ArcView to measure the forest cover within the 24 different sized circles (not rings). At each scale the regressions were repeated several times, with each regression being done on a subset of points that were spatially independent (see description of Focus program

above). The choice of characteristic scale was then made by examining a plot of a measure of model fit against the various scales at which forest proportion was measured.

I chose to conduct my analyses using the same number of data points for each regression at each scale, because the purpose of my analysis was to compare the results at different scales. Since the number of spatially independent points is smallest at the largest scale, the number of points included in each regression at all scales is determined by the number of independent points that can be chosen at the largest scale. This causes a trade-off between the maximum scale of consideration and the number of data points to be used in each regression. Including all scales up to 7km would have limited the number of points in each regression to 5 (figure 2.4). Økland *et al.* (1996) found that the amount of dead wood within 1km² was related to species richness and abundance of saproxylic beetles. Schiegg (2000) found that saproxylic beetle richness was related to the connectness of dead wood pieces within 150m. I found no indication in the literature that saproxylic beetles respond to habitat at scales much larger than about 1km. Therefore, I decided to only include the scales up to 2km. This allowed us to increase the number of points in each regression to 16. Using a much smaller maximum scale, (e.g., 600m), would have resulted in only a very small increase in the number of points that could be included in each regression, while using a larger scale would have resulted in a large decrease in number of points (figure 2.4).

I used 200 regressions at each scale to develop the mean and standard error of the regression statistics. The Focus program allows the user to select any number of regressions. The number of regressions should be large enough that the results are representative of the data (see assumptions below), but not so large that the probability of

some regressions being carried out on the exact same set of selected points is high. Figure 2.2 shows that the number of different possible sets of independent points declines with an increase in scale. This could inappropriately lower the standard error of the statistics that are reported. Deciding on the number of regressions that can be performed without shrinking the standard error bars due to over-sampling is complex because it depends not only on the number of sites in the data and in each regression, but also on their spatial arrangement.

It is important to note that while the Focus program uses linear regression to examine the relationship between the species abundance and the proportion of forest habitat (or whatever other variables are of interest), it is not used to test hypotheses at this stage. It is simply measuring the linear model fit at different spatial scales. Because I am not hypothesis testing, there is no need to examine residual plots and histograms to ensure that the assumptions of ANOVA are met. We are not using ANOVA, only the model fitting stage of linear regression.

To evaluate the relationship between beetle abundance and proportion of forest cover, I used the correlation coefficient (r) as my measure of model fit because for some species there was a range of scales over which this relationship was negative. This suggests that these species may respond to some resource other than forest. The other possible measures of model fit (R^2 , MSE) do not differentiate between positive and negative relationships. R^2 is also problematic as a measure of the strength of the regression at scales where the range of values of r for the regressions done at a single scale extends over both negative and positive values. In this case the average R^2 value could be quite large even though there is no relationship.

For each species I examined the plot of r versus scale to determine the characteristic scale of response to forest cover. Beginning at the smallest scale, the next peak (local maximum) in r that had a higher value and non-overlapping standard error bars was considered to represent a significantly better model fit and became a new “candidate” for the characteristic scale (figure 2.5). Repeating this step, a larger scale was only considered a candidate if it corresponded to a peak in model fit and had a significantly better model fit than the previously chosen, smaller-scale candidate. I used the smallest scale as my initial candidate for characteristic scale of response because it seemed reasonable to assume that the species would be present in larger numbers in habitat than in non-habitat. This method assumes that the abundance will respond to the amount of habitat in a small area around the sampling point. The larger scales, or context, are only considered to influence the abundance if the species responds to habitat at these larger scales significantly more than at the local, or smallest scale.

2.3 RESULTS

I caught 12 species of polyphagous long-horned beetles associated with dead wood in at least five of the traps. The scales at which different species respond to forest cover varied from 20m to 1200m (table 2.1). Figure 2.6 shows the distribution of correlation coefficients from the regressions at different scales for the twelve species. This figure shows that the distributions of the r values did extend over both positive and negative values.

2.4 DISCUSSION

Different species of beetles did respond to forest habitat at different scales. Interestingly, some species showed multiple positive peaks in model fit. It is possible that habitat variables are important at more than one scale for different reasons (Kotliar and Wiens 1990, Jonsen and Taylor 2000, Nathan 2001). For example, Kinnunen *et al.* (2001) and Rukke and Midtgaard (1998) suggest that some habitat variable may cause beetles to select habitat at a fine scale, while larger scale habitat availability may limit areas where a beetle species can occur. Similar responses in our species could for example cause a peak in the response to amount of forest habitat at a small scale indicating a minimum for an area to be suitable, and also at a much larger scale because high forest cover at this scale allows beetle species to recolonize occasional local extinctions.

One species, *Liopinus alpha* (Say), even showed a positive correlation over some scales and a negative correlation over others. Different processes or resources can be important at different scales (Paradis *et al.* 1999). It is possible that the species that had both positive and negative relationships with forest cover at different scales are responding to some resource found outside forest patches at the scales corresponding to negative relationships. As many species of long-horned beetles seek flowers for adult feeding (Speight 1989, Hanks 1999, Gutowski 2002), it is possible that this is responsible for the negative relation to forest cover at some scales. This could be the case if less forest in the area leads to more floral resources.

Some of the beetle species had many sites where no individuals were found. This resulted in some regressions being left out of the analyses because all the data points selected for that regression had no individuals. Therefore, the estimates of the mean

model fit for the less commonly caught species often had large standard errors because the number of regressions used to estimate the fit was small. It would be possible to have Focus resample the pool of data points for regressions that have this problem so that the number of regressions is constant at all scales, but this may lead to another problem: if there are relatively few points where individuals are found, it is likely that the same set of points will be regressed repeatedly using this alternative. This would result in a deceptively low standard error being reported, amplifying the over-sampling problem (see methods) for the rare species.

Some species showed rather clear peaks in response at some scale (e.g.: *Urographis fasciatus* (DeG.)), while for other species the choice of characteristic scale of response is less clear (e.g.: *Strangalia luteicornis* (F.)) (figure 2.5). This suggests that it may be appropriate to place more confidence in the characteristic scales of response for some species than for other species in further analyses that utilize these scales of response. I have not done this in chapters 3 and 4 because I have no information on what is causing the differences among species. If the magnitude of the difference in response among scales is related to a variable that I include in further tests (chapter 3 and 4) weighting the species data based on the clarity of the scale of response could bias the results. Even if only the species which showed a clear choice for characteristic scale of response to forest habitat are considered, the results still show that different species respond at different spatial scales.

In my example the sampling points came from a large area, but because my study included the effects of habitat at scales of several kilometers the number of spatially independent data points was small. However with 190 sampling locations I was able to

use 200 regressions per scale and adequately represent the data without over-sampling. With very small data sets, especially if the sampling points are close together, the issue of over-sampling will be much more restrictive.

The program we describe here should make the use of existing data sets to answer larger scale questions possible as long as the locations where the response variables were measured are known. I did a survey of the literature to see how many studies had data appropriate for this. I used Cambridge Scientific Abstracts to search within the Ecology Abstracts subfile of Biological Sciences. My search criteria were that the listing not contain the term “model” anywhere, but did contain “landscape” or “patch” anywhere. This search yielded 6985 studies. I picked a random sample of 40 abstracts from these studies to check for the proportion that produced data sets that would lend themselves to larger scale questions using the Focus program. To be considered appropriate the studies had to produce numerical response data measured at multiple locations, and these locations had to be spread over an extent large enough that multiple independent data points would exist when the predictor variables are measured beyond the patch level. Twenty of these 40 studies created datasets that met my criteria. The 0.5 proportion (20/40) was quite stable after the first 10 abstracts. This leads me to estimate that there are about 3500 data sets in the ecological literature which would lend themselves to answering large-scale questions of characteristic scale of response of organisms to their environment using the Focus program.

Figure 2.1: Example of areas within which forest cover was measured. For clarity I have only shown 2 scales around 3 plots. At the larger scale the areas within which the predictor variable is measured overlap.

Figure 2.2: Possible sets of spatially independent points. A) Spatial locations of 8 hypothetical points. B) to G) – all possible ways to select 5 spatially independent points to include in a regression. H) At a smaller scale the areas where the predictor variable is measured are independent. At this scale there are ${}_8C_5=56$ ways to select 5 independent points.

Figure 2.3: Locations of beetle sampling sites in the Ottawa, Ontario region. Each of the 19 sampling areas was 1km^2 and had 10 randomly located trapping sites. Black polygons in upper map show sampling areas. The lower map is a detail of one sampling area. In the lower map the black squares show trapping locations and the shaded areas represent forest cover.

Figure 2.4: Relationship between the spatial scale (radius within which forest cover was measured) and the average number of points that could be included in the individual regressions while maintaining non-overlapping predictor variable areas (spatial independence).

Figure 2.5: Focus output showing model fit (Pearson correl. coeff.) between forest cover and beetle abundance for the 12 polyphagous (polyphagous as larvae) species. Error bars are standard errors over 200 iterations excluding regressions consisting completely of zero abundances. Arrow shows characteristic scale of response to forest habitat.

