

**LIMITATIONS OF THE POINT-COUNT METHOD
FOR INFERRING STAND-LEVEL
SPECIES-RESOURCE RELATIONSHIPS:
A SAMPLING SIMULATION APPROACH**

by

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Abstract

In this thesis, I suggest that only under special, simplified circumstances is the point-count method appropriate for deducing stand-level species-resource relationships. As a field evaluation of the point-count method, I developed stand-level species-resource models for two woodpecker species, the red-naped sapsucker (*Sphyrapicus nuchalis*) and the northern flicker (*Colaptes auratus*). Compounding sources of uncertainty severely compromised the usefulness of this exercise in elucidating species-resource relationships. In response to the difficulties with the field data, I developed Sample Sim'on, a program that simulates the repeated sampling of a population of mobile, territorial organisms in a landscape with one or more resources. I show that the spatial distribution of resources, species behaviour, and sampling design can greatly affect the success rate with which species-resource relationships can be determined correctly (i.e., the sampling success rate). Realistic values for parameters describing these elements result in a very low sampling success rate, even when sampling effort is impracticably high. In addition, other variables that are not explicitly defined in Sample Sim'on, including those acting over larger spatial scales, can only *add* variance to species-resource data, further weakening sampling success.

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CHAPTER I: Introduction

At the turn of the millennium, population growth and economic development continue to create increasing pressures on natural resources worldwide. Resource management policies in economically prosperous countries have evolved, with a corresponding growth in public environmental awareness, to consider a more diverse set of interests. In British Columbia, Canada, the introduction of the Forest Practices Code (BC Ministry of Forests 1999) in 1995 marked an important first step towards more sustainable forest management. Forestry companies are encouraged, both by new legislation and informal guidelines, to know and understand the ecological impacts, economic tradeoffs and local community interests associated with any forested area to be harvested (e.g., BC Ministry of Forests, 1995). Adaptive management embodies the contemporary philosophy, whereby successful resource extraction and management is a holistic process in which scientists and non-scientists cooperate to maintain biodiversity and ecosystem function, applying and adapting to new knowledge (Walters 1986).

Conservation biology is a relatively new discipline that has arisen to fulfill part of the role of science in forest management. Attempting to bridge the traditional institutional gaps between zoology, botany, wildlife management and forestry (Cooperrider 1996), conservation biologists seek to identify and provide solutions to problems resulting from new management decisions (Heissenbuttel 1996). Caughley (1994) argued that conservation biology generally addresses two related issues, the viability of small populations, and declining species populations. In the context of adaptive management, the declining species paradigm seeks not only to understand why species may be

declining, but also how to mitigate future declines. In this context, conservation biologists seek how, in the light of harvesting, to manage forest resources to maintain current distributions of species. To answer this question, we must know which habitat attributes limit the populations of wildlife species, and how these attributes are affected by forestry activities.

Because our knowledge of species and ecosystems is fragmented at best (Christensen *et al.* 1996), a hotly discussed topic in conservation biology is whether to concentrate research efforts on pursuing individual species management or ecosystem management. The logical solution is to use both approaches, recognizing the limitations of each (Franklin 1993, Simberloff 1997). Single-species management can ensure the protection of endangered populations, or of umbrella species with broad resource requirements (Launer and Murphy 1994, Simberloff 1997), while ecosystem management encompasses many less conspicuous but equally integral species, and acknowledges the need for maintaining a functioning ecosystem (Franklin 1993, Simberloff 1997).

Whether the means is single species management or ecosystem management, habitat protection is a goal of conservation. In order to identify what habitat attributes need protecting, conservation biologists must extend previous ecological research to refine our knowledge of species-resource relationships. In the context of this thesis, a species-resource relationship is a robust relationship between habitat use and a quantified habitat attribute, reflecting actual use of a resource. Differential habitat use may be indicated by the relative numbers of detections among sampling points. In studies of a single species, variation in reproductive success among individuals can be correlated with variation in breeding habitat attributes, at a particular spatial and temporal scale (Pribil

and Picman 1997). However, if all individuals occupy optimum habitat, there will be no discernable difference among the habitats they inhabit and no relationship will be detected (Pribil and Picman 1997). In studies of many species simultaneously, species-resource relationships may be deduced by comparing the variation in detections of individuals with the variation in habitat attributes across a number of sampling stations (e.g., Mannan and Meslow 1984, Morrison *et al.* 1987, Lundquist 1991, Hansen *et al.* 1995, Bosakowski 1997). Since a greater range of habitat is sampled than just suitable breeding habitat, both where species occur as well as where they do not occur, species-resource relationships may be more readily detected. However, because species operate over different spatial and temporal scales, one spatial and temporal scale of investigation applied to one or many species is not likely to reveal all species-resource relationships (Pribil and Picman 1997, Riitters *et al.* 1997). In addition, the assumption of many species-resource models (e.g., Verner *et al.* 1986, Kangas *et al.* 1993), that use/availability data accurately reflect some aspect of the carrying capacity of a habitat, is not valid under realistic conditions (Hobbs and Hanley 1990). Morrison *et al.* (1987) advised that more intensive studies of individual species, which include species-specific variables, are required to successfully build models predicting their abundance.

One group of species likely to be particularly sensitive to forest practices in BC is cavity-nesting birds (Martin and Eadie 1999). Primary cavity nesters (i.e. woodpeckers) excavate cavities that, once abandoned, are used by secondary cavity nesting species (e.g., mountain bluebird (*Sialia currucoides*), common goldeneye (*Bucephala clangula*), American kestrel (*Falco sparverius*). Forest harvesting removes trees, indisputably disrupting the future as well as the present availability of suitable nesting sites. To investigate interactions, both

among species and between species and habitat within this community, and ultimately to provide guidelines for forest practices, a field study on structure and function of cavity-nesting wildlife was initiated in 1995 in the Chilcotin Region of central BC (Martin and Eadie 1999). This study was designed to determine how associations among cavity-nesting species change in relation to forest type, forest fragment size and proximity to wet (i.e. pond and stream) and dry (i.e. grassland) edges. Two study sites, Riske Creek and Knife Creek, were chosen representing a mixture of coniferous and deciduous forests embedded in a matrix of grasslands, ponds and wetlands. In order to compare bird communities across different forest types, a series of study plots, each consisting of a grid of point-count stations, was created to provide data on species detections and habitat attributes. The intent was that species activity, as indicated by relative numbers of detections, could be correlated with ecologically relevant habitat variables.

The original objective of this thesis was to incorporate habitat quality predictions into FORCEE, a spatially explicit, stand-level forest ecosystem management model (Kimmins *et al.* 1999). Given habitat and structural attributes generated by FORCEE, the goal was to construct a habitat relationship model to predict the suitability of the simulated stand for a particular species, making it possible to compare habitat quality over time or among different simulation scenarios. To build models for many species, it would be necessary to use existing studies and data. The Riske Creek-Knife Creek study presented a good case study. Thus, I selected two primary cavity-nesting bird species, the northern flicker (*Colaptes auratus*) and the red-naped sapsucker (*Sphyrapicus nuchalis*), and attempted to build habitat relationship models for each. Based on the published literature on the resource requirements of each species, I selected a set of resource variables which I

expected to be most important in determining habitat suitability. I then estimated a logistic relationship between probability of use and the selected variables. Models were constructed separately for data collected with and without playback (i.e. a tape of woodpecker calls was played during the point-count survey). The resulting models were error-prone (14 to 47% of cases were predicted incorrectly) and inconsistent between playback and non-playback data (i.e. different methods of data collection resulted in different sets of significant variables in the models). To see if the residual variance could be explained by any of the other variables measured in the study, I repeated this exercise using all measured resource variables. Although the error rates in the resulting models were lower (10 to 25% of cases predicted incorrectly), inconsistent variable lists between the playback and non-playback models reaffirmed that the species-resource relationships inferred by the models could be statistical artifacts, and not ecologically meaningful or robust relationships. The disappointing results of this exercise are presented in Chapter II.

The failure of the Riske Creek-Knife Creek data to consistently confirm ecologically meaningful species-resource relationships suggested that perhaps there were other, unmeasured variables involved, both in determining habitat suitability and in obscuring actual species-resource relationships. In this case study, the data used to investigate species-resource relationships were collected at only one spatial scale. Habitat attributes and factors operating at larger scales, e.g., forest patch size distribution and connectivity or regional population dynamics (Dunning *et al.* 1992), were not quantified. Also, given the low rates of detection for both flickers and sapsuckers, the accuracy of the point count data in implying habitat suitability was likely to be sensitive to stochastic

events (e.g., the detection of an individual in poor habitat) and methodological idiosyncrasies (e.g., varying numbers of rounds among point-count stations).

To explore the effects of some of these other variables on the rate of correctly determining species-resource relationships (success rate), I created a computer program which simulated the sampling of a population of mobile, territorial organisms in a landscape containing one or more resources. This is the subject of Chapter III. The results of simulations run with this program suggest that the spatial distribution of a resource (i.e. its spatial period, or the maximum distance over which spatial autocorrelation acts, and its range in density), the average territory size of the species under study, and the method by which detection data are collected (e.g., method of point placement, number of rounds), greatly influence the possibility of successfully predicting species-resource relationships. In the context of my simulation model, only under special, simplified conditions could species-resource relationships be determined with a realistic sampling effort. For example, if the occurrence of a species is determined by only one resource, and both the average territory size and the spatial period of the resource are large, a minimum of 9 rounds of 27 sampling points was required to predict this relationship, at $p < 0.05$.

The results of the sampling simulation call into question the reliability of the point-count method by which to infer species-resource relationships. Thus in the final chapter, I conduct four additional sampling simulations to summarize the influence of the interaction of average territory size and spatial period on success rate. Applied to the Riske Creek-Knife Creek study, the results suggest that the point count data that resulted from the sampling methods employed should not be used on a "per species" basis to infer

species-specific resource relationships. Whether point-count data may be useful in examining community-level associations at a stand level is a separate issue, not addressed here. For the task of determining habitat relationships for single species, alternative methods such as individual behaviour studies (e.g., Mannan and Meslow 1984, Adams and Morrison 1993) or expert opinion (e.g., Kangas *et al.* 1993, Holthausen *et al.* 1994) may provide more meaningful results. In addition, the approach developed by Dettmers and Bart (1999) may provide a more appropriate method of analysing presence data. In summary, the spatial and temporal scales of both species and resource distributions must be quantified in order to determine a point-count sampling scheme which will enable the accurate prediction of species-resource relationships.

CHAPTER II: Field Work and Analyses

Forest harvesting undoubtedly affects nutrient cycling, vegetation structure, and animal populations. To aid in predicting the magnitudes of these effects, biologists create simulation programs. One such simulation program is FORCEE, a spatially explicit, stand-level forest ecosystem management model (Kimmins *et al.* 1999) which simulates the development of soil, individual trees and plants within one hectare. FORCEE also presents the user with a variety of associated values, including economic costs and benefits and rudimentary predictions of wildlife habitat quality. The original objective of this thesis was to examine the problem of predicting wildlife habitat quality in FORCEE, and to create guidelines which may be used to produce improved models for a variety of species. In this chapter, I discuss the field work and analyses I conducted in pursuit of this goal.

I selected two case-study species and an existing field census study of these species as a source of data with which to work. Based on the literature on the resource requirements for the selected species, I chose a set of stand-level resource attributes from which to predict presence or absence for each species. I used data from the field census and logistic regression to construct models to test the postulated species-resource relationships, with unsatisfactory results. I then used the data to generate a new set of models, but again their performance was poor and the ecological significance of the model variables was ambiguous. These results suggested either that the species-resource relationships that I had postulated do not exist, or that the data were incomplete or too noisy as the result of unidentified variables. Finally, I identified some variables which may

have added variance (noise) to the field census data, and suggested a method for exploring these effects (described in further detail in Chapter III).

2.1 Study site

To serve as a case study in building species-resource relationship models, I used data from a field study of cavity-nesters around Williams Lake, BC, conducted by Dr. Kathy Martin (University of British Columbia). This study provides data on species detections and habitat at the stand level. In 1997, I had the opportunity to become more familiar with the methodology and inherent problems by assisting with data collection.

The study was conducted in the Chilcotin Region (51° 52'N, 122° 21'W) of central BC, Canada, in the very dry warm subzone of the Interior Douglas fir (IDF) biogeoclimatic zone. The area is characterized by varying mixtures of deciduous and coniferous tree species, embedded in a matrix of grasslands, ponds, streams and wetlands (Martin and Eadie 1999). The predominant tree species are trembling aspen (*Populus tremuloides* [Michx.]), Douglas fir (*Pseudotsuga menziesii* [Mirbel]), lodgepole pine (*Pinus contorta* [Dougl. Ex Loud.]) and white spruce (*Picea glauca* [Moench]). All of the sites were unharvested stands, although some had second growth due to fire or other types of disturbance (Martin and Eadie 1999).

2.2 Sampling design

The sampling design consisted of 18 study plots, on average 15 ha in extent, each composed of a grid of points spaced 100 m apart. At each point, we used a 50 m-radius point count (7,854 m² in area) to sample bird populations, and an 11.28 m-radius vegetation plot (400 m² in area) to sample habitat. Although the study began in 1995, I

used only data from 1997. The numbers of study plots and points were not constant from year to year, making comparisons or the pooling of data across years difficult. Grids contained on average 18 points (7 to 35), for a total of 326 point-count stations.

Point counts were conducted from late May until late June, between 0500 and 0930 hours. The observer stood for 6 minutes at each point-count station, recording the species of all individuals seen or heard within an approximated 50 m radius. Every second point was sampled for an additional 2 minutes, after a woodpecker playback tape was played. This was done in order to increase the detectability of woodpeckers, which are typically less vocal than many other species. All points were sampled three or four times in sequential 10-day periods. One complete set of point-counts in a 10-day period is referred to as a round. Thus, each point-count station was sampled over three or four rounds.

Vegetation plots were completed during July. Within each plot, tree species, diameter-at-breast-height (DBH), and decay class were recorded for all trees with a DBH ≥ 14.0 cm. In addition, the number of saplings, with DBH < 14.0 cm and height ≥ 1.3 m, was tallied by species.

In the summer of 1998, I returned to the 18 study plots and estimated, for each sample point, distance to wet edge and distance to dry edge, to the nearest 100 m. I defined a wet edge as the interface between forest and a stream, pond, or wetland with a width or radius of at least 10 m. I defined a dry edge as the interface between forest and a similarly sized grassland or road.

2.3 Study species

The red-naped sapsucker (*Sphyrapicus nuchalis*) and the northern flicker (*Colaptes auratus*), relatively common species in central BC, were chosen because they have contrasting life histories and resource requirements.

The red-naped sapsucker is a migratory woodpecker. In BC, it breeds in deciduous and mixed woodlands and excavates its own nest cavities, typically in live trees with heartwood decay (e.g., aspen, birch [*Betula* spp.]) (Campbell *et al.* 1996a). During the breeding season, its diet consists mainly of sap, which it procures from wells drilled in trees and shrubs such as willow (*Salix* spp.) and juniper (*Juniperus* spp.) (Ehrlich and Daily 1988). Other food items include aspen buds in the spring and insects caught in the air and gleaned from the furrowed bark of large trees (Winkler *et al.* 1995, Steeger *et al.* 1996). Walters (1996) estimated an average home range for the red-naped sapsucker of about 24 ha.

Also a primary cavity-nesting woodpecker, the northern flicker is both migratory and resident in central BC. It breeds in open forests, farmland, and residential areas (Campbell *et al.* 1996b), and prefers large, dead, decaying trees for nesting (Winkler *et al.* 1995, Dobkin *et al.* 1995, Campbell *et al.* 1996b). During the breeding season, the flicker forages on open ground for insects. Ants constitute 50-75% of its diet (Winkler *et al.* 1995). The average home range of the northern flicker is typically 50-100 ha (Moore 1995).

2.4 Analytical approach

Many approaches have been taken in building species-resource models, including habitat suitability, expert opinion, multiple linear regression and logistic regression

models (e.g., Thomasma *et al.* 1991, Conway and Martin 1993, Daust and Sutherland 1997, Kangas *et al.* 1993). All have the common objective to predict habitat use from resource variables. Habitat suitability index (HSI) models have been widely used since the 1970s, originally by the US Fish & Wildlife Service (e.g., Thomasma *et al.* 1991, Conway and Martin 1993). A biologist who has extensive professional experience with a wildlife species selects a number of habitat variables thought to limit habitat use. For each habitat variable, a function is defined predicting suitability. All functions are then combined, producing an equation that predicts overall habitat suitability, sometimes expressed as a probability. Although there are many HSI models in use, few have been tested (Thomasma *et al.* 1991). SIMFOR is one decision-support tool designed to assist forest managers in evaluating the consequences of forest harvesting scenarios on selected landscape and habitat indicators (Daust and Sutherland 1997). SIMFOR uses an approach similar to that of the HSI models, in that for habitat analysis at the stand level, a stand attribute supply trajectory is compared to species requirements to determine habitat suitability (Daust and Sutherland 1997). An HSI model is comparable to a multiple regression model, except that, rather than arriving at coefficients through formal statistical calculations, biologists use their 'expert opinion' to subjectively create a discriminatory function. Kangas *et al.* (1993) employed expert opinion in a formal and statistically verifiable way to estimate habitat suitability for black grouse, in Finland. Experts prioritized each alternate management plan, by making pairwise comparisons. The researchers were then able to calculate the mean priority of each alternative, and determine an equation to predict it.

