EDITED BY

JIANGUO LIU
MICHIGAN STATE UNIVERSITY

WILLIAM W. TAYLOR
MICHIGAN STATE UNIVERSITY

Integrating Landscape Ecology into Natural Resource Management

2002

JULIE M. BRENNAN, DARREN J. BENDER, THOMAS A. CONTRERAS,
AND LENORE FAHRIG

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Focal patch landscape studies for wildlife management: Optimizing sampling effort across scales

3.1 Introduction

With ever-increasing loss and degradation of wildlife habitat, wildlife management decisions depend on a solid understanding of the influence of both patch characteristics and landscape structure on populations. Appropriately designed multi-scale ecological studies are becoming more and more important in determining how current and future land-use management decisions will affect the survival of natural populations. Effective management plans for populations and regions depend on clear and interpretable results from properly designed studies.

Historically, researchers designed studies to examine the effects of patch-scale characteristics on population dynamics. A patch is defined as a discrete area of contiguous and homogeneous habitat. Patch-based ecological studies address the relationship between the inherent characteristics of the individual patches (e.g., patch size, patch quality, patch isolation) and some ecological pattern (e.g., distribution and abundance of organisms) or process (e.g., dispersal, disturbance regimes, predation, or competition) (e.g., reviews by Andrén, 1994 and Bender *et al.*, 1998).

Recently, researchers have begun to recognize the importance of considering the effect of the landscape context of the patch. A landscape-scale ecological study addresses one or more of (1) the effect of landscape structure on the distribution and/or abundance of organisms, (2) the effect of landscape structure on an ecological process(es) (e.g., animal movement), or (3) the effect of ecological process(es) (e.g., fire), or organisms (e.g., beavers; see Johnston, 1995), on landscape structure. Landscape structure implies spatial heterogeneity, which is described in terms of landscape composition and configuration. Landscape composition is the amount of the different landscape elements (e.g., habitat types, road cover) in the landscape. Landscape configu-

ration describes the spatial arrangements of these elements. Without examining the influence of the landscape context in which patches and populations are embedded, it is impossible to assess how changes in the properties of a landscape will affect populations. Studies that examine effects at several spatial scales have suggested the importance of considering landscape factors as well as local or patch factors for successful wildlife management planning (Jokimaki and Huhta, 1996; Findlay and Houlahan, 1997; Sisk *et al.*, 1997; Saab, 1999; Pope *et al.*, 2000).

However, the very nature of landscapes, i.e., their potential complexity and size, can make the definition of landscapes and the design of landscape-scale studies difficult (Allen, 1998; Goodwin and Fahrig, 1998). If landscapes are defined inappropriately and/or the designs of studies are improper, unsuccessful management recommendations may follow from these studies. The purpose of this chapter is to provide guidelines for the design of sampling strategies for landscape-scale studies. These guidelines will assist managers in critically evaluating the studies on which they base their management decisions. We first discuss how to define landscape size relevant to the pattern or process being studied or question being asked. We then address the decision-making process required when designing a multi-scale landscape study and selecting landscapes best suited for answering a particular question. Finally, we provide information on the tools currently available for measuring and analyzing differences in spatial pattern and other landscape properties between sample landscapes, and address some of the data considerations unique to a landscape-scale ecological study.

3.2   How big is a landscape?

In landscape ecology, ecological patterns and processes are defined and studied within the context of a landscape. It is therefore important to define both the functional and physical size of a landscape for a particular study. The size of landscape determines how a researcher or resource manager will interpret observations and assess the impact of spatial pattern on populations.

Landscapes are often defined as a geographical region that has a particular heterogeneity of cover types (Forman and Godron, 1986; Wiens, 1992). However, this definition is based on a human perception of heterogeneity (Allen, 1998; Goodwin and Fahrig, 1998). Since ecological patterns and processes occur over a wide range of scales, the size of a landscape should in fact be tied to the scale of the pattern or process under study. For example, a single hectare of forest may represent a heterogeneous landscape for a species of ant, whereas a fire ecology study conducted in a 1000-ha continuously forested area

should not be considered a landscape-scale study if the area is homogeneous with respect to the process(es) studied. Landscapes are therefore "relative" entities, with the scale and heterogeneity of a landscape being determined by the scale and heterogeneity relevant to the question being asked and the ecological process under consideration (Wiens, 1989; Fahrig and Grez, 1996; King, 1997; Allen, 1998; Goodwin and Fahrig, 1998).

We suggest two criteria for defining the scale of landscapes: (1) what is the hypothesis concerning the relationship between landscape structure and the ecological response of interest? and (2) what are the relevant processes and at what spatial scale do they occur? For example, Henein *et al.* (1998) used empirical data and simulation models to study how the life-history characteristics of two forest species, Eastern chipmunk (*Tamias striatus*) and white-footed mouse (*Peromyscus leucopus*), affect their responses to differences in landscape connectedness. Henein *et al.* (1998) found that chipmunk movements through a landscape were restricted by the amount and configuration of both forest patches and wooded fencerows. White-footed mice, on the other hand, were found to be habitat generalists. Their movements are much less dependent on the amount and configuration of forest patches or wooded fencerows and they range much more widely. From a design perspective, this affects the size of sample landscapes required to assess differences in mouse and chipmunk population responses to landscape structure. The scale of landscape appropriate for assessing effects of landscape pattern on chipmunk populations is smaller than the scale required for white-footed mice in the same region. Therefore, the interaction of ecological processes with landscape heterogeneity will determine the scale of a study. In the above example, a lack of knowledge of dispersal or movement distances could result in inappropriate sampling designs and interpretation of results.