Table 2.1: Characteristic scales of response to forest cover for long-horned beetles, as determined by maximum linear model fit using Focus software. Settings were: 200 regressions/iterations per scale, 16 points per regression, 2 buffer radii for spatial independence.

Species	(buffer radius in m) Scale of max. fit
<i>Bellamira scalaris</i> (Say)	1000
<i>Evodinus m. monticola</i> (Rand.)	160
<i>Gaurotes cyanipennis</i> (Say)	160
<i>Liopinus alpha</i> (Say)	20
<i>Microgoes oculatus</i> (LeC.)	60
<i>Stictoleptura c. canadensis</i> (Oliv.)	1600
<i>Strangalepta abbreviata</i> (Germ.)	120
<i>Strangalia luteicornis</i> (F.)	800
<i>Trachysida mutabilis</i> (Newm.)	1200
<i>Trigonarthris minnesotana</i> (Csy.)	200
<i>Urgleptes signatus</i> (LeC.)	140
<i>Urographis fasciatus</i> (DeG.)	180

Figure 2.6: Example of the distribution of Pearson correlation coefficients from regressions between abundance of a species and proportion of forest cover at different scales. For clarity, only every third scale considered is shown. Species used was *Urgleptes signatus* (LeC.).

CHAPTER 3

LIFE HISTORY AND BODY SIZE AFFECTS THE SPATIAL SCALE OF HABITAT-BEETLE INTERACTIONS

3.1 INTRODUCTION

Animal species respond to their environment at different spatial scales (Riitters *et al.* 1997). Even within guilds, both parasitoid fly species (Roland and Taylor 1997) and long-horned beetle (Coleoptera: Cerambycidae) species (Chapter 2) respond to habitat variables at different scales (spatial extents). Steffan-Dewenter *et al.* (2002) have found that different bee guilds respond to semi-natural habitat at different spatial scales. To study the response of animals to their habitat, we must measure habitat variables at a scale that is appropriate for the animal and phenomena being studied (Addicott *et al.* 1987, Wiens and Milne 1989, Wiens *et al.* 1993, Cale and Hobbs 1994, Schopf and Ivany 1998, Ludwig *et al.* 2000). Using an inappropriate spatial scale can cause the researcher to miss an important relationship between the species and its habitat (Lomolino and Creighton 1996, Rukke and Midtgaard 1998), or even to come to the wrong conclusion (Hanski 1987, Schopf and Ivany 1998).

Several species characteristics have been hypothesized to explain the scale at which different species respond to their environment. One such characteristic is body size. Larger animals may respond to the environment over a larger scale because they perceive the environment more coarsely (Mech and Zollner 2002). This could affect the scale at which they respond to habitat because they move farther, or because they choose habitat

based on what is present at larger scales. Larger species may also respond at larger scales because they move farther to satisfy their greater energetic requirements (Perry and Garland 2002).

Cale and Hobbs (1994) and Elliot *et al.* (1998) have suggested that the distance that organisms move is one factor that must be considered in deciding on a spatial scale at which to consider habitat variables. Økland *et al.* (1996) found that the abundance and richness of flying saproxylic beetles was more strongly related to the amount of decaying wood resources at larger than smaller scales, and that 40m x 40m represented much too small a scale to reveal this relationship. They concluded that habitat measures should be made within at least a 1km² area for studying these species. In contrast, Rukke and Midtgaard (1998) found significant effects of habitat isolation on fungus beetles when isolation was measured within less than 50m from a source habitat. This may be because the beetle species considered confine their movement to walking over distances less than 50m (Starzomski and Bondrup-Nielsen 2002). These studies suggest that beetle species whose movements are confined to walking very short distances respond to habitat at much smaller scales than the beetle species that move by flying. Therefore, movement range may be an important factor determining the scale of response to habitat. It seems likely that movement and body size could be positively correlated.

The distance that a species moves may also be affected whether or not it can meet all of its resource needs in a single area. Species that must search out complementary resources in different areas to meet some requirement during their life may move greater distances than those that can find all necessary resources in one spot. For example, Pope *et al.* (2000) found that both including measures of both breeding habitat and summer

habitat were necessary to statistically model the response of the northern leopard frog (*Rana pipiens*) to habitat. Species that must use resource complementation will probably move more than species that do not. This is yet another factor that could influence the scale of response to habitat through movement.

Another characteristic that may affect the movement range of a species, and hence the scale at which it responds to the environment, is the longevity of its habitat. Hanski (1987) modified Southwood's (1977) habitat templet theory, noting that species that use ephemeral habitats are expected to move considerable distances to track these habitats. Nilsson and Baranowski (1994) suggested that click beetles that use hollow trees have been selected for low vagility because this habitat is quite stable. In a study of stream invertebrates, Gjerløv (1997) found that Southwood's templet theory was supported, but only when the correct scale was considered. This not only supports the idea that species with narrow niches should move more, but also that measuring variables at the correct spatial scale is vital to uncovering such ecological relationships. If movement is related to the scale of response, then long-horned beetle species that develop in ephemeral habitats should be more mobile than species that use longer lasting habitats. The ideas of movement being influenced by resource complementation and by ephemeral habitats were both suggested earlier by Nicholson (1954).

The measure of habitat that I used to determine the characteristic scale of response of the different species (see methods) was the proportion of forested area. This should represent the proportion of habitat for polyphagous species (defined here as those with polyphagous larvae), which can utilize a wide range of host tree species. The proportion of habitat for more specialized species will be some subset of the total amount of forest.

If overall forest cover is a worse measure of habitat for the oligophagous species then they should show weaker relationships with overall forest cover. For this reason I expected that the proportion of forest would be more strongly related to the abundance of the polyphagous species than to the abundance of the oligophagous species.

The purpose of this study was to determine whether body size, movement outside forest and/or longevity of larval habitat (ephemeral or not) were related to the scale at which different species of long-horned beetles respond to forest cover. I predicted that larger species would respond at larger scales. I also predicted that species that move out of forest patches would respond to the amount of forest habitat at a larger scale than species that are not found moving outside of forest. I further expected species whose larvae develop in newly dead wood to respond to forest cover at a larger scale than species whose larvae develop in older, decayed dead wood, because the former represents a more ephemeral habitat than the latter.

3.2 METHODS

3.2.1 NATURAL HISTORY OF CERAMBYCIDAE

Most species of long-horned beetles are associated with forest (Gutowski 2002). Most of their 1-35 year (1-4 years in the Ottawa area) life cycle is spent as larvae that feed by excavating galleries in a single piece of living or dead wood (Hanks 1999, Linsley 1954). Within the species whose larvae develop within dead wood there are differences in the breadth of suitable host wood species. Some species have larvae that can only develop within a limited number of wood species, while other species can use many species, with

some being able to develop within both deciduous and coniferous dead wood (ex's in Yanega 1996). The mobile adult stage is comparatively short, on the order of three to six weeks for many species (Safranyik and Moeck 1995).

Within the Cerambycidae, species differ in their dispersal distances. Several researchers have suggested that species whose larvae and adult feeding resources are segregated in space disperse farther than those whose larvae and adult resources are in close proximity (Shibata 1987, Barbalat 1995, Hanks 1999). Although many species of long-horned beetle adults feed at flowers, there are also species that are never found at flowers (Dajoz 2000) and some species do not need to move from the larval log to feed, mate and oviposit (Craighead 1950). Although there may be a continuum of movement distances or abilities in the long-horned beetles, it seems probable that species that must move to find complementary resources and those that do not, form two distinct groups.

Another trait that differentiates between two groups of long-horned beetles is the condition of the host tree or log. Recently-dead wood (within the first few years of tree death) is used by a different set of wood-boring beetle species than wood that has been dead for decades (Blackman and Stage 1924, Graham 1925, Samuelsson *et al.* 1994). The recently-dead wood represents a much more ephemeral resource than the older stage of dead wood (Kletecka 1996). Hanks *et al.* (1998) suggest that the eucalyptus borer (a long-horned beetle) moves considerable distances because of the ephemeral nature of the larval host, stressed or weakened live trees.

3.2.2 DETERMINING THE CHARACTERISTIC SCALES

To investigate the scales at which long-horned beetles respond to habitat amount I used data on trap catches at 190 beetle trapping sites in the Ottawa area. During 1999 and 2000, 10 Lindgren funnel traps were located within each of 19 1km x 1km sampling areas (Holland *et al.* in revision). I narrowed the list of species included in my analyses to those whose larvae develop within dead wood. As well, species had to have been caught in at least 5 of the 190 sampling sites to be included. I used the abundance of beetles caught at each study site as response variables, with each species considered separately. To determine the characteristic scale of response, I measured the proportion of forested area (the predictor variable) in concentric circular areas around the sampling sites using ArcView (Environmental Systems Research Institute, Redlands, California, USA). The radii I used were 20-200m in 20m increments and 200-2000m in 200m increments. Scale in this study refers to the radius of the area within which the predictor variable was measured. Larger areas around a focal site were inclusive, that is, forested proportion was calculated within circles at all scales, not in concentric rings. I created a raster forest cover layer from digital NTDB topographical maps of the Ottawa area (National Capital Commission 1999). The proportion of forest at each scale was calculated as the proportion of 1m² cells that were forested. The proportion of forest cover ranged from 0 to 1.0 at the 20m to 140m scales, and this range decreased slightly to between 0.062 and 0.808 at the 2km scale.