One of the simplest ways of estimating a resource selection probability function

involves taking a census of the used and unused units in a population of resource units, and estimating a logistic function for the probability of use as a function of variables that are measured on the units (Manly *et al.* 1993). Our field census around Williams Lake, BC is consistent with this sample design. We used vegetation plots to sample what can be thought of as a population of 326 available resource units, each of which has values for a number of vegetation density variables. We used point counts to census each of these resource units, determining whether or not they were used. Given these data, I judged logistic regression to be an appropriate statistical method for constructing species-resource models for two selected species, the red-naped sapsucker and the northern flicker. For these two species, I selected a set of measured resource variables that I anticipated to be reliable predictors of habitat use. I classified each sample point in the field census as used or unused, then estimated a logistic regression function for the probability of use as a function of the selected variables (hypothesis-testing models). In a second exercise, I again used logistic regression, starting with a larger number of candidate variables (hypothesis-generating models).

2.4.1 Hypothesis-testing models

Using the expert opinion approach, I chose a set of variables for each of the two study species that I expected to be reliable predictors of their presence or absence (Ehrlich and Daily 1988, Dobkin *et al.* 1995, Winkler *et al.* 1995, Campbell *et al.* 1996a, Campbell *et al.* 1996b, Steeger *et al.* 1996). With these variables and the field study data, I used SPSS, a statistical analysis software package, to determine a logistic regression function predicting probability of use (<http://www.spss.com>).

I noted that for both study species, the number of detections was significantly

greater at point-count stations where playback was conducted (t-test; $t=4.26$, $df=305$, $p<0.01$). Since I could not pool data from playback and non-playback point-counts, I constructed the models using playback and non-playback data separately. Although the greater number of detections at playback points increased statistical power, there is also the possibility that playback pulled in birds from beyond the 50 m point-count radius.

I derived a series of variables from the raw data, classified according to stem density (N) or basal area (B), tree species (e.g., AT, FD) and decay class (e.g., 1, 2P). For example, N_AT_3P signifies the number of dead aspen stems per (decay classes 3+) per hectare. B_FD_1 signifies the basal area of live, healthy (decay class 1) Douglas fir trees. Basal area increases exponentially with increasing DBH. See Appendix I for a complete listing and description of the variables.

I expected red-naped sapsuckers in the study area to prefer live trembling aspen with decaying heartwood for cavity excavation and nesting (Campbell *et al.* 1996a). Therefore, I chose the variable N_AT_2, or the number of aspen stems of decay class 2. To fulfill foraging requirements, I chose stems of live willow (N_WX_SAP), stems of live juniper (N_JX_SAP), and stems of live Douglas fir (N_FD_1, N_FD_2) for sap wells (Ehrlich and Daily 1988). I chose basal area of aspen (B_AT_1, B_AT_2, B_AT_3P) and basal area of Douglas fir (B_FD_1, B_FD_2, B_FD_3P) for insect gleaning (Steeger *et al.* 1996).

I expected northern flickers to prefer decaying trees for nesting (B_AT_2, B_AT_3P, B_FD_2, B_FD_3P, B_SX_2, B_SX_3P, B_PL_2, B_PL_3P) (Winkler *et al.* 1995, Dobkin *et al.* 1995, Campbell *et al.* 1996b). For their foraging requirement of

open ground (Winkler *et al.* 1995), I selected basal area of all trees (B_TOTAL), total number of saplings (N_AL_SAP) and distance to the nearest dry edge (DRY_EDGE) .

I used SPSS to estimate a logistic relationship between the probability of use and the selected resource variables, for each of the two study species. In effect, I was testing the hypothesis that the selected resource variables could be used to predict presence or absence, with a satisfactory success rate. I chose the forward-conditional (stepwise) method of variable selection (Hosmer and Lemeshow 1989). This method enters variables one at a time, and only enters a variable if its addition significantly improves the fit of the model, using my chosen probability standard of $\alpha = 0.05$. Also, each time a variable is entered, existing variables in the model are removed if they cease to significantly improve the fit of the model. I used the classification table, histogram of estimated probabilities, and the Hosmer-Lemeshow goodness-of-fit test generated by SPSS to assess how well the resulting models predict habitat use (Hosmer and Lemeshow 1989).

2.4.2 Hypothesis-generating models

Performance of the *a priori*, hypothesis-testing models was unsatisfactory (see Results, below). Therefore I constructed a new model for each case-study species to determine whether any species-resource relationships could be detected. If such relationships could be detected, they may identify hypotheses to test in future studies. I again used logistic regression, starting with a larger number of candidate variables.

As a general rule, there should be at least ten observations for each independent variable included in a general linear model. Since my sample consisted of

326 point-counts, I could include up to 33 variables in each model. I therefore included all available variables: density and basal area for each tree species and decay class (24 variables), sapling density for each tree species (6 variables), proximity to wet and dry edges (2 variables), and presence or absence of sapsuckers or flickers (1 variable). As in the hypothesis-testing models (above), I used forward stepwise logistic regression in SPSS to construct the hypothesis-testing models. In addition, because I started with a large number of candidate variables, the $\alpha = 0.05$ probability standard is overly optimistic, and should be reduced via the Bonferroni correction.

2.5 Results

The final or 'best' hypothesis-testing model for the red-naped sapsucker, with playback data, contained only 3 of the 11 postulated variables. The classification table for the model shows that it performed very poorly, with a success rate of only 9% for sampling points where sapsuckers were absent (Table 2.1). In addition, a histogram shows the frequencies of the observed groups (absence, 0s, and presence, 1s) versus predicted probabilities (Figure 2.1). A perfect model would result in the 0s and the 1s being completely separate on either side of 0.5 (the chosen pivot value for a binomial assignment to a group). A perfectly random model would result in a normal distribution of 0s and 1s centered on 0.5.

No variables qualified to be included in the RNSA model with non-playback data (Table 2.2). Similarly, the hypothesis-testing model for the northern flicker, with playback data, contained 5 of 10 variables, with an overall correct classification rate of 62% (Table 2.3, Figure 2.2). The model with non-playback data had a classification success rate of only 4% for sampling points where individuals were observed (Table 2.4, Figure 2.3).

The performances of the hypothesis-generating models appeared marginally better, as was expected due to the larger number of variables available to fit the model with the data. With playback data, the sapsucker model performed fairly (an overall classification success rate of 78%) with 10 variables and a constant (Table 2.5, Figure 2.4). With non-playback data, the model performed fairly (overall 76%) with 11 variables plus an intercept (Table 2.6, Figure 2.5). The northern flicker model with playback data performed fairly (overall 75%) with 10 variables and an intercept but the chi-square diagnostic of an acceptable model fit failed (Hosmer-Lemeshow goodness-of-fit, $\chi^2=19.7$, $df=8$, $p=0.01$; Table 2.7, Figure 2.6). The flicker model with non-playback data performed poorly, with 7 variables and a constant, correctly predicting only 48% of cases where individuals were detected (Table 2.8, Figure 2.7). Because the models using playback and non-playback data had few variables in common (five for the sapsucker, three for the flicker), and the performance of each was fair to poor, I concluded that the results were too ambiguous and that the models did not serve as a useful basis for generating hypotheses on either species' use of resources at the stand-level.

Table 2.1. Classification Table for the hypothesis-testing logistic regression model for the red-naped sapsucker, using playback data ($n = 326$; Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 5.7856$, $p = 0.6712$).

		Predicted		
		0	1	Percent Correct
Observed	0	12	118	9.23 %
	1	5	191	97.45 %
				Overall 62.27 %

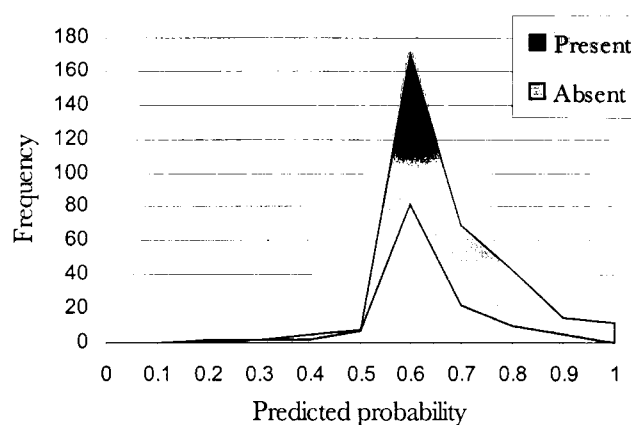


Figure 2.1. An alternate display of the results shown in Table 2.1. This histogram shows the frequencies of the observed groups (Present and Absent) versus predicted probabilities. A perfect model would result in the two groups being completely separate on either side of 0.5. A perfectly random model would result in a normal distribution of both groups centered on 0.5.

Table 2.2. Classification Table for hypothesis-testing logistic regression model for the red-naped sapsucker, using non-playback data. No variables could be included in the model; thus, no accompanying figure could be.

		Predicted		
		0	1	Percent Correct
Observed	0	174	0	100.0 %
	1	152	0	0.00 %
				Overall 53.37 %

Table 2.3. Classification Table for hypothesis-testing logistic regression model for the northern flicker, using playback data ($n = 326$; Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 12.4940$, $p = 0.1305$).

		Predicted		
		0	1	Percent Correct
Observed	0	97	61	61.39 %
	1	62	106	63.10 %
				Overall 62.27 %

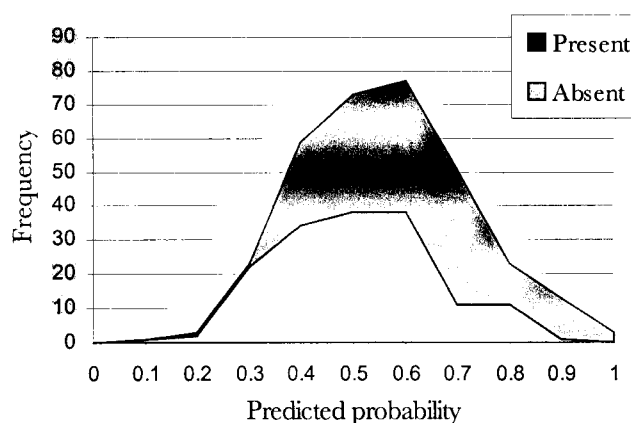


Figure 2.2. An alternate display of the results shown in Table 2.3. This histogram shows the frequencies of the observed groups (Present and Absent) versus predicted probabilities. A perfect model would result in the two groups being completely separate on either side of 0.5. A perfectly random model would result in a normal distribution of both groups centered on 0.5.

Table 2.4. Classification Table for hypothesis-testing logistic regression model for the northern flicker, using non-playback data ($n = 326$; Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 1.8692$, $p = 0.9313$).

		Predicted		Percent Correct
		0	1	
Observed	0	278	1	99.64 %
	1	45	2	4.26 %
				Overall 85.89 %

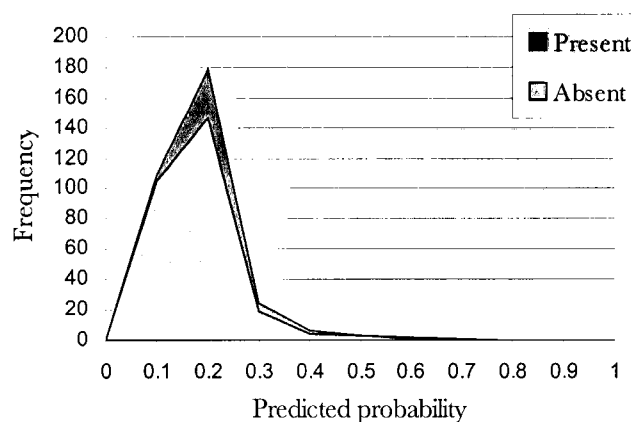


Figure 2.3. An alternate display of the results shown in Table 2.4. This histogram shows the frequencies of the observed groups (Present and Absent) versus predicted probabilities. A perfect model would result in the two groups being completely separate on either side of 0.5. A perfectly random model would result in a normal distribution of both groups centered on 0.5.

Table 2.5. Classification Table for hypothesis-generating logistic regression model for the red-naped sapsucker, using playback data ($n = 326$; Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 9.9783$, $p = 0.2666$).

		Predicted		
		0	1	Percent Correct
Observed	0	85	45	65.38 %
	1	26	170	86.73 %
				Overall 78.22 %

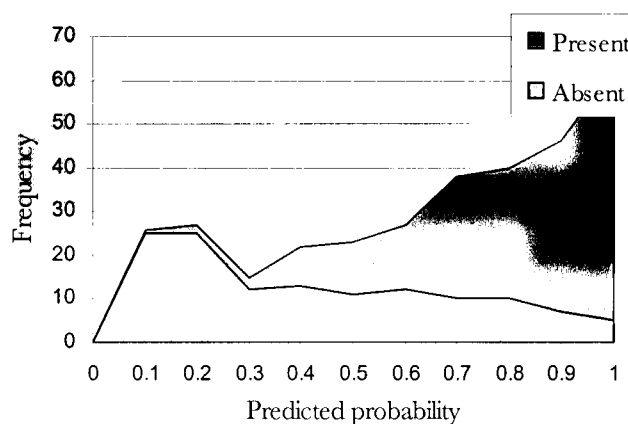


Figure 2.4. An alternate display of the results shown in Table 2.5. This histogram shows the frequencies of the observed groups (Present and Absent) versus predicted probabilities. A perfect model would result in the two groups being completely separate on either side of 0.5. A perfectly random model would result in a normal distribution of both groups centered on 0.5.

Table 2.6. Classification Table for hypothesis-generating logistic regression model for the red-naped sapsucker, using non-playback data ($n = 326$; Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 4.3985$, $p = 0.8195$).

		Predicted		
		0	1	Percent Correct
Observed	0	139	35	79.89 %
	1	42	110	72.37 %
				Overall 76.38 %

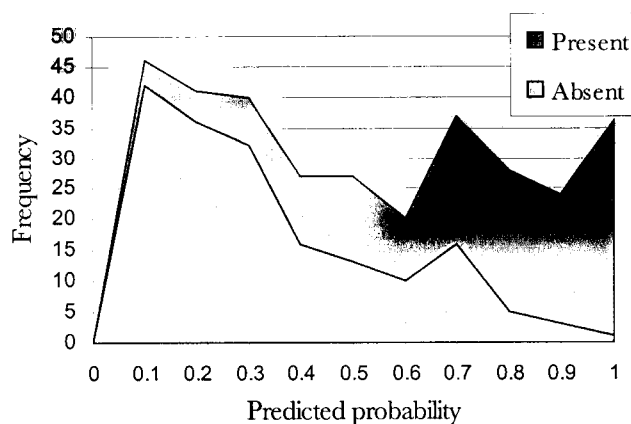


Figure 2.5. An alternate display of the results shown in Table 2.6. This histogram shows the frequencies of the observed groups (Present and Absent) versus predicted probabilities. A perfect model would result in the two groups being completely separate on either side of 0.5. A perfectly random model would result in a normal distribution of both groups centered on 0.5.

Table 2.7. Classification Table for hypothesis-generating logistic regression model for the northern flicker, using playback data ($n = 326$; Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 19.7276$, $p = 0.0114$).

		Predicted		Percent Correct
		0	1	
Observed	0	114	44	72.15 %
	1	39	129	76.79 %
				Overall 74.54 %

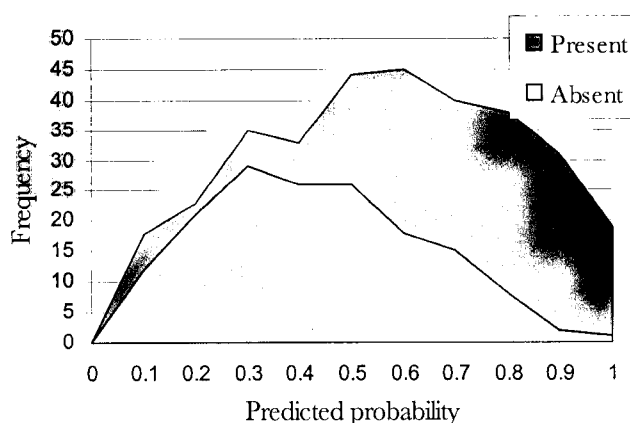


Figure 2.6. An alternate display of the results shown in Table 2.7. This histogram shows the frequencies of the observed groups (Present and Absent) versus predicted probabilities. A perfect model would result in the two groups being completely separate on either side of 0.5. A perfectly random model would result in a normal distribution of both groups centered on 0.5.

Table 2.8. Classification Table for hypothesis-generating logistic regression model for the northern flicker, using non-playback data ($n = 326$; Hosmer and Lemeshow goodness-of-fit test, $\chi^2 = 3.1837$, $p = 0.9223$).

		Predicted		
		0	1	Percent Correct
Observed	0	271	8	97.13 %
	1	24	23	48.94 %
				Overall 90.18 %

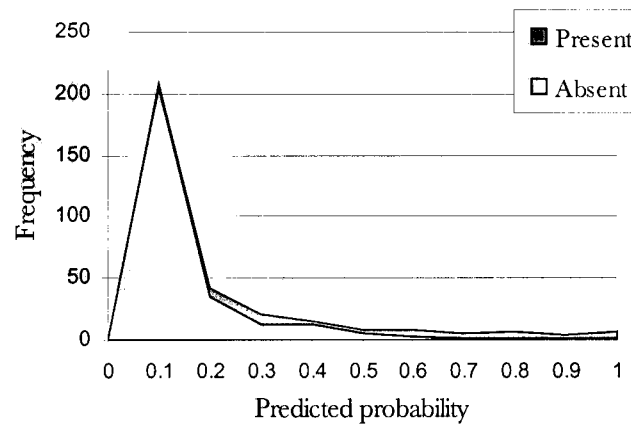


Figure 2.7. An alternate display of the results shown in Table 2.8. This histogram shows the frequencies of the observed groups (Present and Absent) versus predicted probabilities. A perfect model would result in the two groups being completely separate on either side of 0.5. A perfectly random model would result in a normal distribution of both groups centered on 0.5.