Recognizing that a particular landscape scale is appropriate does not always mean that landscapes of that size and type are available, particularly if a large number of sample landscapes is required. It may then be necessary to adjust sampling design to compensate for these problems (see section 3.4). Also, while it is difficult enough to determine the appropriate landscape scale for a single species, in many instances management of natural systems requires consideration of more than one species simultaneously. In these cases, functional groupings of species by habitat use and movement scale may be useful in determining appropriate landscape size (see Noble and Gitay, 1996). Most multi-species studies actually use a single definition of landscape scale (e.g., Findlay and Houlahan, 1997; Jonsen and Fahrig, 1997; Holland and Fahrig, 2000; A. J. McAllister, H. G. Merriam, and L. Fahrig, unpublished data). Since different species respond to habitat structure at different scales, the choice of landscape scale is somewhat arbitrary. When the appropriate

size of the landscape is not obvious (or perhaps even when it is), analyses should be conducted using several landscape sizes (e.g., Findlay and Houlahan, 1997; Pedlar *et al.,* 1997; Pope *et al.,* 2000; Langlois *et al.,* 2001), spanning the known or suspected range of appropriate scales for all the species in the study. The number and sizes of these landscapes will be discussed further in sections 3.4 and 3.6 (case study).

3.3   Importance of measuring multiple landscapes

Landscape ecologists often study the effects of landscape structure on the abundance or distribution of organisms. A landscape-scale study is therefore one that examines the effect of landscape context on an ecological response (dependent) variable. It answers the question: Does the structure of the landscape in which this observation is imbedded affect the observation's value? This question can be answered only by comparing the response variable across several landscapes with different structures. This comparison imposes a particular design on a landscape-scale study, where each data point represents a single landscape. The entire study comprises several non-overlapping landscapes having different structures and the appropriate size of each landscape is determined as described in the previous section. In the statistical analyses, measures of landscape structure are the predictor (independent) variables and measures of abundance and/or distribution are the response variables.

The use of non-overlapping landscapes is important for two main reasons. First, the researcher's ability to uncover effects of landscape structure on ecological response variable(s) depends on the sample landscapes covering a range of different structures. Since overlapping landscapes have similar structures, the range of variation in the predictor variables would be low, and the ability to detect relationships between landscape structure and ecological response(s) would also be low. Second, the use of non-overlapping landscapes reduces problems associated with lack of statistical independence of data points. Lack of independence results in inflated measures of statistical significance in parametric statistical tests.

Such a broad-scale sampling design, using individual landscapes as data points, may seem impractical. However, this constraint is lessening with increasing availability of remotely sensed data, allowing much easier measurement of landscape structural variables. Measurement of the ecological response variable across many landscapes usually presents a greater challenge, and we propose as a practical solution the "focal patch study," in section 3.4. Recent studies of effects of landscape structure on diversity, density, and/or distribution of organisms are listed in Table 3.1.

Table 3.1. *Examples of landscape-scale empirical studies*

Response variable	Number and size of landscapes	Landscape structure variables	Multiple landscape scales?	Major finding	Reference
Wetland species richness	30, 2-km radius	Road density, forest cover in landscapes	Yes	Species richness decreased with increasing road density and decreasing forest cover	Findlay and Houlahan (1997)
Species richness of specialist vs. generalist insects in alfalfa fields	26, 1-km radius	Habitat diversity in landscapes	No	Positive relationship between landscape diversity and insect diversity	Jonsen and Fahrig (1997)
Family richness of herbivorous insects in alfalfa fields	59, 1-km radius	Length of woody field border within landscapes	No	Positive effect of amount of woody border in the landscape on family richness	Holland and Fahrig (2000)
Bird species diversity, richness, evenness	29, 30–86 ha	Agricultural intensity in landscape	No	Negative relationships between agricultural intensity and bird species diversity, richness, and evenness	A.J. McAllister *et al.* (unpublished data)
Density of bird species	30, 250–300 ha	Amounts and configurations of habitat types	No	Most species showed strong density relationships with landscape composition (amounts of different forest types)	McGarigal and McComb (1995)
Relative density of raccoons (*Procyon lotor*)	57, 1-km radius	Amount of forest in landscape	No	Raccoon density highest at intermediate forest amount	Pedlar *et al.* (1997)
Relative density of	34, 1.5-km	Amount of forage habitat and	Yes	Leopard frog density increased	Pope *et al.* (2000)

Response	Sample	Predictor	Significant	Result	Reference
Relative density of leopard frogs (*Rana pipiens*) in ponds	34, 1.5-km radius	Amount of forage habitat and number of occupied breeding sites in landscape	Yes	Leopard frog density increased with amount of forage habitat and the number of occupied breeding sites in the landscape	Pope *et al.* (2000)
Presence/absence of forest breeding birds	94, 10 × 10 km	Amount and fragmentation of forest cover	No	Amount of forest cover had a much stronger effect than forest fragmentation on bird distribution	Trzcinski *et al.* (1999)
Presence/absence of hanta virus antibodies in deermice (*Peromyscus maniculatus*)	101, 4-km radius	Amount and fragmentation of deermouse habitat in landscapes	Yes	Significant quadratic (U-shaped) effect of habitat amount and a (smaller) significant positive effect of landscape fragmentation on distribution of the virus	Langlois *et al.* (2001)

Table 3.2. *Summary of multi-scale landscape study approaches based on the cost of measuring the response and predictor variables*

		Predictor variable cost	
		Low	High
Response variable cost	Low	**Ideal** – more well-studied patches – higher landscape sample size (see Fig. 3.1a)	**Multi-patch landscape study** – more well-studied patches – lower landscape sample size (see Fig. 3.1c)
	High	**Focal patch landscape study** – fewer well-studied patches – higher landscape sample size (see Fig. 3.1b)	**Not feasible**

3.4   Trade-offs in landscape study design

In the previous two sections we outlined the importance of conducting empirical studies at the appropriate landscape scale in many landscapes. Where the process of interest occurs at a small spatial scale, studies designed with these criteria in mind should be feasible. However, there can be logistic limitations, such as time, funding, travel, or number of personnel, to conducting multi-scale studies over a large area. For a given sampling effort, larger landscapes cannot be sampled as intensively as smaller ones. Furthermore, if a manipulative approach is required rather than an observational one, application of the "treatment" may not be feasible at a broad spatial scale, and creating the treatment condition may be impossible if it requires removing threatened habitat. For this reason, manipulative studies are difficult to conduct across many large landscapes; it is usually more feasible to conduct the study at a smaller spatial scale. Careful consideration must then be given to identifying an appropriate compromise among spatial scale, sampling intensity, replication, and degree of experimental manipulation to achieve the most reliable results as a basis for appropriate management decisions.