I conducted linear regressions of the beetle abundance of each species on the proportion of forest. I repeated these regressions at each scale to see where the resulting model best fit the data (Elliot *et al.* 1998) for each species. At the larger scales the

sampling sites were clustered so that the areas within which forest cover was measured were overlapping. This could violate the assumption of independence and artificially inflate the degrees of freedom in the individual regressions. To make use of all points despite the lack of spatial independence I used a randomization procedure encoded in the Focus program (Chapter 2). Focus conducts the regression between abundance and habitat a number of times at each spatial scale using different sets of randomly selected spatially independent sites. The user sets the number of iterations (regressions) to be done at each spatial scale; the output is then the average model fit and associated standard error at each spatial scale. In this way all or most of the data points are included in the final average measure of model fit, even if only a small proportion are used in individual regression because of spatial non-independence. A sample size of 16 was used in all regressions, because 16 was the number of possible spatially independent points at the largest spatial scale (2km).

I considered the scale of maximum model fit to be the scale at which the Pearson correlation coefficient had a local maximum (peak), and had standard error bars that did not overlap those either at a smaller local maximum or at the smallest scale (Chapter 2). For 12 long-horned beetle species the characteristic scale of response is reported in Chapter 2.

3.2.3 DETERMINING BEETLE MOVEMENT

I used data from two sources to determine which species move through non-forest areas. During the cerambycid surveys carried out during the summers of 1999 and 2000, 11 of the 190 traps were >50m from all woodlots and located in non-forest sites such as

wooded fencerows. All beetles caught in traps that were 50m or farther from the edge of any woodlot or forest were considered to be moving outside of forest habitat.

During the summer of 2001 I used flight intercept traps to capture long-horned beetles flying from forest into non-forest areas. I put these traps in seven of the 19 sampling areas from the 1999 and 2000 surveys that had a meadow or old field next to a woodlot edge. The selected woodlot edges all faced roughly northwest, which faces the prevailing wind direction in this area. I used woodlot edges that faced the same way to control for any possible effects of sunlight or photo-taxiing. As well, adult longhorns often use scent to find suitable larval host trees and mates (Linsley 1954, Schowalter 1985, Hanks et al. 1993). Therefore, it is likely that species moving out of woodlots to seek these resources may travel into the wind.

I designed flight intercept traps that had a very large surface area (5.2m^2 on a side), but would not require constant maintenance and would alleviate the need for transporting a large volume of killing/preserving fluid to the traps. The resulting trap was a combination of flight intercept and sticky trap. I used wooden posts to support a 4.3m long by 1.2m tall piece of black window screen (figure 3.1). I stapled clear plastic onto a plywood stage that was 0.3m wide and was supported at a 45° angle below and in front of the screen (figure 3.1). The bottom of the plastic was creased upwards to create a trough that was below and slightly behind the trapping screen (figure 3.1A). I placed two traps in each of the seven locations. One trap was 25m from the forest edge and the second trap 50m from the forest edge. The traps were offset by 50m laterally. Both traps had the “trapping side” of the screen facing the forest, so that they only caught beetles flying from the direction of the woodlot.

To hold any beetles that hit the trap I applied Rat and Mouse Trapping Adhesive (The Tanglefoot Company, Grand Rapids, Michigan, USA) to the plastic sheet. Beetles flying into the screen dropped onto the angled plastic sheet and got caught in the adhesive. I heated the adhesive to about 60°C and poured it into empty plastic caulking gun tubes. I immediately placed the tubes in a cool water bath to cool the adhesive and prevent damage to the tubes. The full tubes were taken into the field, and loaded into a standard caulking gun. When the traps were first set up I applied four beads of adhesive along the length of the plastic sheet. As the adhesive became saturated with insects, pollen, or other materials I laid down additional longitudinal beads of adhesive.

I visited each trap weekly from the beginning of May until the end of August. During each visit I removed all long-horned beetles and placed them in vials of Histo-clear (National Diagnostics, Atlanta, Georgia, USA). I identified the species using Yanega (1996). I placed voucher specimens in the Carleton University insect collection.

Species caught by either the Lindgren funnel traps outside forest in 1999 or 2000, or by the flight intercept traps in 2001 were categorized as species that will move in non-forest areas. Species not caught by either method, but caught in a Lindgren funnel trap within forest in areas with movement traps were categorized as species that do not move in non-forest areas.

3.2.4 DETERMINING WHETHER LARVAE USE EPHEMERAL HOSTS

Cerambycids whose larvae develop in newly-dead wood were considered to be using an ephemeral resource. I searched the literature for information on the condition of larval hosts of the species I caught (Linsley 1962a, 1962b, 1963, 1964, Linsley and Chemsak

1972, 1976, Yanega 1996). Descriptions such as “newly felled,” “recently cut,” “unseasoned” and “sound deadwood” were considered to indicate recently-dead wood. Species whose larvae developed within wood described as “decaying,” “soft,” or “seasoned,” were considered to develop within older dead wood. These larval habitats were considered not to be ephemeral. Of course, such logs do eventually become unavailable to long-horned beetle larvae, but at a rate of decades not one to a few years as for the recently-dead wood habitats.

3.2.5 ANALYSES

To compare the response of oligophagous and polyphagous species to the total amount of forest I used a two-tailed t-test, assuming unequal variances, to compare the average Pearson correlation coefficients of these two groups at the characteristic scale of response (scale corresponding to the maximum model fit) to habitat amount. To determine whether species were oligophagous or polyphagous I consulted Yanega (1996). All species that develop only in one or a few wood species, or that show a preference for certain species were considered oligophagous. Species were considered to show a preference for certain wood species if the description of larval hosts contained “especially...,” or “including...”.

To test the hypothesis that larger beetles responded to habitat at larger scales I conducted a linear regression between the median adult body length of species and the scales at which they responded to habitat amount. For body size I used the median of the range of lengths specified in Yanega (1996). The characteristic scales were transformed by taking natural logarithms before analysis because these ranged over three orders of

magnitude. I used analysis of variance (ANOVA) to check the significance of the resulting linear relationship.

To test the hypothesis that species that move outside forested areas respond to habitat at larger scales than those that do not I used a two-tailed t-test, assuming unequal variances, to compare the scales of habitat response. To test the hypothesis that species that use ephemeral habitat respond to habitat at a larger characteristic scale than other species I again used a two-tailed t-test, assuming unequal variances, on the scale of habitat response data.

3.3 RESULTS

I caught 32 species of dead-wood feeding cerambycid beetle species at five or more of the Lindgren funnel traps. One species, *Phymatodes amoenus* (Say), was not included because it develops in dead grape vines (Yanega 1996), and therefore probably responds differently to the amount of forest than the species that develop in forest tree and shrub species. Twelve of the species were considered to be polyphagous (as larvae) according to my criteria. Figure 3.2 shows an example of the model fit across the different scales for one of these 12 species and shows the characteristic scale of response. Table 3.1 lists all the species and their characteristic scales of response to proportion of forest in the landscape, median body size, as well as whether or not they use an ephemeral larval resource and were caught moving outside of forest (emigrant species).

Four of the species had negative correlations between abundance and forest proportion at all scales (as did *Phymatodes amoenus* (Say), mentioned above), indicating

that proportion of forest may be a very poor measure of proportion of habitat for these species. These species were therefore not included in further analyses. The t-test between the correlation coefficients of polyphagous and oligophagous species was based on the remaining 12 and 15 species respectively. This test did show that the correlation coefficients for the polyphagous species were higher than for the oligophagous species ($df=23$, $t=3.84$, $p=0.000841$, figure 3.3). This indicates that total forest area more accurately represents habitat (or something strongly correlated with it) for the polyphagous species. This does not invalidate the scales at which the oligophagous responded to forest, but it does suggest that not all forest is habitat. For this reason, the analyses that follow were done using only the polyphagous species.

There was a marginally significant positive relationship between the median body length for the forest polyphagous species and the scale at which they responded to proportion of forest (figure 3.4, $df=11$, $F=4.26$, $p=0.0659$). This relationship explained 29.9 percent of the variability in the scale of response.

There was no difference in the scale of response to forest habitat between the species that were found moving outside forest was larger than those that did not move outside forest (figure 3.5, $df=1$, $t=0.800$, $p=0.570$). Species that used ephemeral habitat did not show a greater scale of response to forest proportion than those not using ephemeral habitats (figure 3.6, $df=3$, $t=2.30$, $p=0.105$). In fact the general trend was for the species using ephemeral habitats to respond at smaller scales.

3.4 DISCUSSION

Different species of long-horned beetles responded to habitat amount at different spatial scales, with the characteristic scales of response varying over 3 orders of magnitude (chapter 2). This suggests that it may not be appropriate to use a single spatial scale in studies of multiple species. Single-scale studies can lead to some species showing a stronger response to habitat variables because they happen to be measured closer to the characteristic scale of response of those species. The response of other species will appear to be weaker, simply because the species-habitat relationship is strongest at a different scale.