2.6 Discussion

The unsatisfactory performance of the models suggests that either species-resource relationships do not occur consistently at the stand level, the data were too noisy for such relationships to be detected, or the wrong variables were measured and used. If the intensity of sampling is too low, it does not capture all occurrences of birds in good habitat, creating the illusion that birds do not occupy areas of good habitat. If habitat is less than 100% saturated, then birds actually do not occupy areas of good habitat, creating the impression that these areas are poor. If habitat is over 100% saturated, birds may occupy poor habitat, again weakening the relationship between occurrence and attributes of good habitat. The use of a playback tape may also draw birds from surrounding, good habitat to poor habitat at a sampling point. Finally, if spatial variability is too low, or spatial periodicity is too high relative to a species territory, then no consistent species-resource relationships may be detected. These factors serve to obscure any species-resource relationships that actually exist. Figure 2.8 shows that these factors affecting the quality of presence / absence data can be classified into two types of "error." A "no detection" may occur in occupied and/or suitable habitat (my Type I error), or poor habitat may be observed to be occupied (my Type II error).

Please note that the table in Figure 2.8 is not exactly analogous to the classification tables in Tables 2.1 to 2.8. While the classification tables show observed against predicted presence or absence, Figure 2.8 shows observed presence or absence against *actual* habitat quality. Only if actual habitat quality is correctly deduced can the correct species-resource relationships be identified. In effect, observed occupancy in Figure 2.8 is equivalent to predicted occupancy in Tables 2.1 to 2.8, because the

predictions of the model are derived from the empirical data.

In addition to the factors discussed above, other variables may also influence the frequency with which species-resource relationships are correctly identified. The number of detections of a species may be contingent on aspects of its behaviour, such as its mobility, frequency of vocalizations and territoriality. Aspects of the sampling design may also affect how accurately species-resource relationships can be measured, such as the number of points and rounds, the point-count and vegetation-plot radii, and the method by which sampling points are located. In an attempt to explore and quantify the effects of these variables on the sampling success rate, or the likelihood of detecting actual species-resource relationships, I created a computer program that simulates a population of paired, mobile, territorial organisms in a landscape consisting of one or more resources. This simulation program is the subject of the following chapter.

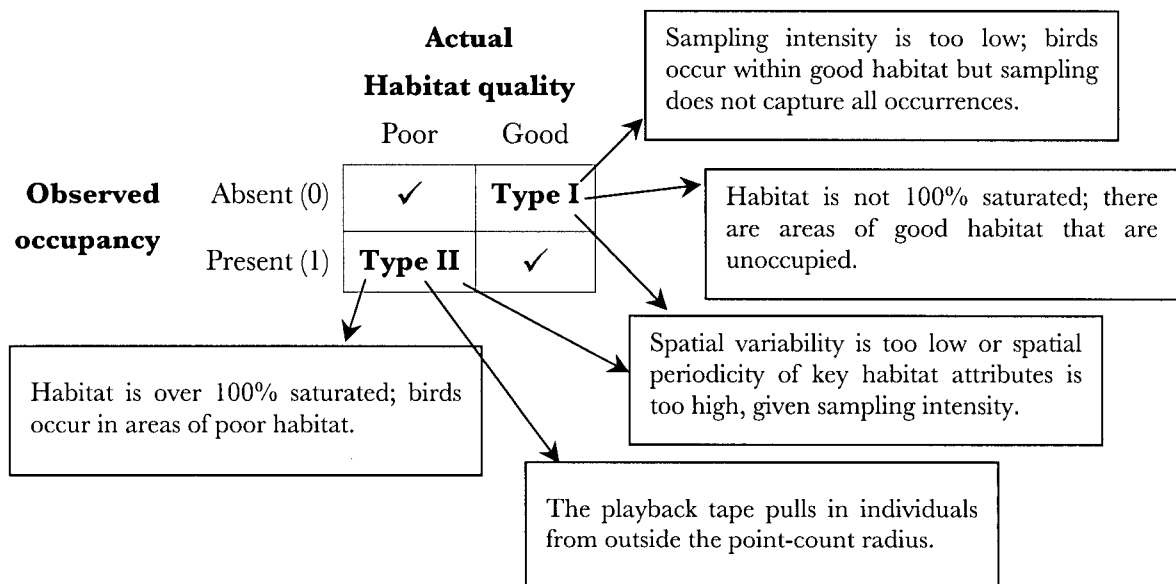


Figure 2.8. Some factors that may confound efforts at detecting stand-level species-resource relationships. Two types of errors, which I define as Type I and Type II, are possible.

CHAPTER III: Sampling Simulation Model

In this chapter I describe a computer program, Sample Sim'on, that simulates the repeated sampling of a population of mobile, territorial organisms within a landscape containing one or more resources. The objective of this exercise is to explore the effects of parameters relevant to the biology of a species and to the sample design, on the success rate with which species-resource relationships can be correctly determined. This exercise was motivated by the unsuccessful attempts to produce informative empirical models for two woodpecker species, the red-naped sapsucker and the northern flicker, described in Chapter II.

In Sample Sim'on, the simulation space consists of a landscape composed of hexagonal cells. The user first defines one or more resources for that landscape. Each cell is assigned a density value for each resource. In nature a resource could be, for example, a species of tree (e.g., decay class 2 aspen) or a type of prey (e.g., flying arthropods). The user defines the spatial distribution of each resource in a simulation by minimum cell value, maximum cell value, cover (how much of the landscape is occupied by the resource), spatial period (average distance among local maxima in the resource density distribution), and associations with other resources. The user defines the species by maximum range, position mode and function, and the amount of each resource required by a breeding pair. The program then populates the landscape with territories, until the landscape is either completely saturated or the user has stopped the process. Each established territory fulfills the defined resource requirements of the hypothetical species. The user defines the sample design by type, point count radius, vegetation plot radius,

number of points, and number of rounds. The user also defines the detection function, which describes the detectability of the species as a function of distance from an observer. Sample Sim'on places sampling points accordingly and generates simulated data, consisting of the number of detections and the resource density at each point.

A simple linear regression is then performed on these data to determine whether the species-resource relationship for each resource is positive or negative, significant ($p < 0.05$) or non-significant. For resources required by the species, a positive and significant relationship is correct, while any other kind of relationship is incorrect. Finally, the sampling process is repeated systematically over varying numbers of points and rounds, and this process is in turn repeated 20 times. The result is a power matrix for each resource, showing the success rate in determining the actual species-resource relationship for each combination of points and rounds. The combination with an acceptable success rate ($\geq 95\%$) representing the least sampling effort can then be identified.

I conducted a series of simulations, each with one resource defined. Each simulation differed from the original, 'baseline' simulation, in the value of one parameter. The effect of each parameter on sampling success rate is thus explored. I conducted a second series of simulations with two or more resources defined. These runs represented more complex scenarios, which move toward approximating the level of complexity likely to exist in nature. I use the results of these simulations to postulate a set of rules which may be used to maximize sampling success rate, given estimates of the parameters used in Sample Sim'on.

The results of the simulations show that the relative magnitudes of point-count radius, average territory size, and spatial period of required resources are critical in

determining whether the detection of species-habitat relationships will be possible. The likelihood of success also depends greatly on the sampling intensity (number of points times number of rounds per point). It turns out that only under the most simple scenarios can species-resource relationships be consistently and correctly identified using the conventional methodology of point counts and vegetation plots.

3.1 Model development and construction

Sample Sim'on, short for 'Sample Simulation,' was written in Microsoft's Visual Basic 5.0 programming environment (<http://msdn.microsoft.com/vbasic/>) under Windows 95 on an IBM-compatible personal computer. The program simulates the repeated sampling of a population of paired, mobile, territorial organisms within a landscape containing one or more resources. The landscape is a space of arbitrary size, divided into a grid of hexagonal cells. A hexagonal grid was chosen because adjacent cells are always equidistant. Any simulation consists of three major steps: generating the resources, populating the landscape, and sampling.

3.1.1 Generating the resources

The first step in a simulation is to define and generate one or more resources. A resource is analogous to any quantifiable environmental attribute, e.g., trees of a particular species or decay class, prey of a particular species, area of open ground. After a resource has been generated, each hexagonal cell in the landscape contains a value in the range $[0, 100]$ which corresponds to the relative density of that resource, e.g., the number of trees, kilograms of arthropods, square metres of open ground. A value of zero represents an absence of the resource, while a value of 100 represents the

maximum possible density of the resource. At least one resource must be required by the simulated species, and all resources required by this species must be defined.

I designed Sample Sim'on to be able to generate resources distributed in space in a variety of ways. I assumed that most resources in nature fundamentally have a spatially autocorrelated distribution, analogous to a topographic map. The closer two cells are to one another, the more similar their density values; cells exhibit spatial dependence. For example, if one were to divide 100 ha of forest into 1-ha cells, and determine the number of trees of species X in each cell, it is unlikely that densities in adjacent cells would prove to be independent. Similarly, if one 1-ha cell were divided into 100 100-m² cells, densities in adjacent cells would tend to be more similar to one another than to increasingly distant cells. However, the maximum distance over which spatial dependence acts, and the range of densities in cells, would vary from species to species. Therefore, to vary distributions in Sample Sim'on, parameters modify the range of cell values in the landscape (minimum and maximum cell values), the proportion of the landscape where they are non-zero (cover), and their period of variation in space (spatial period). It is also likely that many resources exhibit associations, either positive or negative, with other resources.

3.1.1.1 Plasma algorithm

To generate the fundamental, spatially-autocorrelated distribution of a resource, I used the plasma algorithm (e.g., <http://eigen.ee.ualberta.ca/hppd/hpux/X11/Demos/plasma-1.0/>), a recursive procedure which fills in intermediate values at increasingly refined spatial scales. The plasma algorithm is typically used to create cloud-like images or random elevation maps. The version I used operates

on a square grid, so while generating the resources I initially treated the landscape as if it were a square grid. The rules for generating the plasma were as follows:

1. Start with a square grid representing the entire landscape, such that its width is w , e.g., $w = 32$ units. To deal with boundary effects, the boundaries of the grid are wrapped, i.e. cells on opposite edges are treated as if adjacent. Start with a grid of 4 cells, each $g = w/2$ units wide, and assign each cell a random value in the range $[-g, g]$ (Figure 3.1a). The resolution of the grid equals $1/g$.
2. Double the resolution, or equivalently halve the cell width so that $g = w/4$. Assign each new cell a value that is the weighted average of the four cells from the previous step, plus a random value in the range $[-g, g]$ (Figure 3.1b).
3. Repeat Step 2. In each recursive step the resolution is doubled, i.e. the random number range and the width of cells are halved (Figure 3.1c,d). Stop when the width of a cell is equal to 1 (Figure 3.1e).
4. Finally, the square grid is converted into a hexagonal grid with the same number of cells (Figure 3.1f). A hexagonal grid is preferred because adjacent cells are always equidistant.

3.1.1.2 Modifying the distribution

The basic distribution created using the plasma algorithm can be modified by changing the minimum and maximum cell values, cover, spatial period, and associations with other resources. By default, the minimum cell value, u_i , for resource i is 0, and the maximum cell value, U_i , is 100. If the user changes either value, the distribution is re-scaled so that cell values fall in the range $[u_i, U_i]$ (Figure 3.2). If $u_i > 0$, then cover (see below) must equal 100, since at least some of the resource is present in all cells. U_i cannot exceed 100.

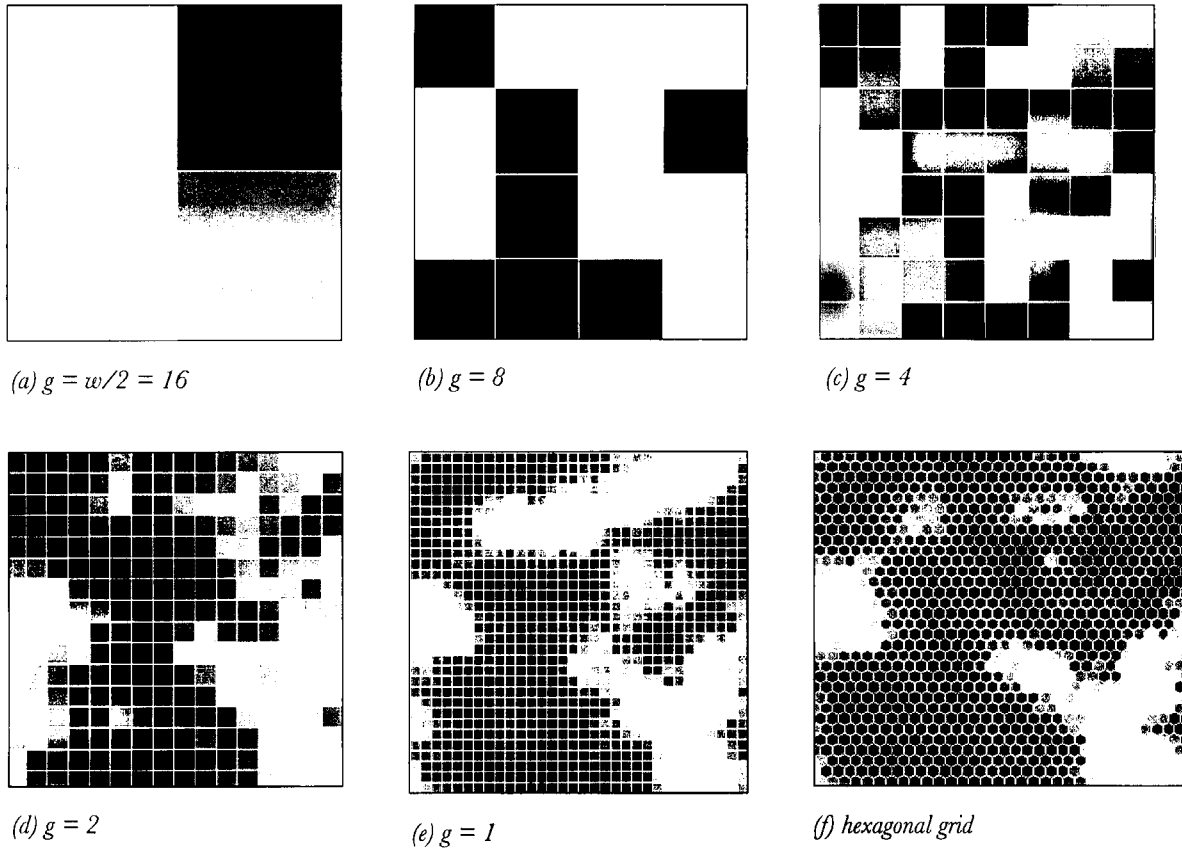


Figure 3.1. Steps followed in the plasma algorithm, which is used to generate the fundamental, spatially autocorrelated distribution of a resource in Sample Sim'on. The darker a cell, the higher the density of the resource. A white cell corresponds to an absence of the resource. g represents the width of each cell.

Cover, c_i , defines the approximate percentage of the landscape which is covered by resource i . If $c_i < 100$, then u_i must equal 0. With cell values falling in the range $[0, U_i]$, a threshold value (t_{ci}) is calculated, such that $t_{ci} = U_i * [1 - (c_i / 100)]$. Cells with a value less than t_{ci} are given a value of t_{ci} , then all values are re-scaled to fall in the range $[0, U_i]$ (Figure 3.3). The relationship between c_i and actual percent cover is not linear, and is more likely to randomly fluctuate at extreme values.

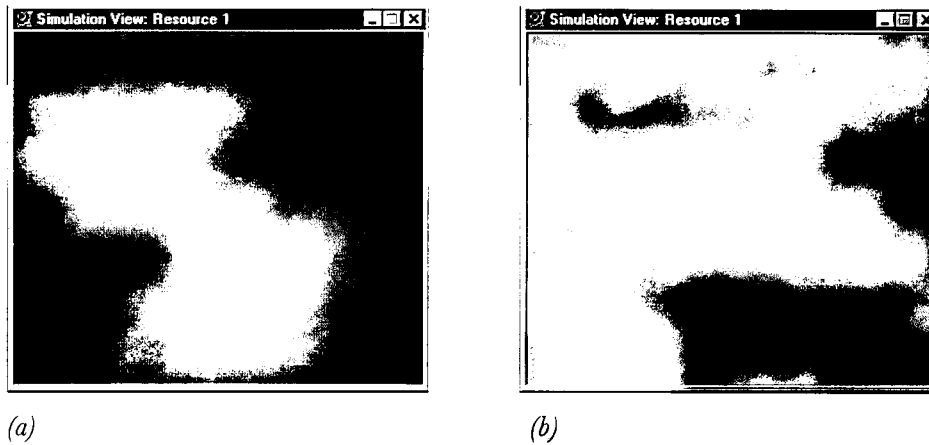


Figure 3.2. Minimum and maximum cell values are used to modify a resource distribution. In this example, minimum cell value, $u_i = 25$ (a) and maximum cell value, $U_i = 75$ (b).