The appropriate trade-off between number of landscapes and within-landscape sampling intensity will depend on whether the cost of obtaining data is higher for the response variable(s) or predictor variable(s) (Table 3.2 and Fig. 3.1). When remotely sensed information can be readily obtained, variables describing landscape structure are usually more easily measured than those describing organism abundance/distribution. In this case statistical power is maximized by maximizing the number of landscapes sampled and minimiz-

ing the intensity of sampling within each landscape. When remotely sensed data are unavailable, the effort required to quantify the structure of each landscape is high, and the number of landscapes sampled will have to be smaller (Table 3.2.). In this case, statistical power can be improved with more intense sampling of the response variable within each landscape, thus reducing the error associated with the response variable.

Another factor to consider is how many scales to include in a study design. Data are collected at both the patch and the landscape scale as defined in section 3.2. However, there is always at least some uncertainty about the appropriate scale for a study because there is never perfect a priori information (e.g., animal movement ranges) from which to determine the appropriate scales. Assessing the influence of landscape structure on the response variable (Fig. 3.2) at several scales can allow one to determine the scale at which the landscape has the strongest influence. Where possible, we suggest the range of scales should cover from about an order of magnitude smaller to an order of magnitude larger than the scale thought a priori to be most appropriate for the process or species. For example, Findlay and Houlahan (1997) determined that wetland species richness was strongly correlated with forest cover and road density up to 1000 to 2000 m away. This distance was an order of magnitude higher than the existing 120 m buffer to protect wetland diversity established in government policy. In cases where landscape-scale measurements can be taken easily, this range can be broken into a large number of sampling scales, thus increasing the accuracy with which the most relevant scale can be determined.

The trade-off between number and size of landscapes and sampling intensity is evident from a comparison of two studies of the effects of landscape forest cover and fragmentation on forest breeding birds. McGarigal and McComb (1995) studied the abundance of breeding birds in 30 landscapes of 250–300 ha each, whereas Trzcinski et al. (1999) studied the presence/absence of forest breeding birds in 94 landscapes of 100 km² each. The smaller number and size (250–300 ha) of landscapes studied by McGarigal and McComb (1995) permitted them to conduct intensive sampling at each location (32–38 samples points for each landscape = 1046 sampling points) for each of 15 species of birds. In contrast, Trzcinski et al. (1999) were limited to using presence/absence Breeding Bird Atlas data resulting in a much less intensively studied response variable.

The trade-off between experimental manipulation and landscape size is illustrated in a study by Wiens et al. (1997). The authors created "mini-landscapes" that were mosaics of grassy patches and bare ground. Each landscape was 25 m², and five different landscape structures (treatments) were studied. The response variable was the movement behavior of tenebrionid beetles across the landscapes. Ten beetles in each of the five treatment areas

a

b
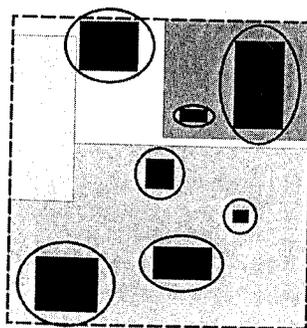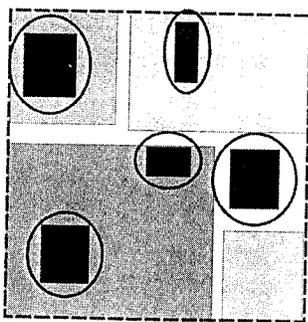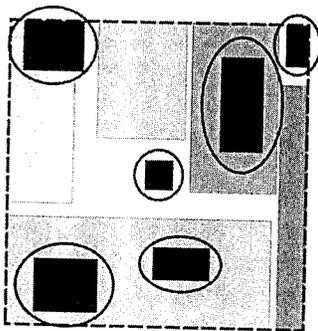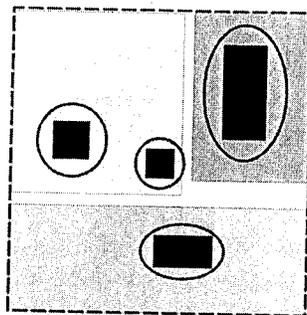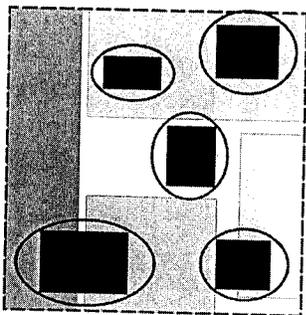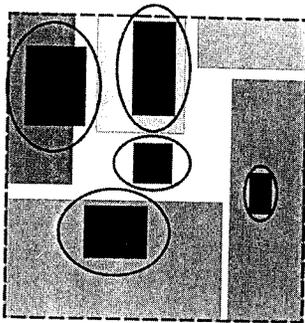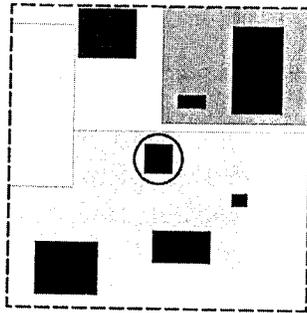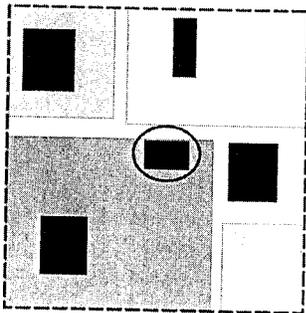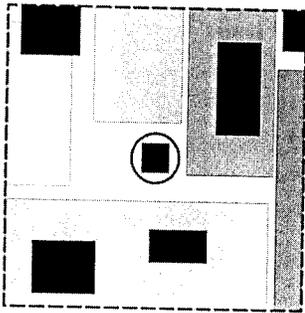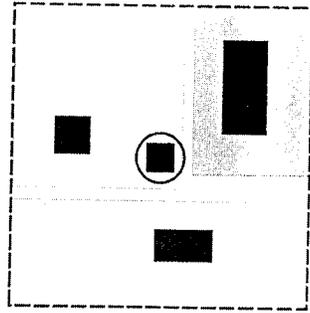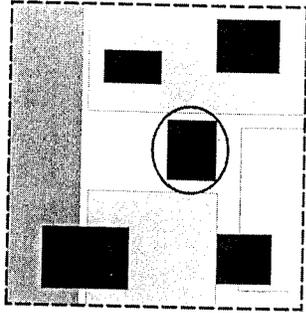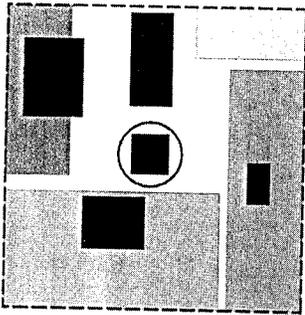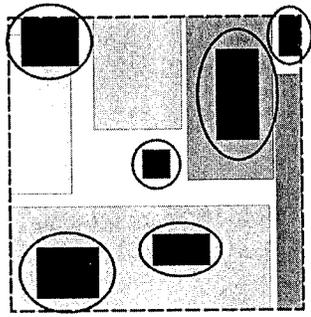
FIGURE 3.1

