Understanding spatial variation in population dynamics: enter the virtual ecologist

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For Brigitte

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Abstract

The importance of spatial variability in ecology has been recognised from the beginnings of ecology as a science. It has also been virtually ignored in ecological analyses, especially in classical population dynamics models. Recent advances in computational power and remote sensing capabilities have enabled the study of spatial variation at larger scales. I review the development of spatially explicit models over the last several years. The range of approaches and applications is enormous, but one clear gap does appear. There are no models that incorporate continuous variation in habitat quality for a species. Many models allow for habitat/non-habitat patches on a range of scales. Some population viability analysis models allow for patches to have different qualities. But no model allows for within patch, between territory variation in habitat quality. It is at this scale that I concentrate my efforts in this thesis.

In Chapter 2, I develop a spatially explicit, individual based simulation of two arboreal marsupials, based on data provided by David Lindenmayer of ANU. I calculate a fractal landscape, the height of which represents a "habitat variable". The habitat variable influences either annual survival rates or fecundity. I develop a range of possible localised dispersal strategies for juveniles, ranging from a random walk through to a complete habitat selector. Average population size varies inversely with the strength of habitat selection behaviour, contravening intuition about the value of habitat selection behaviour. This effect arises through competition for territorial vacancies leading to increased mortality during juvenile dispersal. Habitat selectors tend to spend more time dispersing because their initial directions of movement take them into regions of the landscape that are more crowded. This is especially true on "smooth" landscapes with low fractal dimensions and little interspersion of good and bad habitat.

Wildlife managers often rely on correlations between density or presence/absence and features of the landscape to identify good habitat. In Chapter 3, I sample the landscape model of Chapter 2 with a "Virtual Ecologist" at the home range scale, and subject the resulting data to logistic regression. The habitat quality variable is a good predictor of the presence of the species by standard measures. However, it is not possible to explain all of the variation in territory occupancy by reference to the quality of the habitat. Demographic stochasticity interacts with localised dispersal mechanisms to produce territories that are vacated (by death) and not recolonised immediately. Furthermore, competition for territories means that individuals are often found in poorer quality habitat. The degree of "interspersion" on the landscape is the biggest influence on the quality of the model, with landscapes with a high fractal dimension yielding regression models that are poor predictors. The second conclusion from this work is that a correlation between presence/absence and a habitat variable does not provide information about survival or fecundity rates, but does provide information about the probability that an empty territory of that quality will be reoccupied.

Sleepy lizards are the primary host of an ixodid tick, *Aponomma hydrosauri*. In chapter 4 I explore 15 years of data on tick abundances donated by Prof. C. M. Bull looking for evidence of density dependent population regulation at multiple spatial scales. Tick populations have increased over the period of the study. There is no evidence of density dependence in the time series. Measurements of engorgement success by larval ticks in the lab does show a decrease with density, but only at densities uncommon in the field. In Chapter 5 I develop an individual based, spatially explicit simulation of tick populations on sleepy lizards, and consider the impact on population dynamics of introducing spatial and temporal variability at different levels from individual stochasticity up to extrinsic weather and habitat variation. The primary goal is to see if variability at the individual level leads to "emergent", density independent population regulation. Introducing spatial and temporal variation reduces average growth rates. There is no evidence of “emergent” density independent population regulation. The virtual ecologist in this model demonstrates that counting ticks on lizards is a poor indicator of total tick abundance on the landscape. In chapter 6 I generate predictions for a landscape scale “pulse” experiment that will test some of the components of the model.

In Chapter 7 I analyse a spatially and temporally extensive data set of mark-recapture records of Sleepy Lizards (*Tiliqua rugosa*), collected over 15 years by C.M. Bull of Flinders University. I look for characteristic scales of variation in population numbers using a two techniques suggested in the literature. Lizard population numbers are most variable at scales of less than 3 km, but most of the suggested analysis techniques are shown to have severe problems.

In conclusion, the virtual ecologist is a useful method for linking the output of spatially explicit population models to reality. In the future, such an approach will be valuable for improving the design of field research on spatially complex landscapes.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Andrew J. Tyre
18/5/99
Date

Sasha's contributions

The following excerpts were contributed by my two year old son. The concise eloquence and sparse language were an inspiration.