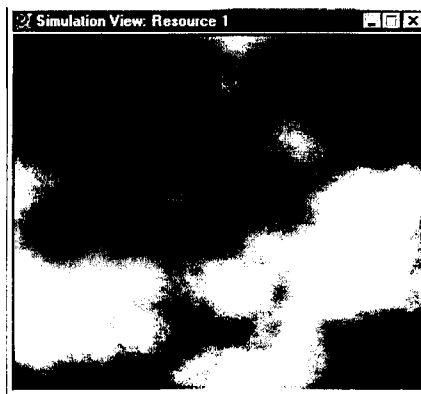


Figure 3.3. Cover is used to modify a resource distribution. In this example, cover, $c_i = 80$.

Spatial period, sp_i , is the average distance between local maxima in the distribution of resource i , or the maximum distance over which spatial dependence acts. The smaller the spatial period, the more ‘lumpy’ the resource appears. Spatial period is changed by altering the relationship between resolution ($1/g$) and the random value range described above. In Figure 3.1, as resolution is increased the random value range is decreased proportionately. If the relationship is made non-linear, then the random value range is only a function of resolution beyond the

threshold resolution, t_n . In Sample Sim'on, the user enters spatial period as a relative value in the range $[0, 100]$, where 0 results in a low spatial period, and 100 results in a high spatial period (Figure 3.4).

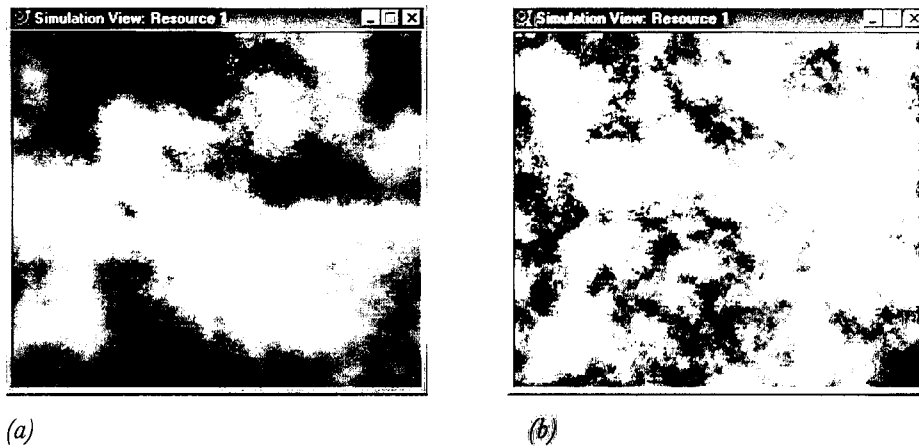


Figure 3.4. Spatial period is used to modify a resource distribution. In this example, spatial period, $sp = 32$ (a) and $sp = 16$ (b).

In nature, the distributions of many resources may be positively or negatively correlated with the distributions of other resources. For example, the number of Douglas fir trees may be negatively correlated with the amount of open ground, or the abundance of arthropods may be positively correlated with foliage density. To illustrate this, let an association (a_{ij}) of + 30% exist between resource i and resource j . First, Sample Sim'on generates resources i and j independently of one another using the plasma algorithm, such that values fall in the range $[0, 100]$. Then, for resource j , cells are recalculated such that the value of each cell equals $100\% - a_{ij} = 70\%$ of its original value, plus $a_{ij} = 30\%$ of the corresponding cell value for resource i . Resource j is then modified according to values of u_j , U_j and c_j (Figure 3.5).

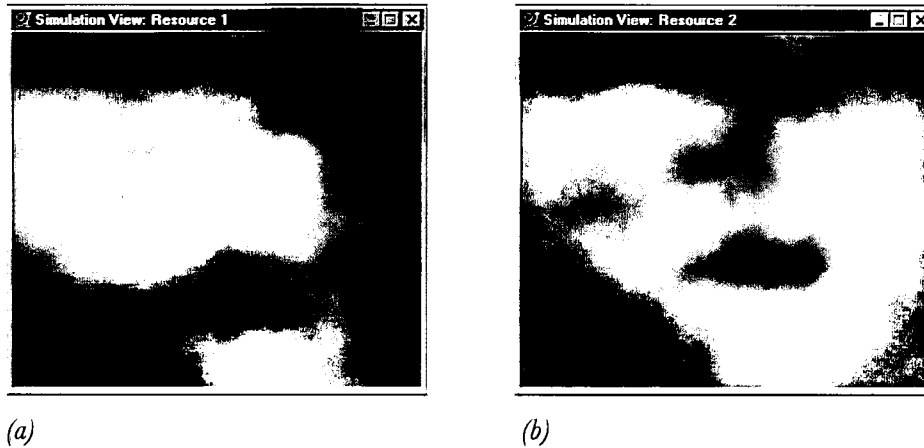


Figure 3.5. Associations may be created among resource distributions. In this example, Resource 1 (a) has a 50% positive association with Resource 2 (b).

Parameters describing minimum and maximum cell values, cover, spatial period, and associations with other resources allow the user to create a wide variety of resource distributions in Sample Sim'on. The effects of various parameter values on sampling success rate are examined later in this chapter. At this stage in the simulation, each cell contains a density value for each resource defined, in the range $[u_j, U_j]$ units.

3.1.2 *Populating the landscape*

Once the spatial distribution of each resource has been defined, the next step in a simulation is to populate the landscape with territories of the simulated species. Maximum range, position mode and function, and resource requirements are defined by the user and used to determine how the landscape is populated. Sample Sim'on makes the following assumptions about the species:

1. The species is mobile and territorial. Each territory is inhabited by two equally detectable individuals (i.e., a breeding pair) who always remain within its boundaries.
2. A territory must fulfill the breeding pair's resource requirements within a maximum

radius defined by the maximum range (m) of the species. The minimum number of units of each resource required by a breeding pair is defined by the user.

3. Territory boundaries do not overlap and do not change, once established.
4. The proportion of time an individual spends in a particular cell within its territory can be a function of the distance to the centre of the territory (*Territory* position mode). This function is called the position function, and is defined by the user. Alternately, the proportion of time an individual spends in a cell can be a function of the resource density in that cell (*Resource* position mode).

3.1.2.1 Algorithm for creating one territory

A territory is created provided that the resource requirements of the species can be fulfilled within a radius bounded by its maximum range (m). First, an unoccupied cell is randomly chosen as the territory origin. The program then wanders from cell to cell around the origin, keeping a running total of resource units as it goes. If the position mode is set to *Territory*, then the resource density available to the species in a particular cell is modified using the position function, $f_p(x)$, which describes the relative amount of time spent in a cell given its distance, x , from the territory origin (Figure 3.6). For example, if the position function is as shown in Figure 3.6, then the probability of a species being in a cell at the edge of its territory is 30% of the probability of it occurring in the centre. Therefore, if the cell at the origin contains 60 units of a required resource, while a cell at the edge contains 80 units, then the effective value of the edge cell is only 24 units. Alternately, if the position mode is set to *Resource*, then the resource availability in cells is not modified, and the proportion of time an individual spends in a cell is a function of resource density in that cell. Once the program has found enough units of each resource to satisfy the resource requirements of the species, without

wandering farther than m cells from the origin, the territory is established. If the program cannot find adequate resources within the maximum radius, then the attempt to create a territory fails, and a new one begins.

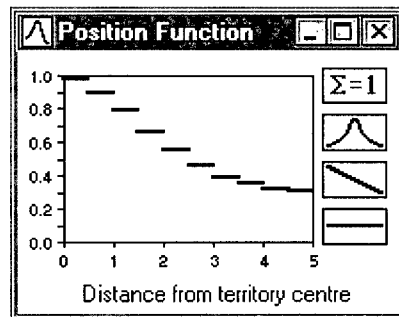


Figure 3.6. The position function, used when the position mode is set to *Territory*, defines the relative amount of time an individual spends in a cell with respect to the centre of its territory. In this example, the position function is a half-normal curve, translated ‘up’ the vertical axis so that it has a minimum value of $f_p(5) = 0.3$.

3.1.2.2 Iterations

Each attempt to create a territory is called an iteration. Territories are placed sequentially in the landscape until a maximum number of iterations is attained. Sample Sim’on plots a territory curve, which shows the number of successfully placed territories against the total number of iterations (Figure 3.7). Uninterrupted, this curve reaches an asymptotic maximum corresponding to 100% saturation of the landscape. The user may interrupt the process before the maximum number of territories is reached, in order to produce levels of saturation less than 100%.

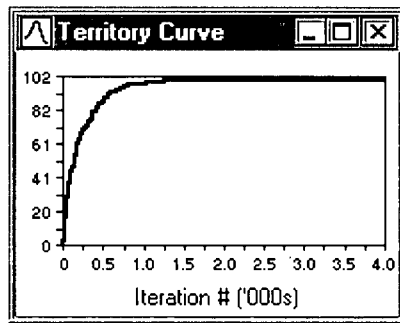


Figure 3.7. The territory curve plots the number of successfully placed territories against the number of attempts at placing territories (iterations). Uninterrupted, an asymptote is approached that corresponds to 100% saturation.

Territories are sequentially placed in the landscape as each territory meets the resource requirements of the species. Territory sizes tend to vary such that territories with a higher average resource density are smaller, and territories with a lower average resource density are larger (Figure 3.8). This is consistent with observations made for many songbird species. For example, black-throated green warbler (*Dendroica virens*) territories are twice as large in white spruce forests as in red spruce forests, probably because of the greater difficulty of foraging on white spruce foliage (Morse 1989). Also, the density of Blackburnian warblers (*Dendroica fusca*) is 40% of that of black-throated green warblers in the same forest, because the high foliage used by the former is 40% of the density of the lower foliage used by the latter (Morse 1989). The maximum size of a territory is bounded by m , the maximum range of the species. Territories are placed in the landscape until no more can be placed, or the user stops the process. Now that the landscape has been populated with the territories of the simulated species, a sample design can be defined.

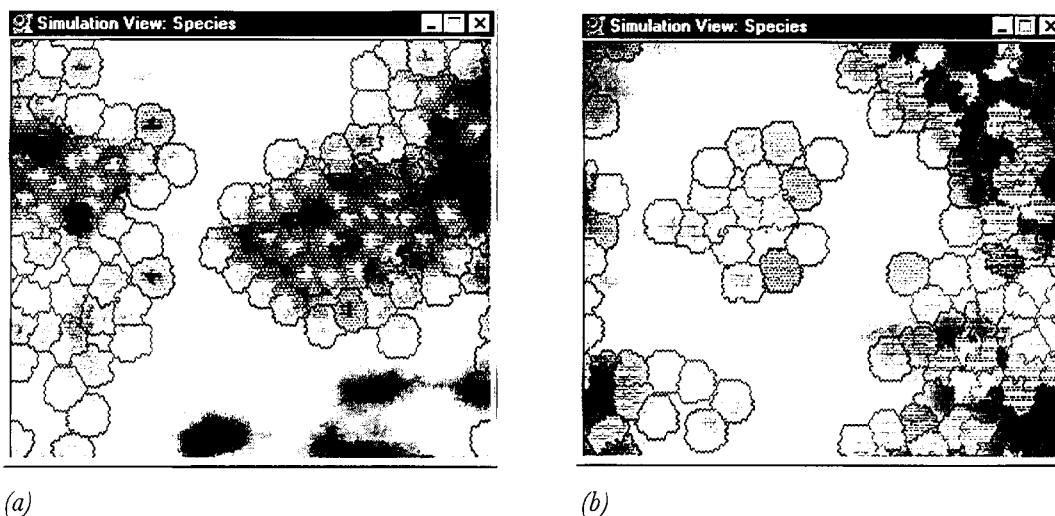


Figure 3.8. The second step in any simulation is to populate the landscape with territories. In this example, the population is at 100% saturation, with the position mode set to *Territory* (a); the population is at 100% saturation, with the position mode set to *Resource* (b). Different colours are used to help distinguish adjacent territories.

3.1.3 Sampling

Once the territories of the simulated species have been placed in the landscape, the user is ready to define the sample design. Each sampling point consists of a point count used to sample the population, and a vegetation plot used to sample the resources. The user must define the type of sample design, point count radius, vegetation plot radius, and a detection function for the species. Over a range of numbers of points and numbers of rounds, Sample Sim'on repeatedly produces simulated data sets. For each data set and resource, a simple linear regression is performed in order to determine whether the observed species-resource relationship is correct. The final result is a power matrix, which shows the relationship between sampling effort and success rate.

3.1.3.1 Sampling the population once

A sampling point consists of a point count and a vegetation plot, centred on the same cell. Sampling points may be placed randomly or in a single transect or grid with a random starting point and direction. The user defines the radii of point counts and vegetation plots, and a detection function for the species. The detection function, $f_d(x)$, determines the detectability of an individual as a function of its distance, x , from an observer (i.e. the centre of a sampling point; Figure 3.9). The user defines this function. By default, the function is flat (i.e. the probability of detection is always 1, no matter the distance from the observer). A more realistic form is a half-normal curve, with the probability of detection approaching 0 at some distance from the observer (Buckland *et al.* 1993). To sample the population once, the user must define the number of sampling points and the number of rounds (i.e., the number of times each point is sampled).

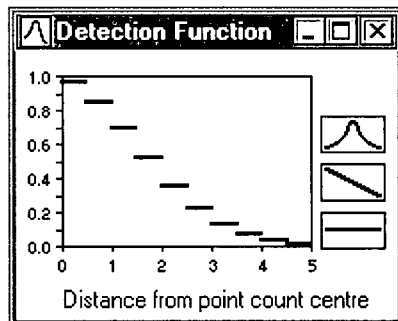


Figure 3.9. The detection function defines the detectability of an individual, with respect to its distance from an observer. In this example, the detection function is a half-normal curve, attenuating to zero beyond a distance of 5 cell widths.

Once the sample design has been defined, Sample Sim'on locates the sampling points according to the chosen method (random, transect, grid or even grid; Figure 3.10). No two sampling points can overlap. Before proceeding with

sampling, the probability of occurrence of an individual is calculated for every cell in the landscape within a point count. If the position mode is *Territory*, this probability, $p_o(i)$, is calculated by dividing the position probability in cell i by the sum of position probabilities across all cells in its occupant's territory. If cell i is unoccupied, $p_o(i) = 0$. For example, if cell i is occupied by individual X , cell i is 3.5 cell-widths away from the centre of X 's territory, and the sum of position probabilities across all cells in X 's territory is 100, then $p_o(i) = f_p(3.5)/100$. If $f_p(3.5) = 0.6$, then the probability of individual X occurring in cell i at any time is 0.006. If the position mode is *Resource*, $p_o(i)$ is calculated by dividing the resource density in cell i by the sum of resource densities across all cells in its occupant's territory.

Within a vegetation plot, the program calculates the average number of units per cell for each resource. Point counts are performed by comparing a random number with the detection probability in each cell, to determine whether an individual is detected. The detection probability, $p_d(i)$, is determined by the probability of occurrence and the detection function. Say, for example, cell i is 2.5 cell-widths away from the observer, $p_o(i) = 0.006$, $f_d(2.5) = 0.8$, and a random number in the range $[0, 1)$ equals 0.0035. Since the random number is less than the probability of detection, $p_d(i) = 0.0048$, an individual is detected. If the random number were greater than $p_d(i)$, an individual would not be detected. The same individual cannot be detected twice in the same point count and round. All point counts are repeatedly sampled according to the number of rounds. Once one sample is complete, Sample Sim'on determines whether the correct species-resource relationship was detected, for each resource.

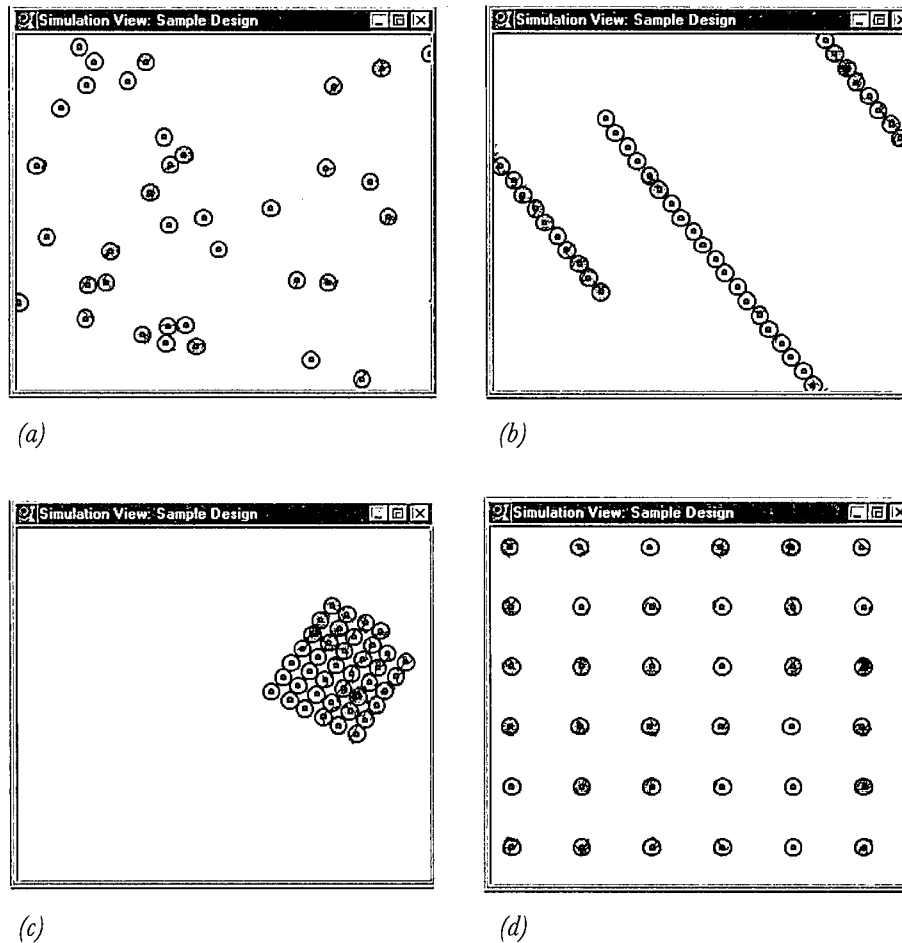


Figure 3.10. The placement of sample points may be completely random (a), in a transect (b), in a grid (c) or in an evenly-spaced grid covering the entire landscape (d).