Sampling strategy to illustrate sampling effort across scales. Black areas represent habitat patches. Circles indicate sampled patches. The remaining areas (white and shades of grey) represent different habitats in the matrix. Dashed lines represent landscape boundaries. (a) Ideal sampling strategy where multiple patches and multiple landscapes are sampled. (b) Sampling strategy where landscape sample size is maximized. Fewer patches are sampled but sampling is more intense. This approach is more suitable when landscape structural variables can be remotely sensed (or are otherwise less costly to obtain). This is the focal patch design. (c) Sampling strategy where fewer landscapes are measured, but each landscape is measured more intensely in more patches. This is a multi-patch landscape study and is more suitable when landscape structural variables are more costly to obtain. (d) Patch-scale study design. This design does not constitute a landscape-scale study.

Focal patch
-Appropriate size for question
-Intensive sampling
        *Dependent variables
            examples:
                Species presence/absence
                Abundance
                Reproductive success
        *Independent variables
            examples:
                Patch habitat quality
                Patch size
                Amount of edge

Multiple scales
    To assess the spatial
    extent of the influence
    of landscape structure

Landscape
-Appropriate size for question
-Less intensive sampling (usually remotely sensed)
        *Independent variables only
            examples:
                Landscape habitat quality
                Amount of forest cover
                Number of paved roads

FIGURE 3.2
Focal patch landscape scale study sampling design.

were followed and their locations recorded for 100 time steps. Because of the short-distance movements of the beetle, the landscape size was large enough to observe the process of in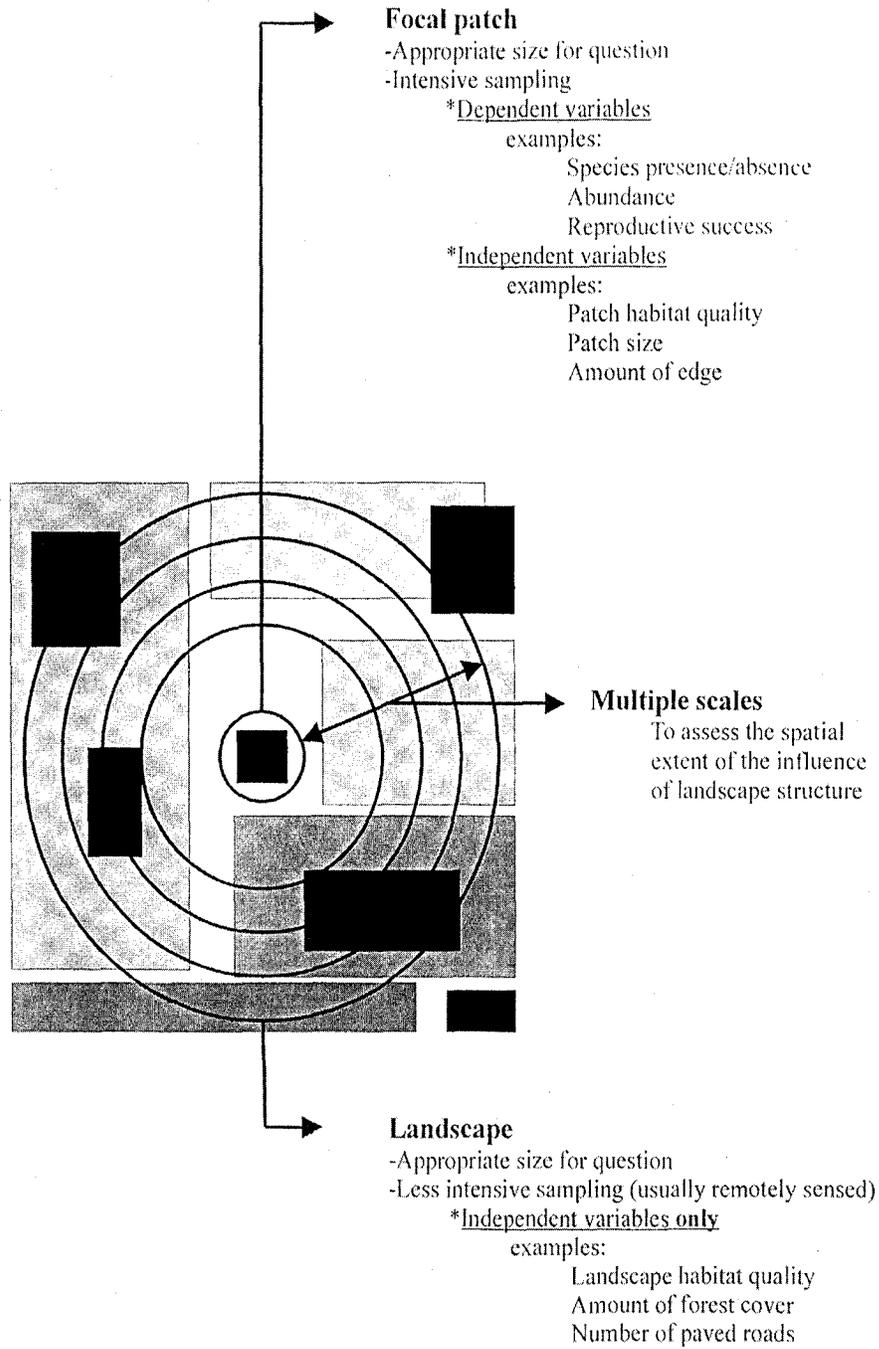terest (section 3.2). The study is thus at an appropriate scale for the question, has reasonable sampling intensity and number of landscapes, and controls for the effects of extraneous variables by the experimental design. The limitation of this type of study is that it is difficult to extrapolate the results to larger scales (e.g., long-distance movements over the life-time of a beetle; larger movement distances associated with other organisms).