The hypothesis that larger beetles should respond to amount of forest habitat at larger scales was supported. The relationship between median body length and scale of response to forest was quite strong, explaining 29.9% of the variation in scale of response (figure 3.4). This is one of the first empirical tests of this hypothesis for any taxa. Roland and Taylor (1997) made a similar discovery in that the scale of response of four parasitoid fly species to forest structure was positively related to body mass. Roslin (2000) found that larger dung beetles moved between pastures more frequently than smaller dung beetles. Researchers have found that larger animals tend to move farther and this may lead to larger animals responding to their surroundings at larger scales. Bowman *et al.* (2002) controlled for the relationship between body mass and movement distance in their study. Although this was not the main focus of their work, they found that body mass explained 50% of the variance in dispersal distance, and 67% of the variance in maximum successful return distance following relocation, in mammals. Sutherland *et al.* (2000) and Peters (1983) have found a positive relationship between body mass and maximum

dispersal distance for both mammals and birds. It seems possible that greater movement of larger species is behind the relationship between body length and characteristic scale of response. Regardless, the larger species are responding to forest cover at larger scales.

There was no evidence that species that emigrate from forest habitat respond to this habitat at larger spatial scales than species which do not emigrate. Given the strong relationship between body size and the characteristic scale of response, it is surprising that movement was not also related to the scale of response, since it seems reasonable that movement could be behind the former result. The statistical power of this test was low (sample size = 9) because we did not have movement data on all our species. As well, the classification of movement 2 classes is much less precise than some movement data that exists in the literature. For example, it would be interesting to check for a linear relationship between the scale of response and the maximum return distance using relocation study data.

Although all the hypotheses regarding what determines the characteristic scale of response that I have tested all deal with movement in some way because this is the most intuitive mechanism for acting on the scale of response. However, the idea that species that emigrate from forest habitat should respond at larger scales than species that do not is not circular. Species that move greater distances can do so within habitat or by moving out of habitat. As well, my results do not show that species that emigrate have larger characteristic scales of response than species that do not emigrate. It would be interesting to know if the movement of the beetles that do emigrate is being driven by the need to emigrate for adult feeding or mating, or if it is determined by an inherently greater dispersal distance than species that don't emigrate, independent of emigration behaviour.

Current studies in the literature suggest the former (e.g.: Shibata 1987) is the case. This could be looked at by designing studies that use some species that usually move long distances and some species that usually move short distances, but where all species must search out some resource (adult feeding sites for example). These species could be placed in small woodlots and larger forests, both with necessary resources outside the forest habitats. The distances moved and probability of emigration from forest could be compared between the 4 categories (usual long/short dispersal distance x small/large forest). This experiment could determine whether emigration is caused by a need to find complementary resources, or simply by some species moving great distances and thereby leaving the forest habitat.

I did not find any evidence that species that develop in more ephemeral habitats responded to forest at greater scales than those developing in longer-lasting habitat. It is possible that the range of host wood conditions that long-horned beetles use is actually broader than the literature currently suggests. There is much less information on saproxylic long-horned beetles than on economically important long-horns that attach living trees (Gutowski 2002), so our knowledge of the hosts and conditions of the saproxylic species may be incomplete. It is therefore possible that the overlap in species compositions between the early, ephemeral stages of decay and the later, more stable stages is greater than is currently suggested in the literature. More information on suitable wood conditions for different species, the longevity of the suitable conditions, and the factors that determine this, would aid in future studies of saproxylic beetles.

If the risk of death is greater during movement (ex: Norrhahl and Korimäki 1998, Carr and Fahrig 2001), then there may be a trade-off between the probability of

movement and the distance moved. In such a case, species that must frequently move because they use ephemeral habitat may not move as far during each movement as compared to species that have a lower probability of moving. This argument considers all movement, not only movement between habitat patches. Such a trade-off in probability of dispersal and distance of dispersal could mean that my prediction that species using ephemeral habitats will have a larger characteristic scale of response to forest habitat is wrong. The beetles are moving to find necessary resources, and it is the spatial distribution of the resources that is behind the movement patterns. Without knowledge of this distribution I can only speculate on patterns such as the trade-off mentioned here.

The higher correlation coefficient values for the polyphagous species than for the oligophagous species (figure 3.3) show that the amount of forest is a better measure of habitat for the polyphagous species. In a loose sense, the polyphagous species are forest generalists, while the oligophagous species are more specialized, and able to use only a subset of the total forest that contains the correct tree species. The oligophagous species were excluded in this study because we wanted to compare the scale of response to amount of habitat, not amount of forest. Reliably determining the scale of response to habitat for the oligophagous species would require the delineation of the parts of the forest that contain the requisite tree species.

This is one of the first studies to test predicted relationships between species attributes and their scales of response to habitat. My results support the hypothesis that larger species respond to habitat at larger spatial scales than do smaller species. They do not support the hypothesis that species that move out habitat patches respond to habitat at larger spatial scales than species moving smaller distances. These results also do not

support the hypothesis that species using ephemeral habitats respond to habitat at larger spatial scales than those using permanent habitats.

Figure 3.1: Details of flight intercept trap. A) Side view. The screen and support post were taller than shown. B) Front view. There were 4 equally-spaced support posts along the length of the 4.3m screen, and 3 equally-spaced 2x4 support structures along the 4.3 length of the plywood sticky trap surface.

A

B

Figure 3.2: Example of Focus software output showing model fit (Pearson correlation coefficient) between forest cover and beetle abundance for a single species. Error bars represent standard errors over 200 iterations excluding those regressions consisting completely of zero abundances. Arrow shows final characteristic scale of response to habitat.

Table 3.1: Species of cerambycid beetles that feed on dead wood and were caught at at least five trapping sites. Poly/Olig refers to whether the species is a polyphagous or oligophagous in the larval stage according to our criteria (see methods). Under Scale, neg means that the scale of maximum fit was negative. Ephem and Emigrate refer to whether the larvae develop within an ephemeral stage of log decay and whether the species was found to move outside of forest patches (see methods) respectively. A blank in the Ephem column indicates that we were unable to assign the larval habitat to either condition. A blank in the Emigrate column indicates that the species was caught only in 1km² trapping areas where we didn't monitor movement so we could not ascertain whether or not the species moved outside forest habitat.

Species	Poly/Olig	(m) Scale	ln(scale)	(mm) Size	Ephem	Emigrate
<i>Bellamira scalaris</i> (Say)	Poly	1000	6.91	21.5	N	N
<i>Evodinus m. monticola</i> (Rand.)	Poly	160	5.08	10.5		
<i>Gaurotes cyanipennis</i> (Say)	Poly	160	5.08	11.0	Y	N
<i>Liopinus alpha</i> (Say)	Poly	20	3.00	6.5		
<i>Microgoes oculatus</i> (LeC.)	Poly	60	4.09	11.5		N
<i>Stictoleptura c. canadensis</i> (Oliv.)	Poly	1600	7.38	12.5		Y
<i>Strangalepta abbreviata</i> (Germ.)	Poly	120	4.79	12.0	N	N
<i>Strangalia luteicornis</i> (F.)	Poly	800	6.68	11.5	N	
<i>Trachysida mutabilis</i> (Newm.)	Poly	1200	7.09	11.5	N	N
<i>Trigonarthris minnesotana</i> (Csy.)	Poly	200	5.30	15.5		Y
<i>Urgleptes signatus</i> (LeC.)	Poly	140	4.94	6.5		N
<i>Urographis fasciatus</i> (DeG.)	Poly	180	5.19	12.0	Y	N
<i>Analeptura lineola</i> (Say)	Olig	200	5.30	9.0		
<i>Anthophylax attenuatus</i> (Hald.)	Olig	400	5.99	14.5	N	
<i>Astylopsis macula</i> (Say)	Olig	20	3.00	8.5		Y
<i>Astylopsis sexguttata</i> (Say)	Olig	80	4.38	8.5		Y
<i>Clytus ruricola</i> (Oliv.)	Olig	20	3.00	12.5	N	Y
<i>Cyrtophorus verrucosus</i> (Oliv.)	Olig	20	3.00	9.0	Y	Y
<i>Hyperplatys aspersa</i> (Say)	Olig	neg		7.0		Y
<i>Hyperplatys maculata</i> Hald.	Olig	100	4.61	6.0		Y
<i>Lepturges symmetricus</i> (Hald.)	Olig	20	3.00	7.5		N
<i>Molorchus b. bimaculatus</i> Say	Olig	neg		6.0		Y
<i>Neoclytus a. acuminatus</i> (F.)	Olig	neg		8.5	Y	Y
<i>Oplosia nubila</i> (LeC.)	Olig	20	3.00	11.5	N	N
<i>Phymatodes aereus</i> (Newm.)	Olig	neg		9.0	N	Y
<i>Saperda imitans</i> Felt & Joutel	Olig	20	3.00	13.0	N	N
<i>Sarosesthes fulminans</i> (F.)	Olig	180	5.19	17.0	Y	
<i>Stenocorus schaumii</i> (LeC.)	Olig	20	3.00	23.5		
<i>Trigonarthris proxima</i> (Say)	Olig	20	3.00	16.5	N	N
<i>Urgleptes querci</i> (Fitch)	Olig	20	3.00	5.0		Y
<i>Xylotrechus colonus</i> (F.)	Olig	20	3.00	11.5	Y	Y

Figure 3.3: Comparison of model fit between polyphagous and oligophagous species. The r-values for each group are the average value at the characteristic scale of response to forest habitat. Error bars represent one standard error.