3.1.3.2 Determining the species-resource relationships

Once the population and resources have been sampled, Sample Sim'on plots the average number of detections against the average resource density, for each resource (Figure 3.11). A simple linear regression is performed to determine the direction (positive or negative) and significance ($p < 0.05$) of the species-resource relationship. For each resource that is required by the species, a correct relationship

is positive and significant. For each resource that is *not* required by the species, a correct relationship is non-significant. Any other kind of relationship is incorrect. Thus, each species-resource relationship determined via sampling may be classified as correct or incorrect. The sampling procedure is repeated over varying numbers of points and rounds, and this is in turn repeated 20 times.

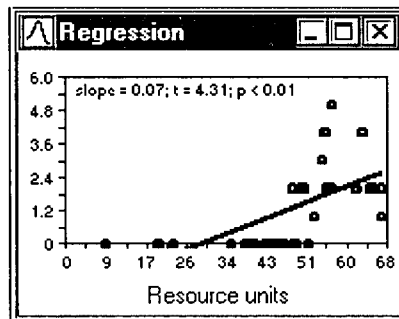


Figure 3.11. Once the point counts and vegetation plots have been sampled, the simulated data are plotted, average number of detections against average resource concentration. Simple linear regression is used to compute the best-fit line. The significance of its fit to the data is shown at the top of the graph.

3.1.3.3 Generating sample matrices and power matrices

Sample Sim'on repeats the sampling process over a range of numbers of points and rounds. The user defines this range. In all simulations presented in this thesis I used a range of 3-40 points and 1-15 rounds, representing extremely low to extremely high sampling effort (number of points multiplied by number of rounds). Performed once, the program produces a sample matrix, showing the correctness of species-resource relationships detected for each resource and each combination of points and rounds. To increase the accuracy of these results, a sample matrix is generated 20 times and the success rate is calculated for each cell in the matrix. The result is a power matrix, showing the success rate in detecting the correct species-

resource relationships, given the sampling effort (Figure 3.12). Combinations of points and rounds exceeding a threshold success rate may then be classified as acceptable. I selected 95% as the threshold; therefore, for each successful cell (coloured black) in the power matrix, the probability of *not* detecting the correct species-resource relationship is $<5\%$. For each simulation, Sample Sim'on conducts a total of 1,960,800 individual point counts. For an equivalent sampling effort to be accomplished in the field, 10 observers would each have to conduct 20 point counts every day of the year for almost 27 years.

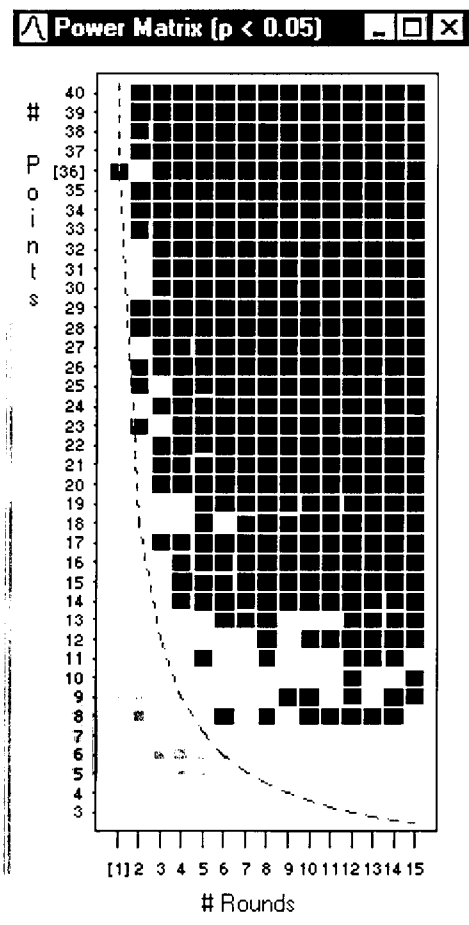


Figure 3.12. The end product of a simulation is a power matrix, for each resource defined. For every combination of points and rounds, a square is drawn whose size corresponds to the success rate in correctly determining the species-resource relationship. Those squares that represent a satisfactory success rate ($\geq 95\%$) are coloured black. A line of equal sampling effort is included (dashed line), passing through the black square representing the smallest sampling effort (denoted by square brackets, []).

3.1.3.4 Determining the minimum sampling effort

Once the power matrix has been created for a simulation, the combination of points and rounds representing the minimum sampling effort, given an acceptable success rate, can be identified. Sampling effort is simply the number of points multiplied by the numbers of rounds, or the total number of point counts conducted. Sample Sim'on identifies the minimum-effort cell, then draws an equal-effort line through the power matrix (Figure 3.12).

Once the user has defined sample design type, point count radius, vegetation plot radius, and a detection function, Sample Sim'on samples the species population using a specified number of sample points. Each point is re-sampled according to the number of rounds specified. A simple linear regression is then performed, and the correctness of the detected species-resource relationship is determined for each resource. This is repeated over varying numbers of points and rounds, to generate a sample matrix. The sample matrix is in turn repeated 20 times to generate a power matrix, which shows the success rate in determining the correct species-resource relationships given the number of points and rounds. Finally, the program identifies the cell representing the lowest sampling effort, given an acceptable success rate, and draws an equal-effort line through it. By changing the simulation parameters over a number of different scenarios, and by generating a power matrix for each scenario and resource, the effects of each parameter on sampling success rate can be explored.

3.2 Simulated scenarios

In order to explore the effects of each parameter on sampling success rate, I ran a series of simulations with one resource defined, changing the value of a different parameter in each run (Table 3.1). Simulation #1 was designated as the 'baseline' to which to compare subsequent runs. In simulation #2, the position mode was set to *Resource*. In simulation #5, a flat detection function was replaced with a half-normal curve (Buckland *et al.* 1993), approaching zero at the point count radius (Figure 3.9). In simulation #6, the minimum value of the position function was changed from 0.3 to 0.6, corresponding to a more dispersed core area of each territory. In simulation #21, I reran the baseline simulation, in order to get an idea of how variable the power matrix can be, given exactly the same parameters. Finally, I conducted simulation #22, again with the same parameters as the baseline run, but with a four-fold increase in the landscape size, in order to see if landscape size affects the resulting power matrix. The remaining simulations differed from the baseline simulation in the value of one parameter, highlighted in Table 3.1.

I also ran a series of simulations with two or more resources defined (Table 3.2). In simulations #1 and #2, two resources are defined with no (i.e. a random) association between their distributions. In the first simulation, the species requires both resources equally; in the second simulation, the species requires little of Resource 2 relative to Resource 1. In simulations #3 and #4, there is a 50% positive association between Resources 1 and 2. In simulation #3, the species only requires Resource 1; in simulation #4 it requires both resources equally. Resources 1 and 2 have a 50% negative association in simulation #5, with the species requiring both resources equally. Simulation #6

presents a more complicated scenario with three resources, all required by the species. The parameters I used for this simulation were arbitrary but, for example, Resources 1 and 3 could represent two species of tree required by the species for foraging, while Resource 2 could represent a rarer resource required for nesting. I reran this simulation (#7) with the position mode set to *Resource*.

Sample Sim'on simulates the repeated sampling of a population of paired, territorial, mobile organisms in a landscape containing one or more resources. Parameters describe the spatial distribution of resources, characteristics of the simulated species, sample design and species detectability. The end result of a single simulation is a power matrix, which shows the success rate in correctly determining the actual species-resource relationships defined in the simulation, over a range of numbers of points and numbers of rounds. A success rate $\geq 95\%$ is deemed acceptable. The combination of points and rounds with an acceptable success rate, where sampling effort is lowest, can be identified. I ran a series of simulations to explore the effects of variability in each parameter on the power matrix, and a second series to better approximate the degree of complexity expected in nature.

3.3 Results and Discussion

In this section, I present and discuss the power matrices for each simulation. Supplementary figures of the resource distributions, territories and other aspects of each simulation, are provided in Appendix II. I discuss the implications of these results in Chapter IV.

3.3.1 Simulations with one resource

Results of simulations with one resource defined are shown in Figure 3.13. Each power matrix includes a dashed line, a line of equal effort passing through the successful combination of points and rounds representing the lowest sampling effort. The addition of this line makes it evident that, for a given sampling effort, increasing the number of sampling points and decreasing the number of rounds consistently leads to a higher success rate. This makes intuitive sense. By chance, a given set of sampling points may be placed such that the likelihood of detecting the correct species-resource relationship is low. Repeatedly resampling these points can improve the success rate only to a limited degree. If one locates a new set of random points, however, the likelihood that they will again by chance produce weaker-than-average results is small. It is arguable, however, that the real effort required to sample new points, rather than resample already established points, is greater. More work must be done in the field to measure out and become familiar with the locations of new points, and to mark the boundaries of new vegetation plots.

The results of simulations #13 to #15 show how stratified-random methods of placing points affect the success of a sampling effort. Using transects (simulation #13) greatly increases the effort required for successful sampling, while using a grid of adjacent points (simulation #14) renders the exercise practically impossible. The less randomized the position of each sampling point, the more likely all points are to fall, by chance, in an area which leads to an incorrect or unsuccessful detection of a species-resource relationship. In addition, when points are placed within a limited area, they are less likely to cover the full range of resource densities, effectively

increasing minimum cell value (simulation #8) and decreasing maximum cell value (simulation #9). Both of these actions necessitate a higher sampling effort than the baseline scenario. Placing an evenly spaced grid across the entire landscape (simulation #15), however, produces better results than a completely random design. If points are placed completely randomly, they may by chance fall within a small portion of the landscape, thus having the same weaknesses as a grid. An even grid ensures that points are always spaced across the entire landscape.

Doubling the point count radius (simulation #16) considerably reduces the sampling effort required for a successful result. Increasing the point count area increases the number of individuals detected per point, thus increasing statistical power. Point count radius, however, cannot be increased indefinitely. The flat detection function used in all simulations except simulation #5 is probably unrealistic. It is more likely to resemble a half-normal curve (Buckland *et al.* 1993), reducing the number of detections and increasing the minimum sampling effort.

Simulations #3, #17, and #18 produced poorer results than the baseline for the same reasons. In simulations #17 and #18, the landscape was less than fully saturated with territories. As a result, some areas of suitable habitat (i.e. high resource concentration) lacked individuals, weakening the possibility of detecting a species-resource relationship. This constitutes the Type I error that I anticipated in Chapter II. Reducing the maximum range of the species (simulation #3) had a similar effect by reducing the total number of territories in the landscape. Increasing the maximum range of the species (simulation #4) also produced poorer results than the baseline. Despite allowing a greater number of territories to be placed in the landscape, this

action resulted in a greater likelihood that individuals would be found in areas of low suitability (i.e. low resource concentration). Changing the position function (simulation #6) also allowed many more territories to be placed in the landscape, and produced poorer results than the baseline. Observing individuals in areas of actually poor habitat results in a Type II error (see Chapter II).

Decreasing the spatial period of the resource (simulations #10 and #12) had among the most devastating effects on sampling success (Figure 3.13). As spatial period decreases, the variance in resource concentration within a vegetation plot and within a point count increases, making it more difficult to distinguish between points. Decreasing the spatial period results in both Type I and Type II errors (see Chapter II).

Changing the position mode from *Territory* to *Resource* (simulations #2, #11 and #19) did not perceptibly affect the results. With position mode set to *Resource*, the time an individual spends in a cell is directly proportional to the resource concentration in that cell. I expected this alternate method to result in a higher rate of sampling success, on average. The fact that it did not shows that other factors, such as the number and size of sampling points, are thus far more important in determining sampling success.

3.3.2 Simulations with two or more resources

Results of simulations with two or more resources defined are shown in Figure 3.14. In simulation #1, the species requires Resources 1 and 2 in equal amounts. The correct species-resource relationships were practically never found for either resource. Because there was no association between the distributions of Resource 1 and 2, the

species was often likely to be present (i.e. observed) in cells that were poor in one resource, but rich in the other. In simulation #2, Resource 2 is required by the species considerably less than is Resource 1. Resource 2 could represent a rare, but vital resource required by the species, such as trees suitable for nesting. However, no relationship whatever is found between the species and Resource 2. Simulation #3 shows how a species-resource relationship can be erroneously detected, if the distribution of an unused resource is correlated with the distribution of a used one. Although Resource 2 is not used by the species, a relationship is readily found for it, because its distribution has a 50% positive association with Resource 1. Simulation #4 presents an identical scenario, except that the species now also requires Resource 2 in equal amounts to Resource 1. Here, a strong species-resource relationship is found for both resources. Simulation #5 shows how species-resource relationships can be missed if the distributions of the resources required by the species are negatively correlated. Even though the species uses both Resource 1 and Resource 2, no relationship is found for either, because their distributions have a 50% negative association. Finally, in simulations #6 and #7, no species-resource relationships are found, even though the species uses all three resources defined in the simulation. The three resources have different values for minimum and maximum cell values, cover, and spatial period. The effects of all of these parameters, first seen individually in Figure 3.13, are compounded such that the detection of species-resource relationships is practically impossible. As in the simulations with one resource defined, the position mode did not greatly affect the results. If the actual patterns in nature resemble those produced in Sample Sim'on, then it seems unlikely that the conventional methodology of using

point counts and vegetation plots to deduce species-resource relationships will be feasible logistically.

The simulations I conducted using Sample Sim'on show how the values of various parameters affecting resource distribution, species behaviour, and sample design may affect success in detecting species-resource relationships. Only under a limited set of simplified scenarios is it possible to correctly and consistently deduce species-resource relationships, using the conventional method of the point count census. More realistic scenarios (e.g., with sampling points placed in a grid; two or more resources required by the species) defy any efforts to do so.

Table 3.1. Simulations with one resource defined. Simulation #1 acted as a baseline for comparison with subsequent runs. Shaded boxes highlight the parameter changed in each run.

Simulation #	Species				Resource				Sampling		
	Max. range	Resource requirement	Detection† function	Position† function	Cover	Minimum cell value	Maximum cell value	Spatial period	Point placement	Point count radius	Vegetation plot radius
1 ^o	5	2500	F	N _{0.3}	100	0	100	64	Random	2.5	0.564
2 ^a	5	2500	F	-	100	0	100	64	Random	2.5	0.564
3	4.5	2500	F	N _{0.3}	100	0	100	64	Random	2.5	0.564
4	5.5	2500	F	N _{0.3}	100	0	100	64	Random	2.5	0.564
5	6	2500	N	N _{0.3}	100	0	100	64	Random	2.5	0.564
6	6	2500	F	N _{0.6}	100	0	100	64	Random	2.5	0.564
7	6	2500	F	N _{0.3}	80	0	100	64	Random	2.5	0.564
8	6	2500	F	N _{0.3}	100	25	100	64	Random	2.5	0.564
9	6	2500	F	N _{0.3}	100	0	75	64	Random	2.5	0.564
10	6	2500	F	N _{0.3}	100	0	100	32	Random	2.5	0.564
11 ^b	6	2500	F	-	100	0	100	32	Random	2.5	0.564
12	6	2500	F	N _{0.3}	100	0	100	16	Random	2.5	0.564
13	6	2500	F	N _{0.3}	100	0	100	64	Transect	2.5	0.564
14	6	2500	F	N _{0.3}	100	0	100	64	Grid	2.5	0.564
15	6	2500	F	N _{0.3}	100	0	100	64	Even grid	2.5	0.564
16	6	2500	F	N _{0.3}	100	0	100	64	Random	5	0.564
17	6	2500	F	N _{0.3}	100	0	100	64	Random	2.5	1.128
18 ^c	6	2500	F	N _{0.3}	100	0	100	64	Random	2.5	0.564
19 ^d	6	2500	F	-	100	0	100	64	Random	2.5	0.564
20 ^e	6	2500	F	N _{0.3}	100	0	100	64	Random	2.5	0.564
21 ^f	6	2500	F	N _{0.3}	100	0	100	64	Random	2.5	0.564
22 ^g	6	2500	F	N _{0.3}	100	0	100	64	Random	2.5	0.564

^o Baseline simulation; position mode = *Territory*

^{a,b,d} Position mode = *Resource*

^c 75% habitat saturation: placement of territories was stopped at 75% of the asymptotic maximum

^e 50% habitat saturation: placement of territories was stopped at 50% of the asymptotic maximum

^f Repeat baseline simulation (to see how random elements in the model can affect results)

^g Area of landscape increased by a factor of 4

[†] F = flat; N_x = normal, attenuating to *x* at the maximum distance from territory centre