One possibility for ensuring large sample size and intensive sampling effort is the "focal-patch study" in which the response variable is measured intensively in several focal patches, each of which is located in the center of a landscape. The landscapes are non-overlapping (section 3.5.2) and predictors are measured at both the patch and whole landscape scales (Fig. 3.2). Focusing sampling efforts of the response variable on focal patches allows for intensive data collection on the species of interest that can then be related to the characteristics of the surrounding landscape. The focus on a central patch for detailed measurement of population response reduces the trade-off between sampling intensity and replication (e.g., Pope *et al.*, 2000).

Furthermore, because it is not always possible, or appropriate, to apply a "treatment" to a landscape, we suggest a quasi-experimental approach to landscape sampling designs (this approach is not limited to focal-patch studies). Landscapes are not manipulated but are chosen using strict, non-random selection criteria to ensure a wide range of values of the predictor variables and to avoid correlations among predictor variables, thus increasing the power of statistical inferences. For example, Trzcinski *et al.* (1999) selected landscapes such that the independent effects of the amount and fragmentation of forest cover on bird distribution could be estimated. We suggest that the combined approach of focal patches and strict selection criteria may be the most appropriate design for obtaining reliable information from landscape ecological studies to be used as the basis for management decisions.

3.5   Overview of analysis tools and data considerations

In a multi-scale landscape study design, the researcher uses hybrid-analysis schemes that examine both patch-scale and landscape-scale analysis. For example, in the focal-patch design we advocate in this chapter, spatial information from patch-scale analysis (e.g., patch size and shape) is combined with landscape-scale attributes (e.g., total amount of breeding habitat in landscape, density of barriers to movement such as roads). This approach is termed multi-scale analysis because it integrates local (patch-scale) information with landscape-scale information. We briefly address the

approach to take in analyzing multi-scale landscape patterns and provide some of the data considerations unique to a landscape-scale ecological study. For a more comprehensive discussion on landscape-scale analysis methods, the reader should consult Klopatek and Gardner (1999) or Turner and Gardner (1991).

3.5.1   Landscape pattern analysis

Landscape pattern analyses can take many forms, but generally they are performed at two scales. One approach is to look within individual landscapes to see how attributes of patches are related to ecological properties within the patches. This approach has been popularized by metapopulation theory (Hanski and Gilpin, 1991) which emphasizes patch occupancy and patch characteristics, such as patch number, size, and isolation, to predict regional population dynamics and persistence. Because this approach explicitly examines patches within a landscape(s), this constitutes a patch-scale analysis. Another approach is the landscape-scale analysis which explicitly studies properties that emerge only at the landscape scale (e.g., landscape connectivity, percentage habitat cover, road density).

Two sets of methods are available for landscape pattern analysis. The first is geostatistical methods, which are applied to data that consist only of mapped points. We focus more on the second method, which is more common in landscape ecology: pattern-based analysis. This method is applied to patch-based or raster maps. A complete review of techniques from both types of methods is beyond the scope of this chapter. For a more in-depth discussion of these techniques, we recommend reviews by Legendre and Fortin (1989), Turner et al. (1991), Legendre (1993), and Gustafson (1998).

Geostatistical methods

Geostatistical methods assume that some properties of a landscape (e.g., rainfall) vary continuously over space, and that one can estimate this variation by sampling it at many (usually irregularly spaced) locations (Burrough, 1995). An example of a useful geostatistical technique is trend surface analysis (Gittins, 1968). Trend surface analysis techniques are used to extrapolate from the sample points to the broad-scale spatial pattern, using two-dimensional non-linear regression techniques. They can be used either (1) among landscapes, to categorize each landscape with respect to some variable, prior to hypothesis testing, or (2) within landscapes, to characterize statistically the trend in a variable so that its effects can be removed statistically (detrended) prior to hypothesis testing with another landscape variable (Cormack and Ord, 1979; Legendre and Fortin, 1989).