Within a single day, the model processes several steps in the following order: ticks board lizards, lizards move between refuges, engorged ticks disembark from lizards, and ticks develop. I will now consider each of these steps in more detail. xfxxxzz

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Lubchenco et al. (1991) list dispersal as one of the "intellectual frontiers" of ecology, hhhhhhhucasl;134 cxvh pppppppppppppppOIOihighlighting thjjjjjjjjjjjj---
mmmmnnnnnnnnnnnnlgvgggggggggggggggggggggggggggggggggggggg66444yyyrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrxcrrxxcrxxrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrre need for further analytical and empirical work in this area.

Acknowledgments

My work was supported in part by an NSERC PGS B award from Canada. I would like to thank my supervisors, both official and unofficial, for their data, guidance, and support over the last three years: Hugh Possingham, Mike Bull, David Lindenmayer, and Sue Carthew. The many members past, present, and temporary of the PHLEM (Possingham HyperLab of Ecological Modelling) discussion group had to listen to me complain on innumerable occasions, and did so graciously, for which I'm eternally grateful. Among these people, Ian Ball, Steve Ball (no relation), Jemery Day, Mick McCarthy, and Shane Richardson have been especially helpful and good friends to boot. Gary Starr gets an honourable mention for trying to convince me that genetics matters, playing volleyball, and otherwise helping to make Roseworthy a fun place. Thanks also to other Roseworthians, especially Dave Campbell, Mike Harte, Danny Brock, Fiona Fisher, and Darren Bos for providing perspective and friendship.

At Roseworthy Campus, Keith Cowley was indispensable for providing the basic necessities of research, whatever they were. Jane Endicott, Tracey Parish, and Sheila Johnson provided mail, conversation, and repeated education on how to use the fax machine. At Waite Campus, thanks to Mike Keller for providing a desk under crowded conditions, and to Terry Feckner, Gary Taylor, and Anke Johnsen for basic support services.

Finally, and most importantly, no thanks are enough for Sasha and Brigitte Tenhumberg. Brigitte read more drafts, listened to more complaints, and tolerated more crap than anyone, and I would never have made it to the end without you.

Publications arising from this thesis to 1998

Tyre, A. J., Possingham, H. P. & Bull, C. M. (1997). Characteristic scales in ecology: fact, fiction, or futility. In: *Frontiers in Ecology: Building the Links.* (Klomp, N. & Lunt, I. eds). Oxford: Elsevier Science. (Chapter 7)

Tyre, A. J., Possingham, H. P. & Lindenmayer, D. (1997). Spatially explicit ecological models: population consequences of individual habitat selection mechanisms. In: *MODSIM 97 International Congress on modelling and Simulation, Proceedings.* (McDonald, A. D. & McAleer, M. eds): Modelling and Simulation Society of Australia.

Tyre, A. J., Possingham, H. P. & Lindenmayer, D. L. (1998). Modelling dispersal behaviour on a fractal landscape. *Environmental Modelling and Software* **14**, 103-113. (Chapter 2)

Chapter 1 General Introduction

> *"For mathematical elegance the first generation of spatially explicit models has asked what dynamics and patterns arise in uniform environments, now we need to ask how habitat heterogeneity alters these patterns."*
>
> *Peter Kareiva and Uno Wennergren (1995)*

Introduction

One of the most salient features of any landscape is variation in space. Moving across a landscape leads to observations of changes. On a sufficiently long timescale, variation in time also becomes apparent. Searching for explanations of this variation, for the underlying mechanisms, is what basic ecological research is about. The domain of applied ecology is understanding the consequences of spatial and temporal variation for achieving specific objectives within landscapes modified by humans. These objectives range from maximising productivity of a particular trophic level, as in agriculture or fisheries, to minimising the loss of biodiversity in a region. Without an understanding of the sources of variation in ecological parameters, both basic and applied ecology will suffer. Moreover, because variation is a function of the scale at which it is observed (Allen & Starr, 1982), it is critical to develop an understanding of the influence of observation scale on ecological variability. The theme of an interaction between an ecological process and the process of observing the ecological process will recur throughout this thesis.