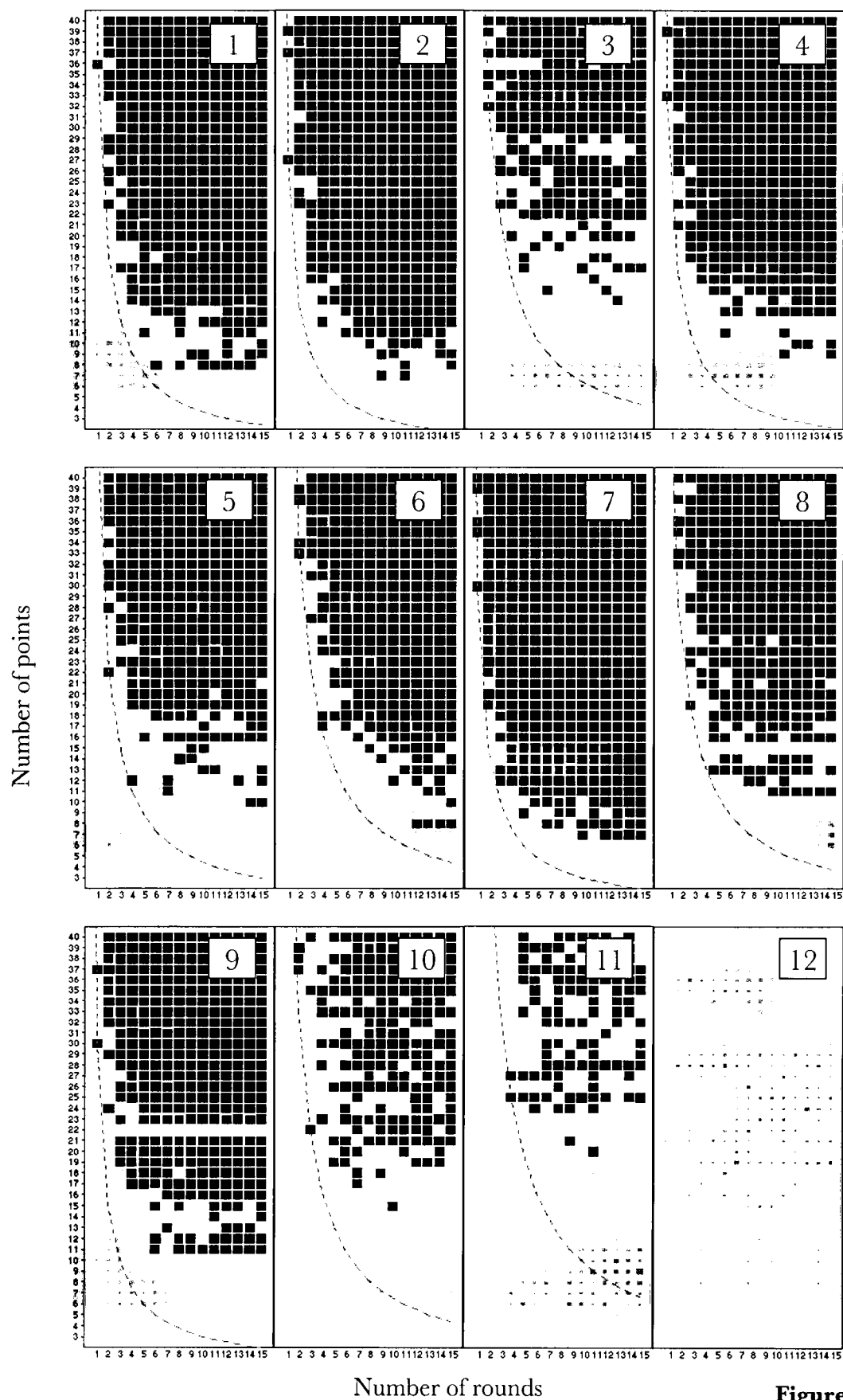


Figure 3.13
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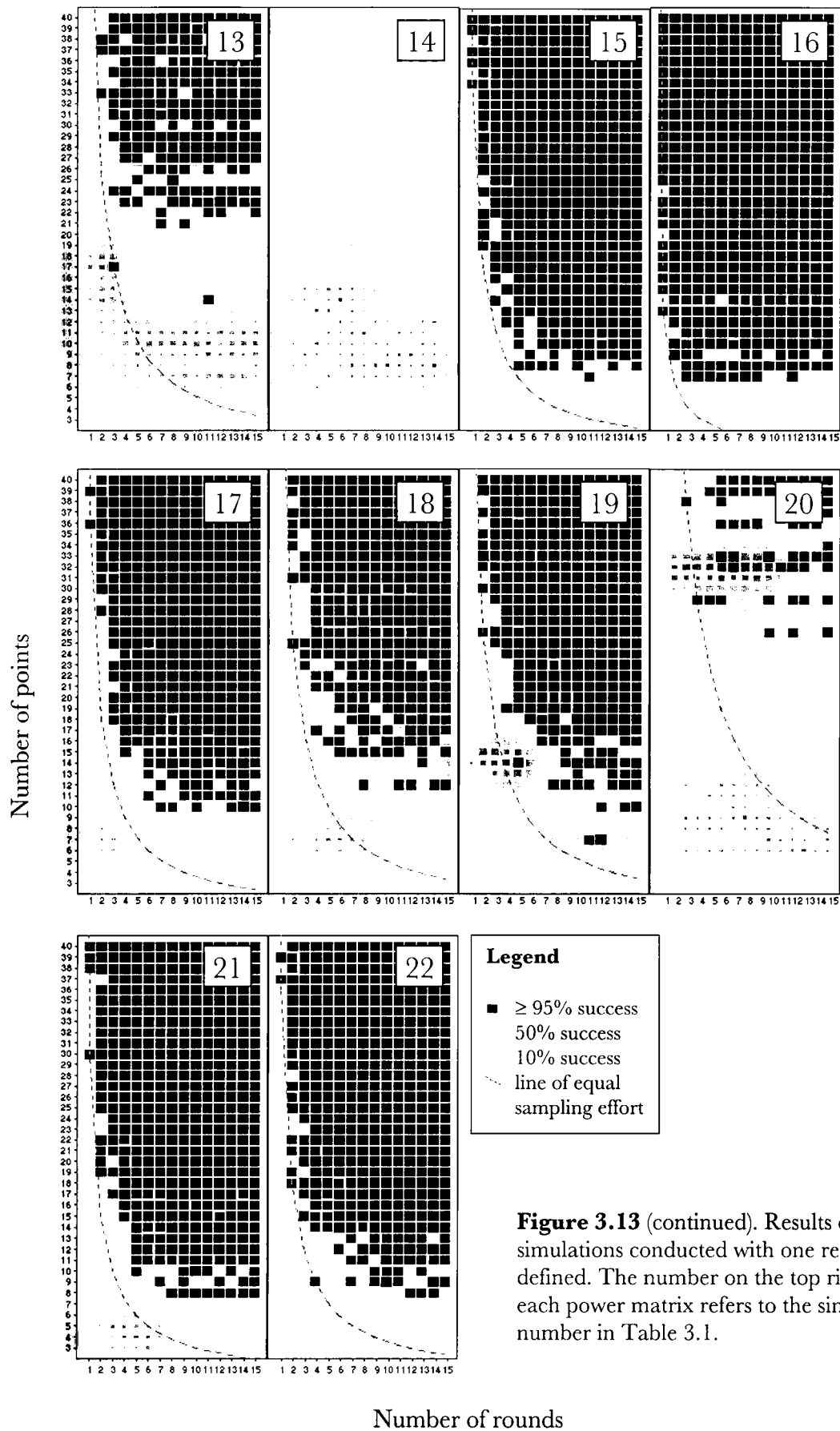


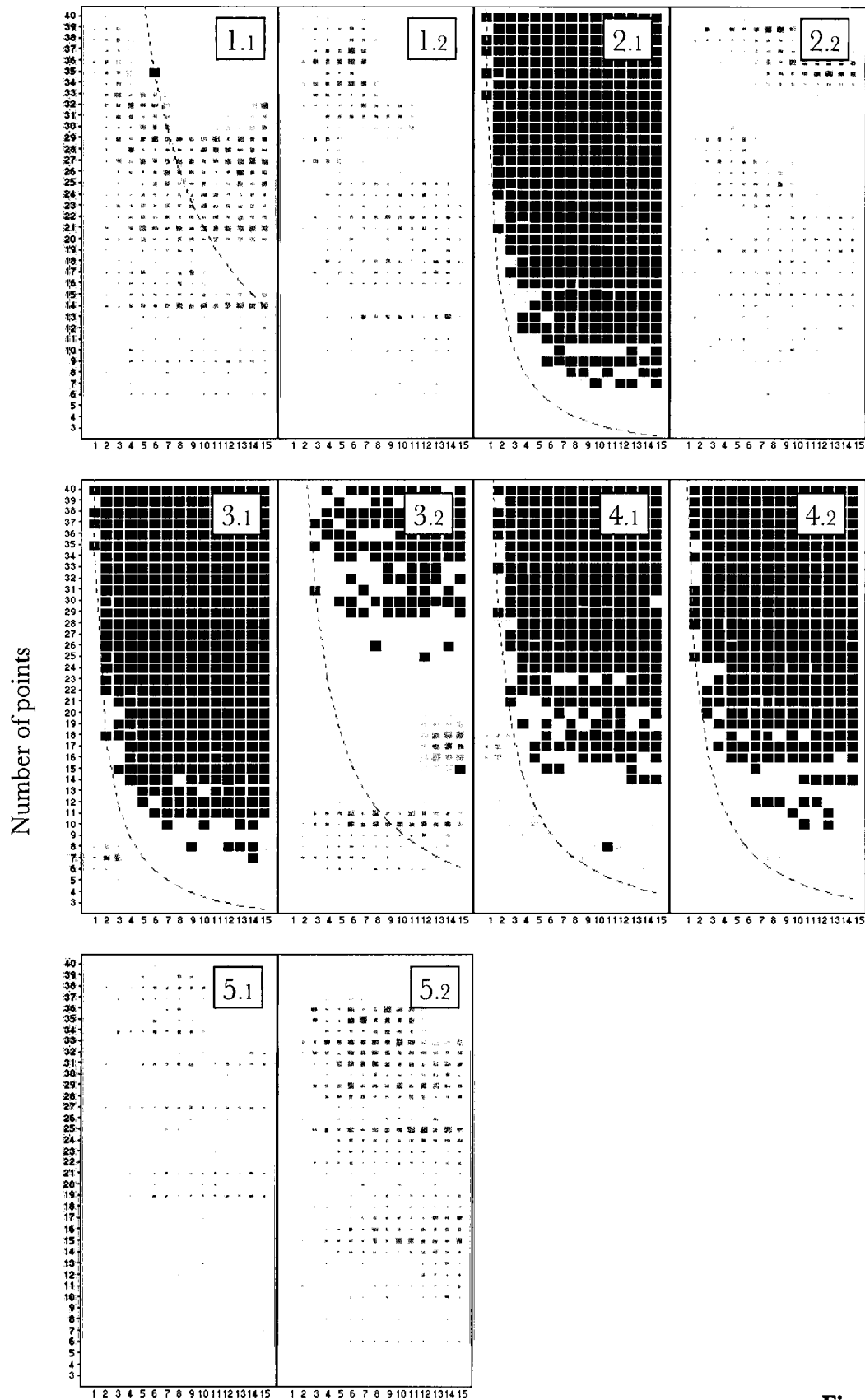
Figure 3.13 (continued). Results of simulations conducted with one resource defined. The number on the top right of each power matrix refers to the simulation number in Table 3.1.

Number of rounds

Table 3.2. Simulations with two or more resources defined.

<i>Simulation #</i>	Species					Resource 1				Resource 2				Resource 3				Sampling		
	<i>Mobility</i>	<i>Resource 1 Requirement</i>	<i>Resource 2 Requirement</i>	<i>Resource 3 Requirement</i>	<i>Detectability function</i>	<i>Position function</i>	<i>Cover</i>	<i>Minimum cell value</i>	<i>Maximum cell value</i>	<i>Spatial period</i>	<i>Cover</i>	<i>Minimum Cell value</i>	<i>Maximum cell value</i>	<i>Spatial period</i>	<i>Cover</i>	<i>Minimum cell value</i>	<i>Maximum cell value</i>	<i>Point placement</i>	<i>Point count radius</i>	<i>Vegetation plot radius</i>
1 ^o	5	1650	1650	-	F	N _{0.3}	100	0	100	64	100	0	100	64	100	-	-	Random	2.5	0.564
2 ^o	5	2000	500	-	F	N _{0.3}	100	0	100	64	100	0	100	64	100	-	-	Random	2.5	0.564
3 ^a	5	2000	0	-	F	N _{0.3}	100	0	100	64	100	0	100	64	100	-	-	Random	2.5	0.564
4 ^a	5	2000	2000	-	F	N _{0.3}	100	0	100	64	100	0	100	64	100	-	-	Random	2.5	0.564
5 ^b	5	1850	1850	-	F	N _{0.3}	100	0	100	64	100	0	100	64	100	-	-	Random	2.5	0.564
6	6	1200	100	1800	N	N _{0.3}	90	0	100	64	75	0	80	24	100	20	80	Random	2.5	0.564
7 ^c	6	1200	100	1800	N	-	90	0	100	64	75	0	80	24	100	20	80	Random	2.5	0.564

^o No (i.e. random) association between Resource 1 and Resource 2^a 50% positive association between Resource 1 and Resource 2^b 50% negative association between Resource 1 and Resource 2^c Position mode = *Resource*



Number of rounds

Figure 3.14
(continued on next page).

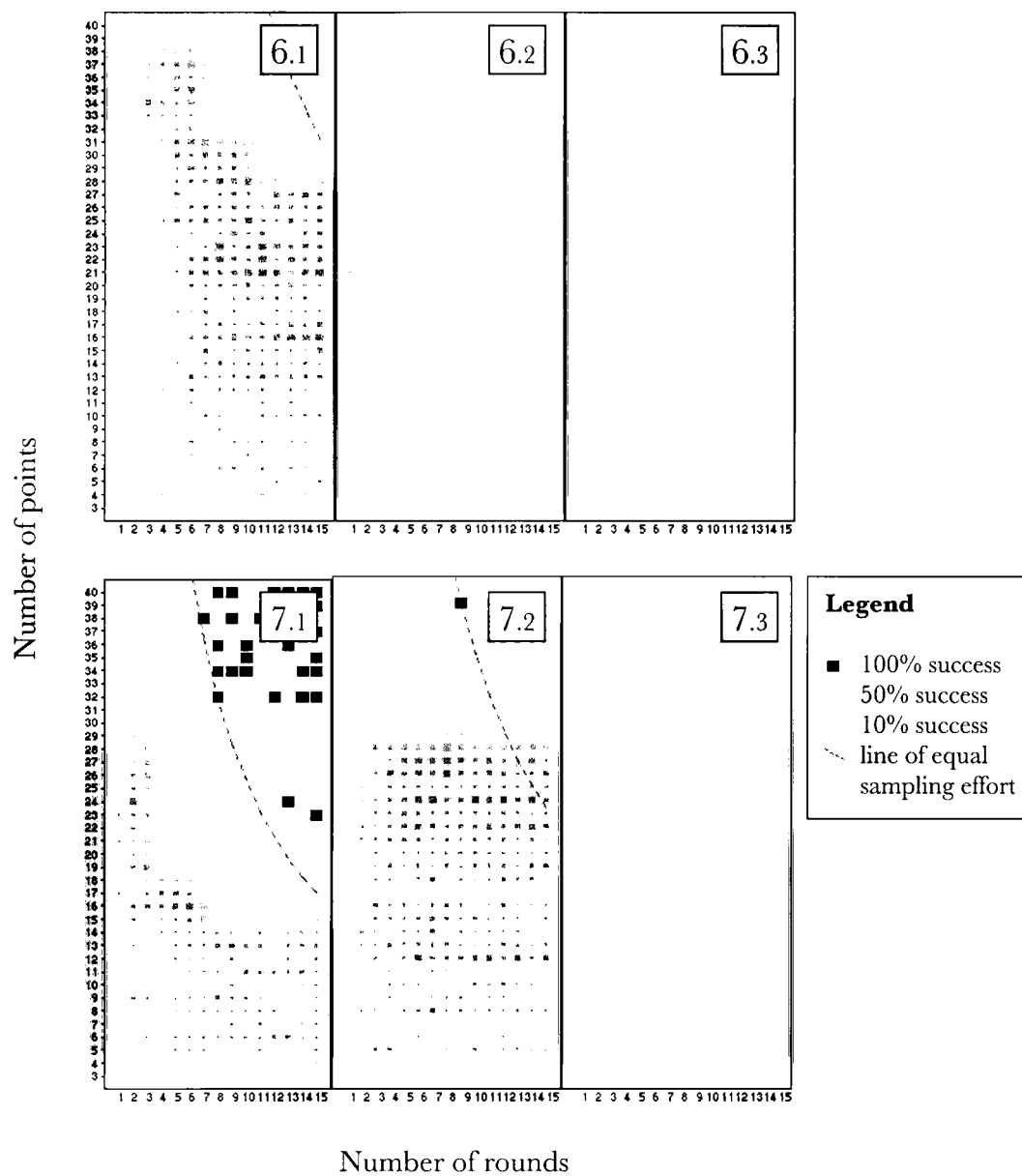


Figure 3.14 (continued). Results of simulations conducted with two or more resources defined. At the top right of each power matrix, the first number corresponds to the simulation # and the second number corresponds to the resource # (see Table 3.2, above).

CHAPTER IV: Improving Predictions of Species-Resource Relationships

In order to infer ecologically meaningful and robust species-resource relationships at a stand-level from field study data, the most appropriate sample design and analysis method must be chosen. Aspects of point-count sample design normally considered include sampling effort (e.g., Barker *et al.* 1993), census method (e.g., Dobkin and Rich 1998), and point-count duration (e.g., Smith *et al.* 1998). However, resource distribution parameters and average territory size must also be considered, as they may greatly influence a study's potential to identify species-resource relationships. The ratio of within-point to between-point variability must be minimized, both for the dependent variable (i.e. species detections) and the independent variables (i.e. resource variables). The effects of these parameters on the performance of my logistic regression models are unknown, because the Riske Creek-Knife Creek study was not designed to quantify resource distributions or average territory size. In fact, I have been unable to find any examples of studies using the point-count method where these potentially confounding parameters were measured.