Pattern-based methods

Pattern-based methods are used to quantify the composition and configuration of landscapes. They include patch-based, landscape-based, and transect-based measures. One should bear in mind that these approaches are not always interchangeable. For example, some landscape properties can be derived from knowledge about the landscape's constituent patches (see below) but the reverse is not true and, therefore, patch-scale pattern analysis is not equivalent to landscape-scale pattern analysis. Nevertheless, the patch paradigm is popular in ecology (e.g., metapopulation theory; Hanski and Gilpin, 1991; see also review by Andrén, 1994). In addition to patch size and isolation, various measures of patch shape, such as edge:interior ratios or patch fractal dimension, are often measured as predictors of ecological variables (e.g., Lindenmayer *et al.*, 1999). Isolation measures, such as nearest-neighbor scores and dispersion indices, are generally calculated from point-based data. However, all the measures can be calculated from patch-based or raster-based maps and can be performed on binary and categorical data, so they are generally applicable. The main deficiency with all pattern-based measures, particularly patch-based measures, is that there is little consensus as to which properties are most significant for ecological analysis in general (e.g., see Andrén, 1994; Bender *et al.*, 1998; Hargis *et al.*, 1998). Also, many of the indices provide similar information, resulting in redundancy when one performs analyses using multiple measures (Ritters *et al.*, 1995; Hargis *et al.*, 1998; see also section "Data Reduction" below).

Comparison of pattern across landscapes requires landscape-based methods for pattern analysis. Common landscape-based properties are the amount of habitat in the landscape and landscape connectivity. Landscape connectivity is an operational term rather than a quantifiable measure, but several landscape-based indices have been reported as indices of connectivity (see Schumaker, 1996; Tischendorf and Fahrig, 2000a). Landscape contagion (O'Neill *et al.*, 1988), fractal dimension (Palmer, 1988; Milne, 1991) and lacunarity (Plotnick *et al.*, 1993) are all indices related to the connectedness or aggregation of one type of landscape element (e.g., breeding habitat for a particular species) for raster-based maps. Other commonly used landscape-based measures use aggregate properties of all the patches within a landscape (e.g., mean patch area, total amount of edge). Some progress has been made in establishing general relationships among landscape-based measures through simulation modeling that examines the behavior of different landscape-based measures in different types of landscapes (see Gustafson and Parker, 1992; Ritters *et al.*, 1995; Schumaker, 1996; Hargis *et al.*, 1998; Tischendorf and Fahrig, 2000b). Empirical support for this work, though, is still lacking.

Transect-based measures differ from the patch and landscape-based measures in that location is expressed in one-dimensional (1D) space. Transects can

be used to estimate landscape pattern (e.g., pattern of forest canopy gaps) by sampling only a small portion of the landscape, assuming that the pattern across the transect(s) is representative of the landscape. Transect-based data can be preferable to mapping entire regions when the spatial pattern under observation is fairly regular across the landscape. Also, some analysis techniques are calculated more easily using 1D data than 2D data. For example, spectral analysis methods such as Fourier analysis, which can determine the characteristic scales of a repeated pattern like the pattern of clumping of grasses, can be performed easily on transect data (Turner *et al.*, 1991).

3.5.2   Statistical considerations associated with landscape-scale data

Landscape studies are subject to the same limitations that must be overcome in any study. Any study should seek to maximize replication and interspersion of observations while also minimizing sampling error (Hurlbert, 1984). However, at least three additional considerations unique to landscape studies must also be addressed. First, spatial autocorrelation among data often arises in landscape studies, and this poses a problem when applying some of the common statistical hypothesis tests, which assume independence of data points. Second, the presence of broad-scale spatial trends in the data may mask finer-scale patterns that may be of greater interest. Third, because many factors that affect variables of interest are spatially dependent, there may be spatially correlated common causes that exist in landscape data. This makes identifying important determinants of the phenomenon under investigation (e.g., the distribution and abundance of a species) more challenging because non-causal factors are difficult to separate from causal ones. Each of these potential pitfalls is discussed below with suggestions to minimize their influence.

Spatial autocorrelation

Spatial autocorrelation is a concern for landscape data, and it should be tested for whenever one is concerned that proximate sites (or worse yet, overlapping landscapes) consistently behave more similarly than distant sites with respect to some variable (e.g., vegetation type). The most common techniques for statistical hypothesis testing are those statistics lumped together under the term general linear models (GLM), which include familiar procedures such as multiple regression and ANOVA (Neter *et al.*, 1990). Uncorrected spatial autocorrelation among study sites (landscapes or focal patches) can artificially inflate the significance of GLM tests, potentially leading the researcher to unreliable conclusions (for reviews see Legendre and Fortin, 1989; Legendre, 1993).

If spatially autocorrelated data must be used, one must resort to alternative means for hypothesis testing. Legendre and Fortin (1989) and Legendre (1993)

advocate the use of techniques such as the partial Mantel test for hypothesis testing when faced with autocorrelated data. However, these methods have not been quickly adopted by ecologists, probably because they are computationally intensive and not entirely straightforward to interpret. Another potential solution is the use of distribution-free statistical procedures, such as randomization and bootstrapping tests (e.g., Manly, 1997). These methods also have not been readily adopted by ecologists, presumably because the randomization routines necessary for calculating the statistics must often be customized on a case-by-case basis, necessitating that the user be familiar with at least a rudimentary level of programming or scripting.

Broad-scale spatial trends

When there are broad-scale trends in the data but the autocorrelation of the response variable is small, one can statistically remove unwanted trends from the data and proceed with the standard GLM statistics. For example, if there are latitudinal and/or longitudinal trends in the data, one can correct for these effects statistically using trend-surface analysis (e.g., Venier and Fahrig, 1998). One creates a polynomial regression model where the response variable is the variable of interest (e.g., species abundance) and the predictor variables are latitude and longitude, expressed in units such as decimal degrees. Performing subsequent statistical analyses on the residuals of the polynomial regression (rather than on the original response variable) eliminates the effect of the spatial trend. A similar method can also be performed using ANCOVA if the unwanted trend varies in only one direction. Randomized blocked-ANOVA (Neter et al., 1990) designs are also useful if there is a natural clustering or grouping of sites, but one must be careful that variables of interest are not similarly grouped. If the predictor variables of interest are not sufficiently interspersed throughout the landscape, then blocking may remove any apparent relationship between the response and predictor variables of interest.