Figure 3.4: Relationship between median body length and scale at which dead-wood polyphagous species responded to proportion of forest.

Figure 3.5: Comparison of the characteristic scale of response of species caught moving outside of forest habitat (emigrate) and those not caught outside forest (don't emigrate).

Error bars represent one standard error.

Figure 3.6: Comparison of the characteristic scale of response of species with larvae that develop within ephemeral wood conditions and those that develop within longer-lasting wood conditions. Error bars represent one standard error.

CHAPTER 4

EFFECTS OF LIFE HISTORY ATTRIBUTES AND FOREST FRAGMENTATION ON EXTINCTION THRESHOLDS IN CERAMBYCIDAE

4.1 INTRODUCTION

Habitat loss due to human activities is the main reason for the current loss of species (Terborgh 1974, Ehrlich and Ehrlich 1981, Winchester 1997, Lande 1998). The conversion of natural areas to suit human activities such as urban development and agriculture (Leemans and Zuidema 1995) leaves less habitat for most other species (Walker 1992, Turner *et al.* 1994). This reduction in habitat results in smaller and more isolated populations, which are at greater risk of extinction due to stochastic demographic and environmental variation (Pimm *et al.* 1988, Raup 1991, Lande 1998). Understanding how habitat loss affects the extinction risk of different species is therefore an important part of improving conservation efforts (Pimm *et al.* 1988, Pearson *et al.* 1999, With and King 1999, Fahrig 2001, Reed and Shine 2002).

An important aspect of a species' response to habitat loss is the possibility of a sudden increase in the probability of extinction at some critical amount of habitat (Lande 1987). This amount of habitat has been termed the extinction threshold (Lande 1987). This phenomenon has been found in spatially explicit models (Bascompte and Sole 1996, With and King 1999, Fahrig 2001), and there is some empirical evidence for it as well (ex: Carlson 2000). Determining the critical amount of habitat that must be preserved to

prevent different species from reaching the extinction threshold should be a key part of conservation research. Moreover, if species characteristics, such as life history traits or behaviour, correlate with the threshold we could predict which species will be at risk at a given level of habitat loss without having to resort to detailed studies on each species. One problem in conservation is that in many cases the necessary remedial actions must be informed by detailed, species-specific studies (Doncaster *et al.* 1996, Eriksson and Kiviniemi 1999). Easily obtained estimates of extinction risk could facilitate conservation efforts (Davies *et al.* 2000, Duncan and Lockwood 2001).

Species characteristics that are likely to influence the risk of extinction include the intrinsic rate of population growth (Ehrenfeld 1970, Bennet and Owens 1997, McKinney 1997) and the rate of movement between habitat patches (Terborgh 1974, Lande *et al.* 1998, Huxel and Hastings 1999). Species with higher reproductive rates should rebound from population declines more quickly (MacArthur and Wilson 1967). Because small populations face a high risk of extinction (Pimm *et al.* 1988, Raup 1991, Boyce 1992, ex: Hecnar and M'Closkey 1997), high reproduction will reduce the time that the population is more vulnerable to subsequent stochastic events. Therefore species with greater reproductive rates should tolerate more habitat loss and so have a lower extinction threshold. A simulation study of factors affecting the extinction threshold predicted that reproductive rate had a very strong effect on the threshold amount of habitat (Fahrig 2001). Species with higher reproductive rate were predicted to tolerate more habitat loss and so have a lower extinction threshold by this model. Vance *et al.* (in press) also found evidence of this relationship in their study of forest breeding birds. They found a negative

relationship between species reproductive rate and the amount of forest necessary for 50% probability of occurrence.

Emigration from habitat patches has also been predicted to affect the amount of habitat at the extinction threshold (Pagel and Payne 1996). Movement between habitat patches is needed for recolonization of patches in which local extinctions have occurred (Hanski *et al.* 1995, Britton *et al.* 2001). For example, Speight (1989) has suggested that many forest remnants in the United Kingdom lack many species of saproxylic beetles even 200-300 years after being isolated because the distance to any source of colonizers is too great compared to the movement distances of the beetles. Dispersing individuals may also prevent local extinctions through a rescue effect (Brown and Kodric-Brown, 1977). Therefore, movement through non-habitat areas is predicted to restock or replenish declining populations, thereby lowering the amount of habitat necessary for persistence.

In contrast, in a simulation study Fahrig (2001) found that increasing the emigration rate leads to an increase in the amount of habitat needed for population persistence. This increase in the extinction threshold was due to the increased mortality associated with movement through non-habitat ("matrix") areas (Fahrig 2001). The amount of habitat at the extinction threshold was further increased by emigration when the probability of mortality in the matrix was increased. Therefore this model predicts that species with a high probability of emigration from habitat patches will require more habitat in the landscape for persistence, or a higher extinction threshold, than species with a low probability of emigration from habitat patches. This difference will be greater in landscapes that contain a more hostile matrix. Baillie *et al.* (2000) found that their

spatially-explicit, deterministic model predicted that emigration from forested habitat would have a negative effect on bird populations, especially when the chance of finding other high quality habitat was lowered. Because emigration has been predicted to have both negative and positive effects on population persistence, determining the effect size and direction for real species should be a conservation priority.

Habitat fragmentation within a landscape may also have an effect on the extinction threshold (Hill and Caswell 1999, With and King 1999). Habitat fragmentation had a weak positive effect on the amount of habitat necessary for persistence in Fahrig's (2001) simulation study. Organisms that live in highly fragmented habitat may have a low probability of colonization and population rescue. In an extreme case, the patches in such a landscape may become completely isolated so that the individual patches are not colonized following local extinctions. This may be happening to saproxylic beetle species in the United Kingdom; there are few species in forest remnants that have been isolated for 200-300 years (Speight 1989). Nilsson and Barnowski (1994) warn that click beetles (Coleoptera: Elateridae) are unlikely to recolonize patches that experience local extinctions if they are isolated by more than 10km from a suitable source habitat. Habitat fragmentation has probably been responsible for local extinctions of several species of ground beetles with low dispersal ability from heathland fragments within several decades of isolation (de Vries *et al.* 1996).

Studies of the effects of habitat fragmentation are usually confounded by the effects of habitat loss (Trzcinski *et al.* 1999, Fahrig 1997). In most studies, landscapes that are more fragmented also have less habitat. The isolation effects mentioned above are caused by the removal of the habitat between the remaining fragments, and not necessarily by

fragmentation *per se* (Fahrig 1997). The correlation between habitat loss and habitat fragmentation may lead to misguided management if fragmentation is perceived to be an important determinant of species persistence after habitat loss is accounted for when this is not, in fact, correct. It is important to know whether the configuration of habitat resulting from habitat loss can help mitigate that loss (Fahrig 1997). I therefore looked for the effects of fragmentation after accounting for habitat amount.

The purpose of this study was to test the effects of reproductive rate, emigration, and fragmentation on extinction thresholds using abundance data on saproxylic long-horned beetles (Coleoptera: Cerambycidae). I predicted that the effect sizes would be ordered reproductive rate > emigration > fragmentation, following Fahrig's (2001) simulation study results. Determining whether extinction thresholds are a real pattern in species response to habitat loss is important if conservation efforts are to be successful because this would indicate that additional incremental losses of habitat may lead to extinction rather than a small incremental reduction in a population with an associated small increase in the probability of extinction. As well, it is important that we understand how the characteristics of different species and landscapes affect the extinction threshold in order to predict the effects of habitat loss and to guide conservation efforts.

4.2 METHODS

I found the amount of habitat at the extinction threshold for 12 species of saproxylic (dead-wood feeding) long-horned beetles. The extinction threshold was defined as the lowest proportion of forest for which the species was present (Eriksson and Kiviniemi

1999). I only used species that have larvae that can develop within many different species of dead wood to ensure that the amount of forest was a good measure of the amount of habitat available to these species. Using only these species also avoided the possible confounding effect of more specialized species being more prone to extinction (McKinney 1997, Kotze and O'Hara 2003). The forest measurements were collected using digital topographical maps (National Capital Commission 1999) within ArcView GIS (ESRI Corp., Redlands, California, USA).