Once point-count data have been collected, the most appropriate analysis method must be chosen. Conventional statistical methods (e.g., logistic regression) treat non-detections to mean that no individuals are present. In reality, individuals may be present but not recorded, leading to incorrect model construction. An analysis method which, unlike conventional methods, treats non-detections to mean only that no individuals were recorded (Dettmers and Bart 1999), is more appropriate for the analysis of point count data.

4.1 Sample design

Studies using the point-count method to infer species-resource relationships typically describe the number, size, spacing and duration of point-count circles (e.g., Mannan and Meslow 1984, Morrison *et al.* 1987, Lundquist 1991, Hansen *et al.* 1995, Bosakowski 1997). The primary concern in such studies is that sampling intensity will be high enough that ecological relationships can be inferred with reasonable statistical confidence. However, even if these parameters are satisfactory, resource distribution and average territory size may still preclude the point-count method from correctly identifying species-resource relationships (see Chapter III). Quantification of these variables is therefore essential in determining a sample design that will maximize the chance of success. The proliferation of GIS databases has enabled the development of increasingly sophisticated spatial analysis tools, which may be used to measure spatial distribution parameters of resources (e.g., Dettmers and Bart 1999). In addition, average territory size may be inferred from body weight (Irwin 1994) or via alternate census methods such as the spot count (Dobkin and Rich 1998).

4.2 Minimizing the ratio of within-point to between-point variability

Another critical issue in successfully detecting species-resource relationships, which is rarely alluded to in the literature, is the ratio of within-point to between-point variability in both detections and resource variables. In order to detect a relationship, it must be possible to accurately distinguish points representing suitable habitat from points representing unsuitable habitat. In order to differentiate mean attribute values among sampling points, the ratio of variability of both resource variables *and* species detections within points to their variability between points must be low. Link *et al.* (1994) examined

an analogous ratio for species detections, using data from the North American Breeding Bird Survey (BBS). They defined lambda (λ) as the ratio of within-site variability in detections to total variability within and between BBS sites. They showed that if a species is rare or difficult to detect, the value of λ is high and it is difficult to detect differences in the numbers of birds among sampling routes (Figure 4.1). Increasing sampling intensity (i.e., increasing the number of points and/or rounds), within practical limits, is the most obvious way to overcome this problem (Link *et al.* 1994). It is also possible to minimize λ by placing sampling points over a wide variety of habitat types, maximizing the range of values for all resource variables.

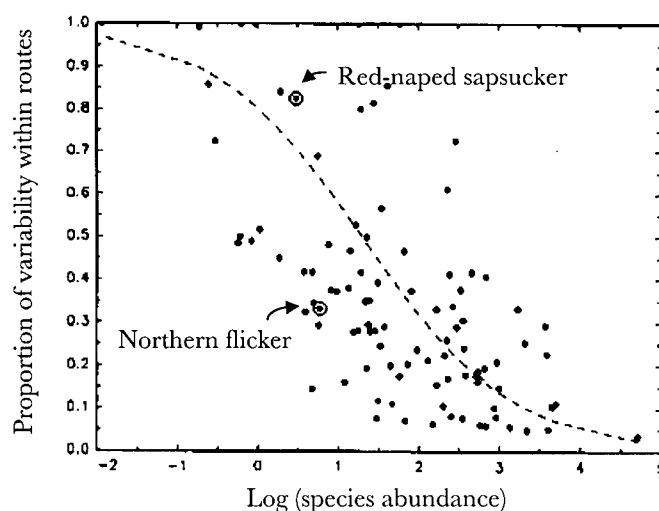


Figure 4.1. Proportion of within-route variance to total variance (λ) plotted against the natural logarithm of abundance (mean number of birds seen) by species, showing a decreasing trend. The (dashed) trend line explains 40% of the variance in the data ($r^2 = 0.40$). From Link *et al.* 1994, p. 1100.

In Chapter III, I showed that the average territory size of a species and the spatial period of its required resource both greatly influence the sampling success rate. If the ratio of average territory size to point-count radius is large, or the ratio of spatial period to vegetation plot radius is small, then the ability to correctly deduce species-resource

relationships is compromised. The ratio of average territory size to point-count radius ultimately affects the ratio of within-point to between-point variance in species detections. The ratio of spatial period to vegetation plot radius determines the ratio of within-point to between-point variance in resource variables. In either case, in order for a sampling effort to provide consistently correct results, the ratio of within-point to between-point variability must be minimal.

Using Sample Sim'on, it is possible to produce scenarios where within-point to between-point variability, for both species detections and resource variables, is low or high. Assuming that the species requires just one resource and that the ratio of maximum range to resource requirement is such that most territories are regular in shape (i.e. nearly round), Table 4.1 and Figures 4.2 to 4.5 show how spatial period and territory size, relative to vegetation plot radius and point-count radius, interact and affect sampling success rate. If spatial period is small enough, the density of a resource will vary more within a vegetation plot than it does between vegetation plots, eliminating any possibility of distinguishing resource characteristics among points (Figures 4.2 and 4.4). The smaller the spatial period, the higher the ratio of within-point to between-point variability. Similarly, as average territory size increases, the number of species detections decreases, decreasing statistical power (Figures 4.2 and 4.3). The presence of a species becomes less likely to correspond to actual habitat suitability, and the ratio of within-point to between-point variability in species detections increases. The ideal situation is one where spatial period is large and average territory size is small, relative to the point count radius (Figure 4.5).

Spatial period may be quantified by repeatedly measuring the correlation between

cells in a grid at varying distances. Thomson *et al.* (1996) measured spatial autocorrelation among cells in a 0.1-ha grid in a subalpine meadow in western Colorado. They used correlograms to illustrate the maximum range over which spatial autocorrelation acts, for each of six variables (Figure 4.6). All correlations are significantly positive within 5-10 m, and significantly negative at 15-20 m. Therefore, in this example the spatial period for these variables is approximately 25 m. This method could have been applied to the Riske Creek-Knife Creek data, but because the number of sampling points per study plot varied between 7 and 35, it was too difficult to determine a consistent measure of spatial period for each study plot. Rather, a study must first be designed such that spatial period may be more simply quantified.

Table 4.1. Spatial period and territory size, relative to vegetation plot radius and point count radius, affect the ratio of within-point to between-point variance in resource and species variables, $1/\lambda$. This ratio in turn affects the sampling success rate.

Spatial period ¹	Territory size ²	$1/\lambda_{\text{resource}}$ ³	$1/\lambda_{\text{species}}$ ⁴	Sampling success rate
Small	Large	Low	Low	Very poor
Large	Large	High	Low	Poor
Small	Small	Low	High	Fair
Large	Small	High	High	Good

¹ Average distance between peaks in resource concentration, relative to vegetation-plot radius

² Average territory size, relative to point-count radius

³ Ratio of within-point to between-point variation in resource variables

⁴ Ratio of within-point to between-point variation in species detections

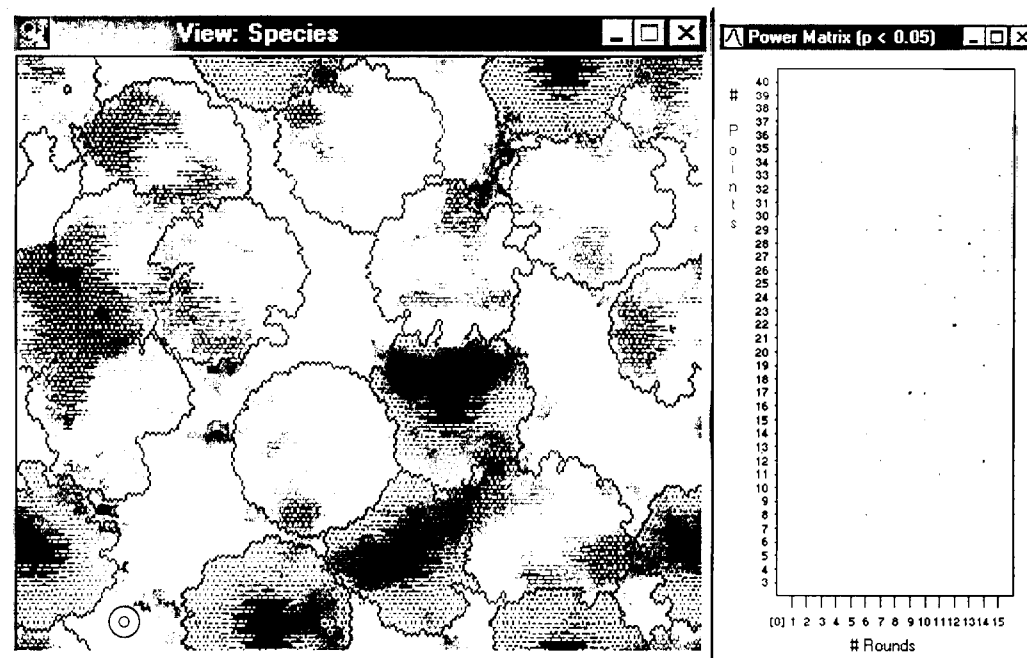


Figure 4.2. Spatial period is small relative to the vegetation-plot radius, and average territory size is large relative to the point-count radius. The ratio of within-point to between-point variability for both species detections and resource variables is high, making the species-resource relationship undetectable. Sizes of point counts (outer circle) and vegetation plots (inner circle) are shown at lower left.

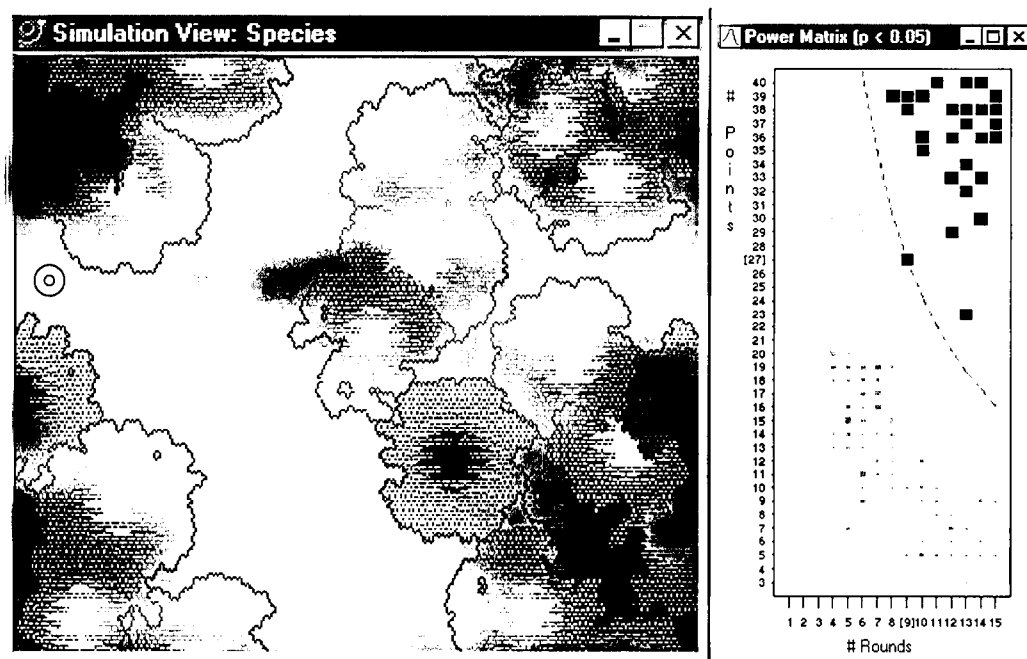


Figure 4.3. Spatial period is large relative to the vegetation-plot radius. The ratio of within-point to between-point variability for resource variables is low, making the species-resource relationship marginally more detectable. Sizes of point counts and vegetation plots are as in Figure 4.2.

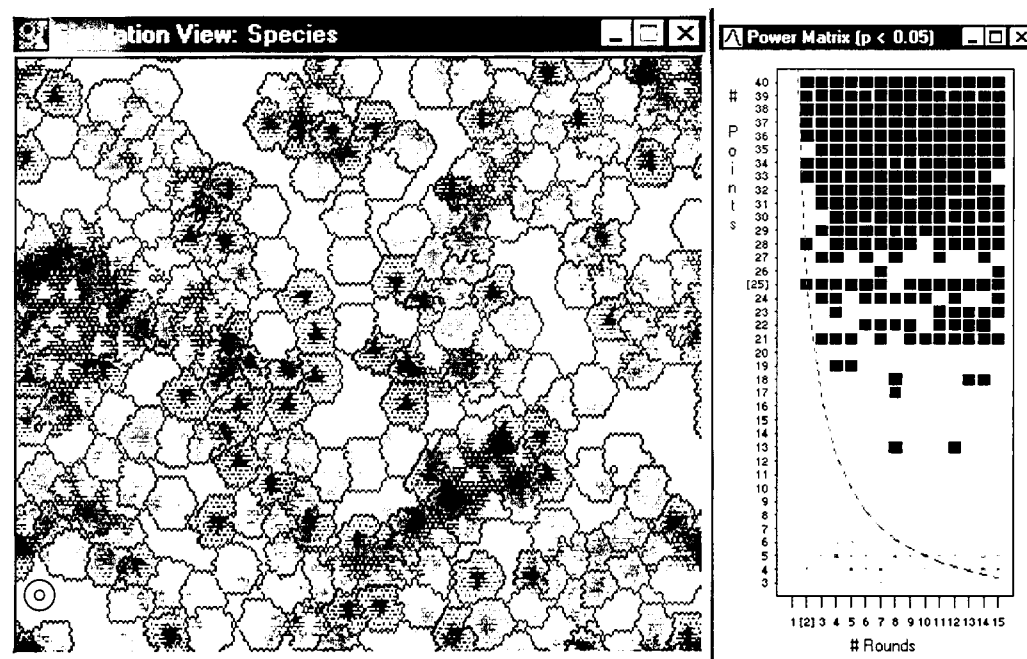


Figure 4.4. Average territory size is small relative to the point-count radius. The ratio of within-point to between-point variability for species detections is low, and the total number of species detections is greater, making the species-resource relationship more detectable. Sizes of point counts and vegetation plots are as in Figure 4.2.

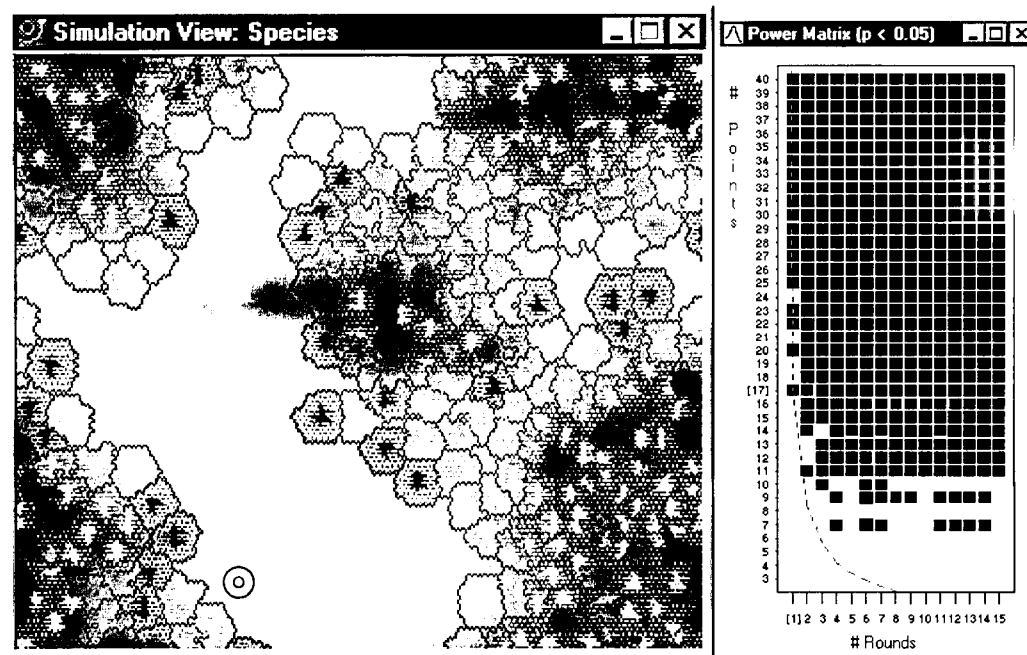


Figure 4.5. Spatial period is large relative to vegetation-plot radius, and average territory size is small relative to the point-count radius. The ratio of within-point to between-point variability for both species detections and resource variables is low, making the species-resource relationship easily detectable. Sizes of point counts and vegetation plots are as in Figure 4.2.