In this first chapter I intend to set the context for the remainder of the thesis, rather than provide an introduction in the sense of an introduction for a paper. I will initially discuss my view of the different sources of variability in population ecology. Then I will review a representative sample of spatially explicit models published between 1990 and 1996. Finally, I will outline the structure and motivation of the remainder of the thesis.

The first source of spatial and temporal variation in ecological processes is the obvious one, and it has been primarily the concern of empirical ecologists. This is variation imposed by variation in abiotic factors: soil type, salinity, moisture, slope, elevation, latitude, rainfall, average temperature. This list of examples is not exhaustive, and there are clearly correlations between them, as well as feedbacks from many biotic features. For example, the degree of salinity in the root zone is influenced by both the degree of rainfall (or irrigation), and the proportion of cover provided by large trees.

Spatial variation of this kind is often dramatic; a good example are the samphire (*Sarcocornia quinqueflora*) flats around salt lakes in Australia. Samphire is tolerant of high salinity, and so exclusively occupies the region immediately around the lake. As the land rises away from the lake samphire is abruptly replaced by other shrubs, and then mallee eucalypts as the salinity near the surface decreases. In other cases, the variability is more subtle. The probability that any particular hectare within the Ada forest block in the central highlands of Victoria, Australia, is occupied by a greater glider is a non-linear function of the number of hollow bearing trees, and the density of acacia trees which provide its food (Figure 3.1). It comes as no surprise that most of the work on this sort of variability has been done on plants (eg. Austin et al., 1990). The sessile nature of plants means that they respond strongly to the conditions in the immediate vicinity of where they are observed. The greater mobility of animals means that they can frequently be observed in areas away from the abiotic and biotic factors that sustain them, making the detection of the appropriate correlations difficult. The second reason is that animals are at least one trophic level removed from abiotic factors such as soil nutrients, salinity, and moisture that are crucial for plants.

The second source of variation has only recently come to light, and has been primarily the domain of theoreticians and modellers. This variation can arise in the absence of variability imposed by abiotic factors, and is endogenously generated by the local nature of movement and interactions between organisms. In a landscape entirely devoid of variation, a simulated population of greater gliders (*Petauroides volans*) forms patches and clumps simply as a result of the restriction that juveniles disperse step-by-step, and dispersal is risky (Figure 7.2). This spatial pattern is exceptionally dynamic in time, despite the absence of any fluctuation in the population as a whole. Similar results have been found for simulated predator prey systems (De Roos et al., 1991), host-parasite systems (Comins et al., 1992), disease dynamics (Hood, 1997), systems of competing corals (Johnson, 1997), and single populations suffering disturbance (Levin & Buttel, 1986; Green, 1989). Recently, empirical evidence supporting the formation of self-organised patterns in populations has come to light in host-parasitoid systems (Maron & Harrison, 1997), and predator-prey population cycles (Ranta et al., 1997).

These two different sources of variability can be referred to as exogenous (generated by factors outside the organism), and endogenous (generated by factors internal to the organism/population). Despite the fact that they have been studied in complete isolation from one another, in real systems both operate simultaneously. Exogenous variability is a fact; it cannot be avoided or ignored — all organisms must deal with it. However, what appears as critical variation to one organism, may not matter at all to another. The spatial variability in salinity that opens a niche for samphire in the mallee represents only temporary variation in food availability for a group of emus (*Dromaius novaehollandiae*) walking across the lake. The exogenous variation that matters to the emus occurs at much larger scales. The significance of such exogenous variation has been little explored in spatial models of population dynamics.

Likewise, ecologists studying the effects of exogenous variation have ignored the potential influence that endogenous variation can play. Within regions that are relatively uniform, such as the samphire flat, there may be many organisms that live out their entire lives confined to that one region. An ecologist studying the population dynamics of an insect living here considers the variability from one quadrat to another to be "noise". However, this "noise" may be generated in part by spatial processes that can be understood. Even at scales where exogenous variation is significant for a species, endogenously generated variability is overlaid. The consequences of this interaction are almost completely unstudied. Empirical ecologists have largely ignored the endogenous variation, and theoretical ecologists have largely ignored the exogenous variation, or reduced it to a very simple view — patches of good habitat in a sea of bad habitat.