A promising method for dealing with spatially correlated data is generalized additive models (GAM) (Hastie and Tibshirani, 1990; Hastie, 1992). GAM statistics are an extension of GLM techniques, but make fewer assumptions regarding the data, and are capable of modeling non-linear relationships. Preisler et al. (1997) propose a method based on a GAM that (1) estimates the spatial effects in the data, and (2) statistically controls for these effects while simultaneously examining the effects of other predictor variables. The authors claim that this method offers good explanatory power using predictor variables of interest, even when there are other unmeasured variables that also vary spatially. The method is also appealing because it can be performed using the standard output of existing statistical packages, and there is a broad choice of designs (e.g., ANOVA, regression, ANCOVA, etc.).

Spatially-correlated common causes

Another problem that is common in landscape studies occurs when apparent relations among the data are due to spatially correlated factors with a common cause. For example, imagine that a researcher was interested in sampling frog populations in areas with differing amounts of forest cover to assess the relationship between forest cover and frog abundance. One may select multiple landscapes for investigation, choosing sites that display a wide range of amounts of forest cover. However, also imagine that continuous forest cover only occurs in areas where the soil is poorly drained, and areas with little forest cover tend to occur in well-drained soils that have been cleared mostly for agricultural purposes. Once the samples have been analyzed, it would be difficult to interpret any observed relationships between forest cover and frog abundance because of the effects of soil drainage (and therefore, presence of natural wetlands) and human land use. It may be that forest cover is correlated with frog abundance, but there is no direct relationship between the two variables (i.e., forest cover has no causal effect on frog populations). Instead, the relationship arises because frog abundance and forest cover have common causes (human impacts due to difference in drainage) that produce a spatial correlation.

Although such confounding effects are not unique to landscape data, there is certainly a strong likelihood that they will be encountered in landscape studies because so many environmental and human factors are spatially dependent. Statistical techniques such as path analysis (Li, 1975) and structural equation modeling (Maruyama, 1998) have been developed to analyze and interpret causal relations among many variables. However, it is often easier to eliminate confounding effects in the design stage by carefully selecting landscapes so that confounding factors are not correlated. Non-random selection of landscapes can also help to eliminate problems with spatially autocorrelated data at the source, and certainly can minimize broad-scale spatial trends when landscapes with varying degrees of some attribute are carefully interspersed. Although this advice (non-random sampling) seems to violate statistical dogma, we feel that the benefits of carefully selected landscapes far outweigh the potential introduction of bias that might occur when sample landscapes are selected in a non-random, quasi-experimental fashion.

Data reduction

Finally, one is often faced with a barrage of potential landscape pattern indices with no a priori conception of which variables will be most useful and which will be redundant. Although it is possible to construct statistical models that test all possible predictor variables, this is undesirable because (1) more predictor variables results in lower statistical power, (2) there is an increased chance of spurious statistical relationships, and (3) the computations necessary for

finding the exact parameter solutions may take a long time or may not be possible at all. Thus, some form of variable reduction may be desirable.

Gustafson and Parker (1992), Schumaker (1996), and Hargis *et al.* (1998) demonstrate where redundancies are likely among landscape metrics, and provide guidance as to what metrics should be used. An alternative solution is to combine the landscape structure variables in some form of factor analysis, such as principal components analysis (PCA), and use the first few PCA axes as predictor variables in subsequent statistical analyses in place of the original larger set of intercorrelated variables (e.g., Saab, 1999). This both reduces the number of predictor variables and ensures that the predictor variables are uncorrelated. This method has been used by McGarigal and McComb (1995) and Trzcinski *et al.* (1999) to derive measures of habitat fragmentation that are independent of habitat amount in the landscape.

3.6   Case study: Effects of landscape structure on the abundance of the northern leopard frog

Pope *et al.* (2000) examined the effects of landscape structure on the abundance of northern leopard frogs (*Rana pipiens*) in the region surrounding Ottawa, Canada. The authors studied 34 circular landscapes, each with a radius of 1.5 km (or 3 km in diameter). Within each landscape they (and 34 volunteers) assessed the abundance of northern leopard frogs over four census periods. They also surveyed all other potential breeding sites within these landscapes for a total of 107 sampling sites. The authors demonstrated that the relative abundance of *R. pipiens* in a landscape was influenced by the amount of summer foraging habitat (grassy field or meadows), the amount of breeding habitat (adjacent ponds), and the water pH and amount of spawning habitat in the focal ponds.

Focal patch design
Thirty-four non-overlapping landscapes were selected in which the response variable, relative abundance of the northern leopard frog, was measured intensely at one focal pond in each landscape. The landscapes were selected using the criteria described in the following section. The predictor variables were measured at both the patch (pond characteristics) and the landscape scale (amount of breeding and summer habitat based on remotely sensed information).

Strict selection criteria
This study was not an experimental one where "treatments" were applied. Instead, it used a quasi-experimental approach where the ponds were chosen to minimize correlations between the predictor landscape-scale variables. The

landscapes were selected to minimize the correlations between the amount of summer foraging habitat and the density of potential breeding areas in the landscapes, taking advantage of existing difference in landscape structure. In practical terms, this means the authors selected ponds that had one of the following four categories of landscape structure: summer foraging habitat near/breeding area near, summer foraging habitat near/breeding area far, summer foraging habitat far/breeding area near, and summer foraging habitat far/breeding area far.