The results of Chapter 2 demonstrate that each beetle species responds to forest habitat at a different characteristic scale. The characteristic scale of response refers to the scale (radius of circular area around a sampling site) at which the species responds most strongly to the amount of forest habitat. Therefore, in this study the forest that is available to each species was measured at the scale appropriate for that species (table 2.1). Figure 4.1 shows the abundance of each species across the range of forest habitat proportions, with this proportion measured at the characteristic scale of response for each species. I wanted to include small treed patches and fencerows when measuring fragmentation, so digital 1:15000 colour air photographs (City of Ottawa 2000) were used to digitize all treed patches that were not included in the original digital topographical maps (National Capital Commission 1999) using ArcView (ESRI Corp., Redlands, CA). Fencerows were digitized as continuous features whenever the canopy gaps (in direction of fencerow) were less wide than twice the canopy width (perpendicular to fencerow) at the gap. All treed fencerows and small treed patches within 2km of the trapping sites were digitized. We then created 2 separate forest habitat coverages ("themes" in ArcView) with which to measure fragmentation: one with all originally mapped forest patches, plus the smaller

patches that we digitized, and one that further included all treed fencerows. Within each coverage we merged all contiguous and overlapping patches and fencerows. Therefore two patches joined by a fencerow were considered a single patch.

The reproductive rate for each species was determined by dissecting 20 female beetles of each species and counting the number of developed eggs. I used the maximum number of eggs rather than the mean because some beetles would have already oviposited some eggs and this was not possible to determine from the dissections. Reproductive output should also include generation time (or number of clutches per year for some taxa). For the 3 species for which I was able to find this information in the literature the generation time was 1 year. I assumed a generation time of 1 year for the remaining nine species and used the natural logarithm of the maximum egg production as a relative index (“reproductive rate”) of population growth rate. Cerambycidae species were classified as emigrating outside forest habitat patches or remaining within forest habitat in Chapter 3 (table 3.1). In this study I used flight intercept traps, and in an earlier study (Holland *et al.*, in revision) I used Lindgren multiple funnel traps, both placed outside forest patches, to catch species emigrating from forest. In both cases this was done in areas where I was trapping within the forest patches as well and therefore knew which species were present. This allowed me to categorize 9 of the 12 species used here as emigrating or not emigrating. The other 3 species were not caught in the forest or matrix in areas with non-forest traps, and so these species could not be classified.

Each species was used as a data point in my analyses. Extinction threshold was the response variable. To test the prediction of the effect of reproductive rate on extinction threshold I used linear regression analysis. To test the effect of emigration from forest on

the extinction threshold I used a two-tailed t-test (assuming unequal variance) to compare the proportion of forest at the extinction threshold for species caught moving outside forest habitat and those caught only within forest. I tested the effects of these two variables separately because the lack of movement data for 3 of the species meant these could not be included in a multiple linear regression. Using a multiple linear regression with the remaining 9 species would have resulted in very low power to detect an effect of reproductive rate, but I did use multiple regression analysis to check the emigration results after taking reproductive rate into account.

A possible confounding factor in the analysis of the effect of emigration is the difference in commonness among the different species. If all species are caught in direct proportion to their relative numbers and not because there is a real difference in movement, this would lead to the more common species being assigned to the “species moving” category despite the lack of a difference. To see if this was occurring I conducted a two tailed t-test (assuming unequal variance) to compare the mean total number of individuals caught in the moving and not moving categories.

I used the Effective Number of Habitat Patches to measure forest fragmentation (Jaeger 2000, Jaeger 2002, Jaeger *et al.* in prep.). The formula for this is: $1 / (\sum (A_i/A_t)^2)$, where A_i is the area of habitat patch i , and A_t is the total area of all habitat patches. Conceptually, this measures the probability that any two points randomly placed in the habitat will occur in the same habitat patch. The Effective Number of Habitat Patches was calculated by measuring the proportion of habitat within a given radius of the trapping sites represented by each forest patch, using a custom ArcView script (D. Patterson, pers. comm.). The fragmentation both with and without fencerows was

calculated at spatial scales of 20m - 200m in 20m increments, and 400m - 2km in 200m increments. I compared the range of values of the fragmentation values across all scales both with and without fencerows included. Both these measures of fragmentation had a relatively large range of values at 1400m so I used this as the scale at which to compare the effects of habitat amount and fragmentation. The tests for the effect of fragmentation included the proportion of habitat at 1400m (radius around trapping sites) and the fragmentation at 1400m. To test for effects of habitat amount and fragmentation I used multiple logistic regression with occurrence as the response variable and habitat amount and fragmentation at 1400m as predictor variables. I included species as a class variable. The measures of fragmentation with and without fencerows were highly correlated (Pearson $r=0.87$) so I used 2 models, each including one of these. Therefore one logistic model had occurrence regressed on species, habitat at 1400m, and fragmentation measured including fencerows at 1400m, and the other logistic model had occurrence regressed on species, habitat at 1400m, and fragmentation measured without fencerows at 1400m. These tests had inflated power because they used data from all 190 plots despite the fact that the measured predictor variables were not from spatially-independent areas at the 1400m scale. I adjusted the results for this by applying a correction factor to the standard error of the estimates before calculating the Wald statistic and testing for significance. At 1400m, randomly sampling spatially independent sites (separated by at least 2800m) yields an average of 18 sites possible (figure 2.3). I therefore multiplied the standard error values by $(190/18)^{1/2} = 3.249$.

4.3 RESULTS

The proportion of forest at the extinction thresholds for the 12 species ranged from 0.0476 to 0.9897 (table 4.1) forest cover. The maximum number of eggs per female within a species ranged from 9 to 236, corresponding to reproductive rates of 2.20 to 5.46 (table 4.1). There was a significant negative effect of reproductive rate on the extinction threshold (figure 4.2, $R^2=0.617$, $F=16.1$, $df=11$, $p=0.0025$). Species with higher reproductive output were able to persist in areas with less forest habitat, as predicted. This relationship explained 61.7% of the variance in the extinction threshold values. This relationship was not driven by an extreme value. I redid the regression analysis 12 times, each time with a different point removed. The relationship was always significant, and the R^2 value remained well above 0.5 for all regressions.

The mean number caught (in all traps, not just emigration traps) and associated standard errors of the emigrating and not emigrating categories were 40.0 ± 11.0 and 46.1 ± 13.8 respectively. This test clearly showed that the species assigned to the emigrating category were not more common than those in the non-emigrating category ($t=0.371$, $df=5$, $p>0.3$). Therefore the difference in the probability of emigration from forest between the two groups is real, and not simply driven by a difference in commonness. The t-test revealed a significant difference ($t=3.935$, $df=7$, $p=0.0056$) in the extinction thresholds between the species I caught moving and those not caught moving outside forest habitat (figure 4.3). The species that were caught moving had lower extinction thresholds. To ensure that this result held after accounting for reproductive rate, I used a multiple linear regression with emigration and reproductive rate as predictors of the extinction threshold. Despite the lowered power of this analysis,

reproductive rate remained a strong predictor of the extinction threshold amount of habitat, but emigration was not significant.

The two logistic regressions of occurrence on habitat amount and fragmentation were done with all 190 sites, and then the test statistic was corrected by multiplying the standard error by a factor of 3.249 before calculating the Wald statistic to reflect the number of spatially-independent sites that could be chosen. The model that included had fragmentation calculated with fencerows was not significant even before correcting for the number of spatially-independent trapping locations and was not analyzed further. The model that had fragmentation not including fencerows was significant initially so the test statistic adjustment was applied. After adjusting the Wald statistics for the possible number of spatially independent sites, fragmentation measured without fencerows was not significant (Wald=1.0566, df=1, $p>0.3$) while habitat amount was still a marginally significant positive predictor (Wald=3.8075, df=1, $p=0.051$) of occurrence.

4.4 DISCUSSION

The results support the prediction that reproductive rate has a strong negative effect on the extinction threshold amount of habitat (Fahrig 2001). Species with low reproductive rates were only found in landscapes with a large proportion of forest remaining, whereas species with higher reproductive rates were found in landscapes with less forest habitat remaining. This result implies that, as habitat is lost in a landscape, species with lower reproductive rates experience local extinctions before species with higher reproductive rates. This agrees with the empirical study of forest breeding birds by

Vance *et al.* (in press). They found that the amount of habitat at which species had a 50% probability of occurrence decreased with an increase in reproductive rate. Similar to my study, their results imply that species with lower reproductive rates will become locally extinct first as habitat is lost.

Had we used an arbitrary spatial scale to determine the extinction threshold we would have missed the reproductive rate-extinction threshold relationship, even if the scale chosen was suitable for some of the species. To test this idea I arbitrary chose a 1km scale, and measured forest and plotted the abundance of each species against the proportion of forest within a 1km radius. I again considered the extinction threshold to be the minimum proportion of forest at which a species occurred, with the forest being measured at the 1km scale for all species. A regression of the extinction thresholds against the reproductive rate of the species now reveals a much weaker relationship (figure 4.4). The variance explained by this regression is about one-fifth that explained by the relationship that I found by using the characteristic scale of response for each species ($R^2=0.121$, $F=1.378$, $df=11$, $p>0.2$). The non-significance of the results obtained using the same arbitrary 1km scale for all species would have led to the conclusion that reproductive rate does not have an effect on the extinction threshold. The difference between this result and that found using the characteristic scale of response for each species underscores the importance of conducting studies at an appropriate spatial scale for the species under study. In studies with more than one species, using the same scale for all species may further obscure trends that actually exist. In my study the wide range of spatial scales at which the different species responded to forest habitat (table 2.1) shows that any scale would have weakened our ability to find the reproductive rate-

extinction threshold relationship if we had applied it across all species. Therefore the determination of the scale of response is an important step to discovering ecological relationships.