There are exceptions to this final generalisation. Many recent population viability analysis models have incorporated variability in population parameters among different patches (Day & Possingham, 1995; McCarthy, 1996). However, by averaging the density of individuals within patches, these models have removed much of the endogenously generated variability considered above. Essentially, by rendering the system at the level of patches, these models have reduced the number of connections between elements, and thereby reduced the "complexity" *sensu* Green (1997). A new level of variability is possible here; the spatial correlation of occupancy of patches.

The realisation that some models incorporate exogenous variability at different scales raises the question of which scale is appropriate to model a system. This question is frequently ignored, but it is crucial if the insights derived from general models of spatial processes (Durrett & Levin, 1994) are to be applied in real ecosystems. Cellular automata (CA) models in particular assume that each fundamental spatial unit, or cell, can be in a limited number of states. Often this is reduced to occupied or not. Clearly, the scale of these units is important for understanding the processes. Does each cell represent a home range, or an entire patch? If the former, than changes from occupied to unoccupied represent mortality of individuals, and the reverse state change a combination of birth and dispersal. If the cells represent entire patches, then a newly unoccupied cell arises from a population level process of extinction. Colonisation of empty patches is still a process of birth and dispersal, but now aggregated over a larger range.

The literature prior to 1990 on both theoretical and empirical efforts to understand spatial ecology has been summarised by Kareiva (1990). Kareiva and Wennergren (1995) have also attempted to extract some principles for conservation biology from more recent models. For the remainder of this chapter, I will review a representative sample of spatially explicit models in ecology published between 1990 and 1996, and try to identify gaps in the methods and topics covered that could be usefully exploited in this thesis.

Spatially Explicit Population Models

Okubo (1980), in his classic text on reaction diffusion models in ecology, split models into two sorts: educational and practical. Educational models make simplifying assumptions to lay bare the underlying mechanisms. Practical models attempt to incorporate enough reality to answer specific questions. In this review I will show that the field of spatially explicit population modelling has reached a stage where educational models should be just that: for education. Future progress in ecology will come from practical models, addressing questions about real populations.

Spatially explicit population models (SEPM) are characterised by the specification of a spatial location for the units of interest in the model, whether those are individual organisms, patches of habitat, or entire populations. This clearly distinguishes them from earlier models based on differential or difference equations, such as the Lotka-Volterra competition model (May, 1974), or the discrete logistic (May, 1975). These earlier models assumed that the populations they described were homogenously mixing, and therefore all individuals in the population experienced the same conditions. Early meta-population models (Levin, 1974; Gotelli & Kelley, 1993), while they assumed that populations were subdivided, also assumed that the component sub-populations were homogenously mixing. This within-patch "infinite dispersal" assumption still persists in more recent analytical metapopulation models (Hanski et al., 1996). The only way to relax this assumption of homogenous mixing is to describe the location of individuals, populations, or at least regions of a particular density. This extra demand dramatically increases the computational complexity of the models, and this is why the development of spatially explicit population models has paralleled the development of powerful, readily available digital computers.

Given the added complexity of these models, it could (and should) be asked why they are useful or even necessary. Empirical ecologists, particularly those working on plants, have long intuitively felt that spatial heterogeneity was a key factor driving patterns of distribution and abundance. Kareiva (1990) considered the notion to be so common as to be scarcely worth mentioning. Cowles (1899) classic study of dune succession in Michigan highlighted the importance of spatial interactions between species. Gleason (1926) also emphasised that the spatial distribution of neighbours could influence the species present at a particular site. The growth of individual oat plants depends on the spatial distribution of their neighbours (Lindquist et al., 1994). Recruitment of marine fish onto tropical reefs is spatially variable, and a primary determinant of reef fish population dynamics (Doherty & Fowler, 1994). Johnson et al. (1992) considered an understanding of how landscape pattern influences ecological processes to be crucial to the further development of ecology. Husband and Barrett (1996), in a review of metapopulation studies of plants, emphasised that individual, spatially explicit models were necessary because they could be parameterised for real plants, avoiding the difficult to measure colonisation and extinction parameters of classical metapopulations. Doyle (1991) and Hughes (1996) both called for models of weed management systems to account for spatial heterogeneity and spread. The need for SEPM has been around for a long time, and now the tools to create them, and more importantly to understand and compare their output with empirical data, exist.