Landscape size

A circular landscape with a 1.5-km radius from the focal pond was selected because it represented the shortest distance in which there was at least one site (pond, stream, or large drainage ditch) from which dispersers might move. Northern leopard frogs typically move 1 to 2 km between habitats within a year, so the size of the landscape reflected this movement distance. Given the size of the area sampled, the intensity of sampling conducted at each landscape, and the number of survey sites, a landscape sample size of 34 was the largest possible.

Multi-scales – the patch, the landscape and sizes in between

The variables in this study were assessed at both the patch scale (the pond) as well as at the 1.5-km radius landscapes scale, a size determined by the movement habits of the northern leopard frog. The 1.5-km radius landscape was also the largest possible, given the requirement of non-overlapping landscapes and that all breeding sites within each landscape had to be surveyed for leopard frogs. The landscape structure variables were also quantified at several smaller landscape scales to determine the scale at which the effect of landscape structure is strongest.

Patch-scale variables The pond's habitat was assessed in detail to determine pond quality (patch scale predictor variables). The authors examined pond perimeter length, amount of spawning habitat, and water pH.

Landscape-scale variables The amount of all possible types of summer habitat was assessed in the surrounding landscape using remotely sensed data that were later ground truthed. The number of all possible breeding sites was also determined within 1.5 km of the pond based on remotely sensed data; the number of sites with calling males was based on the surveys.

Multiple-scale variables The amount of all possible types of summer habitat was also assessed within four smaller landscapes sizes of 0.25, 0.5, 0.75, and 1 km from the focal pond, based on the remotely sensed information.

Multi-scale analysis methods The authors conducted a multi-scale analysis that simultaneously included variables from all scales in the study. They used a stepwise Poisson regression analysis of the landscape and patch variables on their estimates of core pond leopard frog relative abundance. They found a significant effect of two of the patch variables (water pH and the amount of spawning habitat) and two of the landscape structure variables (amount of summer habitat within 1 km of the pond and number of breeding sites with calling males within 1.5 km) on the relative abundance of the northern leopard frog. There was a potential challenge in interpreting the results of the analysis because of the presence of strong correlations among the landscape structure variables across the five scales. The authors addressed this by calculating the landscape variables in non-overlapping rings and re-analyzing the data. They found qualitatively similar results, suggesting that the multi-scale analysis can be used to determine the strongest scale of influence of landscape structural variables.

Management implications

This case study illustrates the importance of managing populations at both the local scale and the appropriate landscape scale. Leopard frog population survival depends on both pond characteristics and landscape structure up to 1.5 km away from the pond. Adequate amounts of both breeding habitat and summer forage habitat must be maintained in the landscape. Maintaining good breeding habitat is intuitively critical to maintaining frog populations, but in the absence of good summer foraging habitat in the landscape, leopard frogs may not survive to maturity. Considering only the number and arrangement of breeding ponds would have led to erroneous conclusions about the potential persistence of leopard frog populations.

3.7   Implications and guidelines for conducting multi-scale landscape studies for wildlife management

In conclusion, we recommend the following four guidelines for conducting landscape-scale studies: (1) determine the appropriate landscape scale, (2) use multiple landscapes, at multiple scales if possible, (3) consider both patch- and landscape-scale factors, and (4) consider design trade-offs of intensity of sampling vs. adequate sample size.

To determine the appropriate scale the researcher or manager must first formulate a hypothesis, with response and predictor variables clearly defined. The response variable determines the species of interest and the measures required (e.g., presence/absence, abundance, species richness). This in turn determines the intensity of sampling required for the response variable. The hypothesized

relationship between the predictor variables and the response variable determines the appropriate landscape size. For example, if the hypothesis relates landscape structure to an individual-level response (e.g., foraging success), then the appropriate landscape size depends on short-term (e.g., daily) movement distances. If the hypothesis relates landscape structure to population abundance, then the appropriate landscape scale depends on the scale of interpopulation dispersal events.

In most landscape ecological studies the objective is to relate landscape structure to an ecological response. Therefore, many landscapes with different structures are needed. When the application of an experimental "treatment" is inappropriate (as it often is), sample landscapes should be chosen using strict a priori selection criteria to minimize correlations among predictor variables, and to ensure wide variation in the landscape structure (predictor) variables.

Studies have shown that failing to consider the effects of both patch and landscape characteristics may lead to unsuccessful management decisions. Findlay and Houlahan (1997) examined the effect of landscape structure on species richness in 30 wetlands (Table 3.1). They determined that an increase in road density and a decrease in forest cover surrounding each wetland had a negative effect on species richness. They also determined that larger wetlands were positively related to species diversity. One of the results suggested that increasing the amount of road surface by 2m/ha within 1 km of the wetland, or decreasing forest cover by about 20% within 2 km, had a similar effect on species richness as reducing the size of the wetland by 50%. This illustrates the point that the context of a patch is important. Management policies that only considered wetland quality might have failed because the landscape context was not addressed.

In studies where large landscapes are required, trade-offs between sampling intensity and sample size (number of landscapes) will be particularly severe. The number of sample landscapes should be maximized in spite of these limitations. We suggest that the focal-patch approach with strict landscape selection criteria is the best compromise when landscape structure variables can be measured relatively easily. The focal-patch design reduces the trade-off between sampling intensity and replication. It also increases the power of statistical tests through the use of strict criteria to select landscapes, thus reducing the required sample size.

3.8   Summary

A multi-scale landscape study must be designed properly to provide appropriate information for management of natural populations. Multi-scale studies address the effects of both patch characteristics (e.g., patch size or

quality) and landscape structural characteristics (composition, configuration) on an ecological response variable. The size of the landscape must be determined based on knowledge of the organism and the research question. In a multi-scale landscape study, the unit of observation is the landscape. Therefore, several non-overlapping landscapes should be selected that differ in structure. Because of the size of study landscapes, however, logistical limitations may reduce landscape sample size. To counter these limitations we suggest the use of the focal patch design, where the ecological response variable is measured intensely at patches located at the centers of non-overlapping landscapes.

Acknowledgments

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