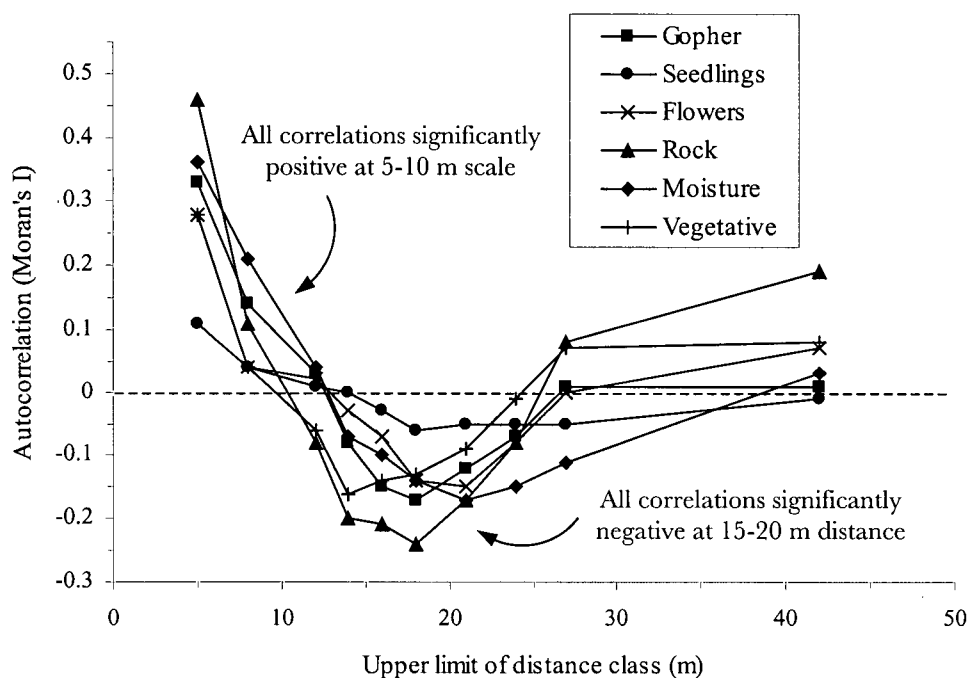


Figure 4.6. Correlograms for six variables measured in 256 2 x 2 m quadrats in a subalpine meadow in Colorado (from Thomson *et al.* 1996). For all variables, there is significant positive autocorrelation among nearby quadrats (at distances of 5-10 m) and significant negative autocorrelation among distant quadrats (at distances of 15-20 m). This indicates that all variables are highly patchy and show similar scales of patch structure (Thomson *et al.* 1996). Furthermore, the spatial period for these variables may be estimated at about 25 m.

4.3 Other obscuring variables

In addition to average territory size and spatial period, many other variables serve to increase the variance in species-resource data. As demonstrated in Chapter III, if an area is under-saturated with territories, there is a greater chance that areas of suitable habitat will yield no detections of individuals. Decreasing the species' maximum range has a similar effect, because this limits the number of territories that can be successfully placed in the landscape. Increasing the minimum cell value of a resource has a similar effect to decreasing its spatial period – the variability between points decreases, weakening the ability to distinguish differences in resource characteristics among points.

The simulation results discussed in the previous chapter deal with highly simplified scenarios. Many variables not included in Sample Sim'on can only increase variance in field census data. Unpaired individuals may be detected, whose presence does not necessarily reflect optimum habitat (Gibbs and Wenny 1993). Stochasticity in regional population dynamics may increase or decrease habitat saturation (Dunning *et al.* 1992). The ability of individuals to adapt their behaviour for specific situations (i.e. behavioural plasticity, Root 1967) or competition with other individuals, especially of other species, may result in the substitution of one resource for another, or variable resource use among individuals in a population (Root 1967). Individuals in a population may respond differently to the presence of an observer, especially one with a playback tape, such that individuals are attracted to or repelled from the observer. Larger-scale variables such as habitat fragmentation, or time lag in response to a major disturbance, may also modify how an area is used by a species, despite the actual value of the resources that are available (Dunning *et al.* 1992).

4.4 Data analysis method

The logistic regression method used in Chapter II to construct species-resource models operates on binary presence/absence data. Point-count stations where individuals were detected are given a value of 1 (present) whereas point-count stations where no individuals were detected are given a value of 0 (absent). Thus, logistic regression attempts to find a discriminating function of the independent (resource) variables that best distinguishes between presence and absence. This method, along with linear regression, discriminant analysis, principal component analysis and others, are commonly used to build predictive habitat models (Dettmers and Bart 1999). However, if no individuals are

detected at a sampling point, this cannot be implied to mean 'none present,' but only 'none recorded' (Dettmers and Bart 1999). A Type I Error may be committed, such that individuals which are actually present fail to be detected (Figure 2.1). Conventional analytical methods fail to recognize this possibility. Dettmers and Bart (1999) outline an alternate analysis method whereby 'optimum' habitat is defined as the multivariate vector of the means of the habitat variables, calculated using only those points where individuals were present. Habitat quality for a remaining point can then be calculated as its multivariate distance from this optimum. This way, while the detection of an individual implies 'present' or 'suitable habitat,' the non-detection of an individual only implies that habitat suitability is unknown. It does not make the assumption that non-detection implies absence, or poor habitat. Although still under development, this method holds great promise for analyzing point-count data to yield more accurate predictions of species-resource relationships (Dettmers and Bart 1999).

4.5 Implications for field studies

The point-count simulations presented in this thesis show that resource distribution, species behaviour and sample design may greatly affect the possibility of detecting species-resource relationships, at one spatial and temporal scale. This result reaffirms the importance of investigating species-resource relationships over a broad range of spatial and temporal scales (e.g., Block *et al.* 1994, Irwin 1994, Holt *et al.* 1995), because a snapshot of limited scope is not likely to provide very clear or complete information about the resource use of a species.

While efficient because it allows the simultaneous sampling of many bird species, the point-count method is of limited use in determining resource relationships for

individual species. To determine microhabitat use (e.g., tree species preferred for foraging), studies of individual behaviour provide more direct evidence of selective resource use. Observers follow individual birds throughout the day, recording at predetermined intervals the foraging substrate, mode, and tree species being used (e.g., Adams and Morrison 1993). These data on use can then be compared with resource availability as measured in systematically positioned vegetation plots. The expert opinion approach (e.g., Kangas *et al.* 1993) is essentially a less quantitatively rigorous way of drawing upon a number of people's observations of individual behaviour. Point-count surveys are more appropriate for providing data on the presence of species over broad areas, and how its distribution varies over time.

Spatially explicit databases can provide data on broad-scale patterns of vegetation structure and composition, as well as abiotic variables such as slope and soil moisture (Dettmers and Bart 1999). Daust and Sutherland (1997) integrated different spatial scales in predicting habitat suitability for various species in simulated, managed forests. They based predicted species distributions on home range and dispersal ability as well as resource requirements. In addition to incorporating multiple spatial and temporal scales, a species-resource model must stress process over empiricism (Daust and Sutherland 1997). Species-resource relationships which reflect an ecologically relevant, theoretically confirmed process are more likely to be correct than those which are only supported by a significant multivariate correlation.

In this thesis, I have demonstrated that a computer simulation can be useful for exploring the effects of hitherto unmeasured variables on the success rate of detecting species-resource relationships, using the point-count method. Average territory size and

the spatial period of a resource are key variables that can greatly affect the ratio of within-point to between-point variability. If the point-count method is to provide useful information about resource use for a species, such confounding variables must be quantified. At best, a study should be designed explicitly to minimize the variance-increasing effects of these variables. Only then can point-count data be useful in creating species-resource relationships models that can be successfully applied, whether to real scenarios or in simulation exercises, to provide accurate predictions of species abundance.

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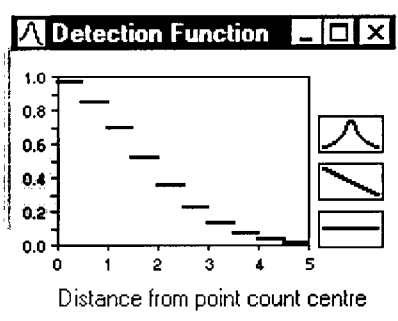
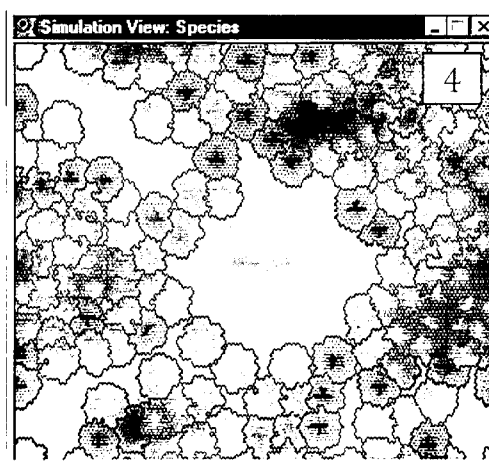
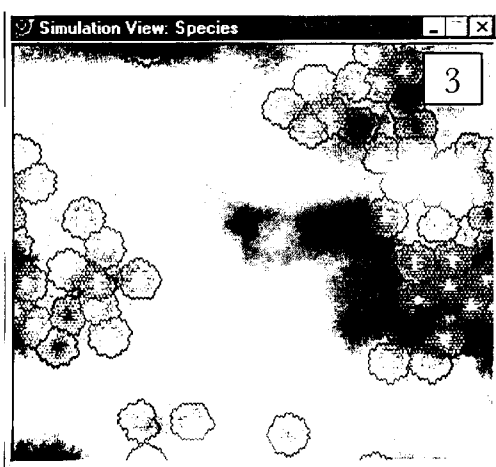
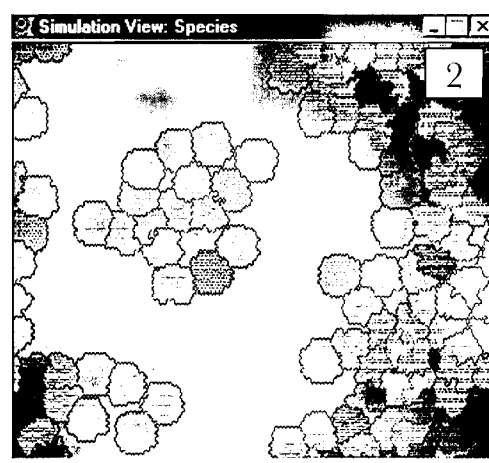
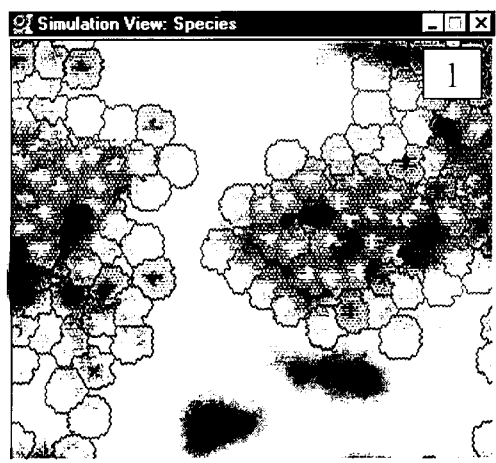
Appendix I: Key to model variables

List of all variables used in logistic regression models.

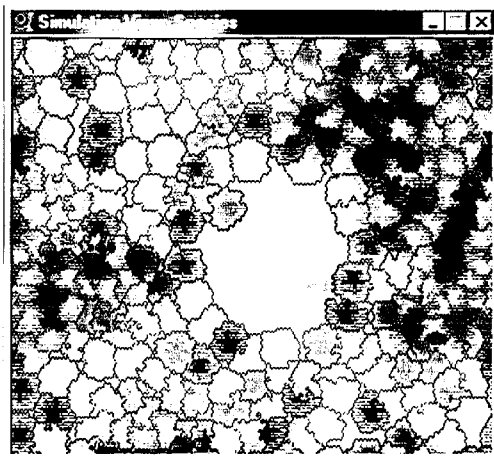
B_RNSA_Y	presence/absence of red-naped sapsucker, playback data
B_RNSA_N	presence/absence of red-naped sapsucker, non-playback data
B_NOFL_Y	presence/absence of northern flicker, playback data
B_NOFL_N	presence/absence of northern flicker, non-playback data
AT_1	stems of live, healthy (decay class 1) aspen (#/plot)
AT_2	stems of live, decaying (decay class 2) aspen (#/plot)
AT_3P	stems of dead (decay classes 3+) aspen (#/plot)
FD_1	stems of live, healthy (decay class 1) Douglas fir (#/plot)
FD_2	stems of live, decaying (decay class 2) Douglas fir (#/plot)
FD_3P	stems of dead (decay classes 3+) Douglas fir (#/plot)
PL_1	stems of live, healthy (decay class 1) pine (#/plot)
PL_2	stems of live, decaying (decay class 2) pine (#/plot)
PL_3P	stems of dead (decay classes 3+) pine (#/plot)
SX_1	stems of live, healthy (decay class 1) spruce (#/plot)
SX_2	stems of live, decaying (decay class 2) spruce (#/plot)
SX_3P	stems of dead (decay classes 3+) spruce (#/plot)
AX_SAP	stems of aspen saplings (#/plot)
FD_SAP	stems of Douglas fir saplings (#/plot)
JX_SAP	stems of juniper saplings (#/plot)
PL_SAP	stems of pine saplings (#/plot)
SX_SAP	stems of spruce saplings (#/plot)
WX_SAP	stems of willow saplings (#/plot)
BA_AT1	basal area of live, healthy (decay class 1) aspen (m ² /plot)
BA_AT2	basal area of live, decaying (decay class 2) aspen (m ² /plot)
BA_AT3P	basal area of dead (decay classes 3+) aspen (m ² /plot)
BA_FD1	basal area of live, healthy (decay class 1) Douglas fir (m ² /plot)
BA_FD2	basal area of live, decaying (decay class 2) Douglas fir (m ² /plot)
BA_FD3P	basal area of dead (decay classes 3+) Douglas fir (m ² /plot)
BA_PL1	basal area of live, healthy (decay class 1) pine (m ² /plot)
BA_PL2	basal area of live, decaying (decay class 2) pine (m ² /plot)
BA_PL3P	basal area of dead (decay classes 3+) pine (m ² /plot)
BA_SX1	basal area of live, healthy (decay class 1) spruce (m ² /plot)
BA_SX2	basal area of live, decaying (decay class 2) spruce (m ² /plot)
BA_SX3P	basal area of dead (decay classes 3+) spruce (m ² /plot)
WET_EDGE	distance to nearest wet edge (m)
DRY_EDGE	distance to nearest dry edge (m)

Appendix II: Supplementary simulation views

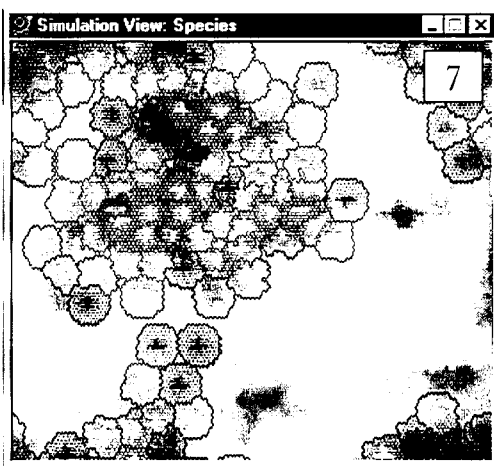
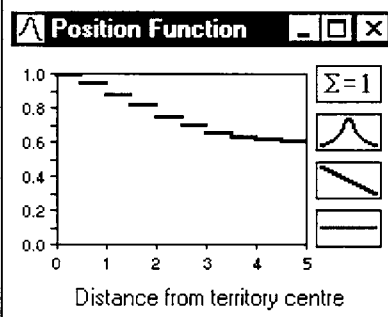
Supplementary views from simulations conducted with one resource. Numbers in upper right corner correspond to simulation number (see Table 3.1).



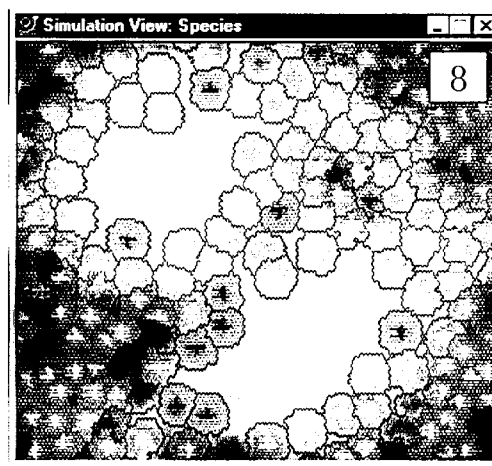
5



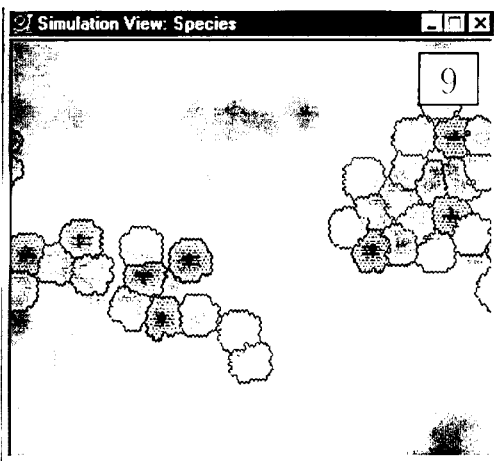
6



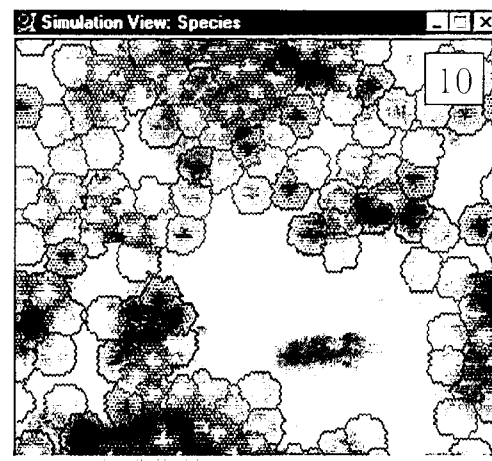
7



8



9



10