Vance *et al.* (in press) used the same spatial scale for all species in their study of forest breeding birds. Interestingly, the variance explained by the reproductive rate-habitat necessary regression in their study ($R^2=0.16$) is very close to the value I obtained when using a constant scale for all species ($R^2=0.121$). This suggests that the magnitude of the reproductive rate effect on the extinction threshold amount of habitat may be similar in different taxa. It seems likely that they would have found an even stronger effect if the habitat necessary for 50% probability of persistence had been measured at the characteristic scale of response for each species. Although the variance explained in their study is only slightly higher than in my results with a constant scale, they did find a significant effect of reproductive rate this way, probably because they had a larger number of species ($n=41$).

My results indicate that species prone to emigration out of forest habitat may have a lower extinction threshold than species that do not move out of forest habitat. However this result did not hold in the (admittedly low power) multiple regression with reproductive rate. It is possible that the increase in non-forest area does not lead to an increase in mortality during movement for the species that move out of forest. The idea that non-habitat matrix is completely hostile is an ideological artifact of island biogeography (D'Eon 2002) and does not always apply to species moving between terrestrial habitat patches (Huxel and Hastings 1999). As adults, many species of long-horned beetles eat pollen and nectar (Yanega 1996, Dajoz 2000) and are commonly found

on flowers of shrubs and herbaceous vegetation in fencerows (Samways 1994) and other non-forest habitats. For species that are commonly found feeding as adults within non-forest habitat, movement into non-forest areas may actually increase survival of these species. Some species have evolved either mimicry or cryptic colouration (Yanega 1996), suggesting that they are at least partially adapted to predators. Laurance (1991) found that the extinction proneness of 66 species of rainforest mammals was negatively related to their tolerance of the matrix.

It is also likely that species that move outside forest to obtain floral resources are more likely to recolonize forest patches that experience local extinctions than are species that do not readily move through non-forest areas. Females of species that move outside forest must locate suitable larval habitat for laying eggs. Shibata (1987) has found evidence to suggest that species of long-horned beetles that must move to find food and then oviposition sites disperse farther than species that are not required to do so. It is very likely that in these species, females lay eggs in a forest patch other than the one they are from. Therefore, the species that leave forest habitat likely have higher rates of patch recolonization and higher rates of rescue from low numbers than species that do not move outside forest habitat. Unfortunately, we were not able to reliably separate the effects of reproductive rate and emigration to test the effect of emigration.

In the long-horned beetle species I used for this study there was a strong positive correlation between the body size and the reproductive rate ($r=0.843$). Therefore, there is a chance that the strong relationship I found between reproductive rate and extinction threshold is in fact driven by some other factor that scales with body size. The only reasonable hypothesis I can come up with is that there may be a negative relationship

between the body size and extinction threshold because larger beetles move further. Greater movement could allow species to avoid isolation effects help avoid local extinctions. This seems reasonable given the result that larger species respond to habitat at larger characteristic scales (chapter 3). We did not, however, find that species that moved out of forest habitat necessarily responded at larger spatial scales. To reliably look at the relative contributions of movement and reproductive rate to lowering the extinction threshold I would need quantitative data on the distances that different species moved. In the meantime, the strong correlation between body size and the reproductive rate should be borne in mind when considering the result that species with greater reproductive rates have lower extinction thresholds.

My results show that fragmentation is not important in determining the occurrence of these species. In this test I gave considerable weight to the fragmentation variable by conducting the multiple logistic regression at a spatial scale where the range of fragmentation values was greatest. In fact, they had a much greater range than did forest habitat amount at this scale; but habitat amount was still a marginally significant predictor of occurrence while fragmentation was not. This result agrees with other studies that have found that habitat amount is much more important than habitat fragmentation (McGarigal and McComb 1995, Trzcinski *et al.* 1999). Conservation efforts directed at these species should focus on habitat retention (Fahrig 1997), and should not be misguided by the idea that configuration can ameliorate habitat loss.

Measuring habitat to determine the extinction threshold must be done carefully for “interior” species. The edges of a patch that are not suitable habitat for the species must not be included in the measurement of habitat. Obviously, a simple measure of forest

cover will not be sufficient for a forest interior species. If the width of the unusable edge is large relative to the characteristic scale of response, taxa that respond to habitat at relatively small scales may seem to have very high extinction thresholds only because they are “interior species”. This could cause the species to seem to occur only in areas that are surrounded by close to 100% forest “habitat”, but only because the edge is not properly included in the measurement of the amount of habitat (Fahrig 1997). Any studies that report extinction threshold amounts of habitat should also report the spatial scale at which the habitat was measured while determining this threshold. Researchers studying interior species should be aware of the possibility of such “false” extinction thresholds. While such responses are more correctly viewed as a response to habitat type, they could still provide information on suitable conditions for the species of concern. This was not a problem in the present study, as none of the long-horned beetles in this study have been described as interior species to my knowledge. Eight species considered here responded at small scales (arbitrarily designated as up to 200m), but within these species the observed extinction thresholds ranged from 0.0478 to 0.9897. The only species with a small characteristic scale of response and a high extinction threshold was *Liopinus alpha* (Say).

One species (*Liopinus alpha* (Say)) had a very high extinction threshold and was also relatively rare based on our trap catches (figure 4.1). It could be that this species was not caught in lower habitat cover areas as often as others by random chance simply because it is rare (Didham *et al.* 1998). It may at first seem reasonable to weight the regressions so that species with more data (caught at more locations here) have more bearing on the analysis. However, we do not know if the species is rare because of habitat loss, or if it

was rare before habitat loss occurred. If less weight is put on species which have few catches, and these species also have high extinction thresholds, the analysis could be biased if habitat loss, and consequent local extinctions, has been the cause of rarity. The fact that the rarest species in this analysis had the highest extinction threshold suggests that habitat loss may have been the cause of this species' rarity. Future studies may be able to guard against the possibility of false extinctions in rare species by increasing sampling effort in areas where the species is not initially found.

Ideally, studies that compare some ecological trait across many different species should take phylogeny into account because species responses may be driven because of many correlated traits (Harvey and Pagel 1991). This problem can be addressed using methods such as independent contrasts (Harvey 1996) if the necessary phylogenetic data are available. Unfortunately, detailed phylogenetic data does not exist for my species below the tribe level. This should not be a large problem in my case however, because the species used are spread over 3 tribes, and all come from different genera.

My findings show that the minimum amount of habitat required for population persistence depends on life history attributes of the species. Species with greater reproductive rate occurred in landscapes containing less forest habitat than species with lower reproductive rates. Relationships between species and their environment are obscured if the scale of investigation is not relevant to the species being studied. I suggest that the first step in such studies should be the determination of the spatial scale at which the studied relationship is relevant.

Figure 4.1: Determining the extinction threshold for the Cerambycid beetle species. The number of individuals caught at each sampling sites is plotted against the proportion of forest within a specific radius of the site. The radius of forest measurement equals the characteristic scale of response to forest habitat for that particular species. The arrow indicates the extinction threshold amount of habitat for each species.

Table 4.1: Reproductive rate, emigration, extinction threshold and characteristic scale of response data for the 12 polyphagous cerambycid beetle species. Reproductive rate is the natural logarithm of the maximum egg count.

Species	Maximum eggs	Reprod. rate	Emigrate?	Extinction threshold	(radius,m) Scale of resp.
<i>Bellamira scalaris</i> (Say)	236	5.46	N	0.231	1000
<i>Evodinus m. monticola</i> (Rand.)	37	3.61		0.4707	160
<i>Gaurotes cyanipennis</i> (Say)	101	4.62	N	0.413	160
<i>Liopinus alpha</i> (Say)	10	2.30		0.9897	20
<i>Microgoes oculatus</i> (LeC.)	20	3.00	N	0.6409	60
<i>Stictoleptura c. canadensis</i> (Oliv.)	160	5.08	Y	0.1014	1600
<i>Strangalepta abbreviata</i> (Germ.)	40	3.69	N	0.3685	120
<i>Strangalia luteicornus</i> (F.)	9	2.20		0.4973	800
<i>Trachysida mutabilis</i> (Newm.)	80	4.38	N	0.0476	1200
<i>Trigonarthris minnesotana</i> (Csy.)	152	5.02	Y	0.0478	200
<i>Urgleptes signatus</i> (LeC.)	14	2.64	N	0.5461	140
<i>Urographis fasciatus</i> (DeG.)	58	4.06	N	0.5589	180

Figure 4.2: Relationship between reproductive rate and the extinction threshold. Each of the twelve species had the extinction threshold determined at the spatial scale that it responds most strongly to forest habitat, the characteristic scale of response to forest habitat.

Figure 4.3: Comparison of extinction thresholds of species caught outside forest habitat (N=2) and species not caught outside of forest habitat (N=7). The species caught outside forest habitat had a lower mean habitat amount at the extinction threshold. Note: emigration was not significant when included in a multiple linear regression with reproductive rate as a second predictor variable.

Figure 4.4: Relationship between the reproductive rate and the amount of forest habitat at the extinction threshold when an arbitrary 1km scale is used for all species. The extinction threshold was determined by plotting the abundance against the proportion of forest within 1km of the sampling site for each species. This relationship is not significant when analyzed at this scale.

CHAPTER 5

GENERAL CONCLUSIONS

5.1 HABITAT LOSS AND SPECIES PERSISTENCE

Habitat loss is important in determining local extinction in the studied species of long-horned beetles. Figure 4.1 shows that all 12 species were found at high forest cover areas, but had some critical amount of forest cover below which they were no longer found. Other studies have found that habitat loss is important in determining local extinction in beetles (Klein 1989, Hanski and Ovaskainen 2002). Such knowledge is important because if the aim of conservation is to conserve the largest number of species possible then these efforts should be largely aimed at conserving insect populations (Major *et al.* 2003). It is evident that retaining beetle habitat is an important part of conserving species. Saproxylic beetles are important agents of nutrient recycling in forest ecosystems (Gutowski 2002) and should be considered when managing forest habitat (Maeto *et al.* 2002).

My results show that generalizations are possible in terms of the spatial scales at which species respond to forest habitat (Chapter 3) and with the amount of habitat at the extinction threshold (Chapter 4). Body size is a strong positive predictor of the scale at which species respond to forest habitat and reproductive rate is a strong negative predictor of the extinction threshold. These are relatively easily measured quantities compared to the collection of detailed demographic data. These could therefore be useful in the conservation and monitoring of populations of species. The relationship between

reproductive rate and extinction threshold suggests that conservation efforts should be focussed on species with low reproductive rate because these will most likely be most at risk from habitat loss. The increase in the characteristic scale of response with body size suggests that when monitoring a species the spatial scale that should be used to detect populations trends will scale positively with body size. My results also stress the importance of using the correct spatial scale for such endeavors. Côté and Reynolds (2002) stress the need for knowledge of such relationships of easily measured parameters and risk of extinction. The strong relationship between reproductive rate and extinction threshold could be especially useful in prediction of the effects of habitat loss on different species.

An especially interesting result is the very similar values for the variance explained between our study (when done at a spatial scale of 1km^2) and that obtained by Vance *et al.* (in press) for forest breeding birds. It would be interesting to see if the variance explained by their relationship between reproductive rate and the habitat necessary for a 50% probability of occurrence, with this probability measured at the characteristic scale of response for each species, is similar to the value of 61.7% that we obtained. I would at least predict that the R^2 value would greatly increase because of the increased ability to detect the relationship. Regardless, the similarity of the R^2 values does suggest that there may be a common effect size of reproductive rate on the extinction threshold. Such general relationships are very important in the conservation of biodiversity because it is already impossible to conduct detailed studies for all the species currently listed as threatened by habitat loss (Lawton *et al.* 1994, With 1997). These lists are probably not comprehensive (Côté and Reynolds 2002), especially for insect species, so conservation

efforts will require some general guiding principals such as trends found here because of the staggering numbers of species actually at risk of extinction. I would suggest that reproductive rate is of primary importance when comparing the extinction risk faced by different species because of habitat loss.

5.2 THE IMPORTANCE OF SPATIAL SCALE

My results show that the characteristic scale of response increases with an increase in body size. A similar result has been found by Roland and Taylor (1997) for parasitic fly species responding to forest fragmentation. I predict that this is a general effect that will be found in many taxa. I plan to use data on different taxa to test this idea in the future. It will be especially interesting to see if it is also found in vertebrate groups.

My results show that the spatial scale at which ecological investigations are carried out can have a large impact on the ability of such studies to reveal important relationships. Different beetle species did respond to habitat at different scales (Chapter 2), and using these spatial scales allows ecological relationships to be uncovered (Chapter 3 and 4). Using an inappropriate spatial scale can result in a real ecological relationships being missed by the researcher (Chapter 4). The relatively smooth curves in figure 4.1 suggest that the idea that the strength of the underlying ecological relationships lessen as the spatial scale is shifted away from the scale at which they operate is correct.

It may seem that first doing a multiple-scale analysis to find the spatial scale at which a species responds most strongly and then continuing to investigate relationships at this scale is somehow compromising the analysis. This is not so because we are not actually

hypothesis testing at this stage. The measures of model fit that are used to find the scale of response are actual measures, just as the equation of the best fit line is fixed given some set of data points. There is no need to apply a correction for multiple tests because I am not actually testing a hypothesis; I am simply looking for the scale that maximizes this model fit. It is not until I use the different scales, or extinction thresholds, as data points in an analysis that I am actually hypothesis testing and then must apply the rules of statistical analysis. This is an effective way of advancing ecological research because the analysis focuses on the spatial scale where the relationship should occur if it is in fact real. If the relationship is not found here, then it is very likely not going to be found at any scale, or at least not at any scale that was covered by the initial multi-scale analysis. Looking for ecological relationships at an inappropriate scale is a waste of time and resources, although many studies have been done at spatial scales that are not relevant to the study question (Cale and Hobbs 1994).

Scientific hypotheses that cannot be rejected are not useful (Platt 1964). Focusing on the spatial scale at which a relationship should be at its strongest allows ecological hypotheses to be rejected outright. Obtaining insignificant results using an arbitrary spatial scale can always beg the question of whether the relationship is in fact present, but the spatial scale was not appropriate to identify it. Therefore I would suggest that ecological questions can almost always be improved by first identifying the spatial scale at which the relationship should be operating and then doing analyses at this scale. This can help ensure that ecological hypotheses are refutable and thereby streamline ecological research.

5.3 IMPLICATIONS

The strength of the relationships between body size and scale of response to habitat, and between reproductive rate and extinction threshold along with similar results from other researchers suggest that these may be useful “rules” for comparing the scale of response and the extinction risk of many different species. In addition to the general trends discussed above, I also found the extinction thresholds for the 12 long-horned beetle species. These values are the habitat required for persistence at the characteristic scale of response to forest habitat. This does not imply that what happens to forest habitat outside of the scale of response does not have an impact on the persistence of these species. While it may represent something about the scale and habitat amount necessary for a local population, these cannot persist for long if separated from other habitat by inhospitable non-habitat (Baillie *et al.* 2000, Davies *et al.* 2000). The individual extinction thresholds do however have obvious utility in the conservation of these species. As well, the characteristic scales of response can be used in further studies of these species, as they indicate the spatial scale at which forest habitat amount should be measured.

With a method of determining the characteristic scale of response to habitat and the extinction threshold analyses such as the ones present here for Cerambycid beetles, these can be determined for a great many species. Most of the information necessary for this probably already exists for many. There are many estimates of abundance and occurrence of species in the literature. As long as there are exact locations associated with the survey data, remote sensing and GIS can be used to obtain the necessary habitat data. Therefore,

such estimates of extinction threshold should be easily obtainable for many species, as long as the survey data exists and the habitat can be measured using GIS.

The result that forest fragmentation was not important shows that conservation efforts should be focused on maintaining and restoring habitat rather than with trying to manage landscapes for an optimal configuration for these species. As discussed in chapter 4, this is probably because the adults of many species use resources in the “matrix” and are likely to move between different forest patches. It would be interesting to test the effect of fragmentation on a set of species that all tend to remain within forest, but our small sample size of such species precluded this. The result that fragmentation is not important in persistence is in agreement with the predictions of Fahrig (1998). This modeling study predicts that configuration of habitat will only be important when the mortality within the matrix is much higher than the mortality in the habitat. Since many species of long-horned beetles appear to be adapted to using resources in the matrix the mortality here might not be greatly inflated compared to the mortality in the forest habitat.

The information on the scale of response to habitat and the extinction threshold could be useful in the future for efforts other than conservation. For example, if one of these species became an introduced invasive species elsewhere this information could help guide control efforts. The information on the characteristic scale of response to forest could help the design of monitoring for the species and in uncovering relationships between the species and forest habitat. The extinction threshold value could be useful in delineating areas where there is enough forest habitat for the species to become established.

APPENDIX A

HABITAT AND BEETLE DATA

MICROSOFT EXCEL FILES ON 3.5" DISC

Cerambycid abundance.xls: Abundance data for all species of Cerambycidae that use dead wood and were caught at at least 5 of the trapping sites. Separate worksheets contain abundance catch data and presence/absence data (occurrence). A third worksheet contains the full scientific names and authors that correspond to species codes used on the first two worksheets, and whether or not each species is among the 12 polyphagous saproxylic species used in these studies.

Forest proportions.xls: The proportion of forest habitat around each beetle trapping site measured within different radii, from 20m to 7km.

Fragmentation no fencerows.xls: Effective number of habitat patches index measured around each beetle trapping site after adding all small woodlots but not fencerows. This was calculated within radii from 20m to 2km.

Fragmentation with fencerow.xls: Effective number of habitat patches index measured around each beetle trapping site after adding all small woodlots and treed fencerows. This was calculated within radii from 20m to 2km.

Plot-plot distance matrix.xls: Symmetric matrix of distances from each beetle sampling plot to every other beetle sampling plot. Distances are in metres.

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