SEPM do not constitute a homogenous group of models describing the locations of organisms and their resulting dynamics. The diversity of models in this category is exceeded only by the diversity of researchers constructing them; and not by much at that. SEPM vary in the way they represent space, in the basic unit they model, and in the temporal and spatial resolution. There are analytical SEPM, but the vast majority are computer simulations. They range in reality from analytical models of stochastic point processes (Durrett & Levin, 1994) to detailed descriptions of the foraging movements of a particular species on a particular landscape (Turner et al., 1994). This immense diversity raises a further issue: can the effect of spatial structure on the dynamics of a population be generalised?

I will first describe the diversity of methods that have been employed in constructing SEPM. Then I will examine the conclusions reached by general, or educational, models. Finally, I will discuss the uses to which practical SEPM have been put, and the kinds of problems they might usefully illuminate in the future.

A Diversity of Modelling Methodologies

I begin this section by describing several axes along which spatially explicit models can be separated, along with examples of each sort. The sorts of axes that I consider include:

- Analytical versus Simulation models
- "General" versus system specific models
- Scale of spatial representation
- Basic biological unit modelled - individual, habitat patch, population
- Number of interacting species

With these descriptions in hand I classify a large number of models to determine if there are patterns in the way models are constructed. The goal is to highlight possible directions for future research.

Spatially explicit models can be fundamentally divided by considering whether they have closed form analytical solutions, or if they are numerical simulation models. Analytical models generally take the form of reaction-diffusion equations, representing space in a continuous fashion (eg. Cantrell et al., 1996). Day and Possingham (1995) have constructed the only example of an analytical spatially explicit metapopulation model. With an analytical solution, the global behaviour of the model can be completely known. However, increasing complexity makes achieving an analytic solution more difficult, or even impossible. For example, Day and Possingham (1995) could find analytical solutions for patch configurations with up to 9 patches, but increasing the number of patches beyond that requires simulation. Given the difficulty of solving systems of reaction-diffusion equations, even these are frequently solved numerically on a computer. Analytical spatially explicit models are correspondingly rare in the literature, and all other models are computer simulations. While computer simulations loosen the limitations on model structure, it is frequently as difficult to understand the results of a simulation as it is to understand the natural system being modelled.

Spatially explicit models can also be separated by examining whether a specific species or group of species motivated the model. "General" models are often constructed without reference to a particular organism in an attempt to derive ecological principles that apply to many species (eg. Bartha et al., 1995; Wood & Thomas, 1996). In some cases models are even constructed without reference to nature. The authors of such artificial life systems (eg. Sipper, 1994; Olson & Sequeira, 1995; Laval, 1996) frequently claim that by creating alternate "natures" in the computer they can discover general ecological or evolutionary principles. At the other extreme, models are constructed that closely match the biology of a selected species (eg. Moloney & Levin, 1996). Some models also incorporate actual landscape features (eg. Akcakaya & Baur, 1996; Mason & Brandt, 1996), limiting the conclusions not only to the species, but also to the particular landscape.

Spatially explicit models also vary in the way they represent space. Conceptually, spatial variation can be either continuous or discrete. In practice, only an analytical reaction-diffusion model can represent continuous space; all simulation models must necessarily break space into discrete chunks at some scale. Distinguishing models based on continuity of spatial representation overlaps with the Analytical/Simulation axis. A more useful classification is to examine the scale, or resolution, at which the system is modelled. The scale is determined by the area below which heterogeneity is assumed to be unimportant for the processes being modelled, and should be considered relative to the organism in question. For animals, fine grained models discretise space at scales smaller than the average foraging movement distances of the organism (eg. Turner et al., 1994). Models with intermediate grain still represent individuals, but only at the scale of an average home range (eg. McCarthy, 1996). Coarse grained models represent space at scales larger than the foraging movement distances of individuals, generally at the scale of a patch of habitat or larger (eg. Possingham & Davies, 1995). For plants, fine grained scales correspond to the size of an individual, while coarse grained models average over areas larger than single individuals.

Another axis of variation is defined by the basic biological unit being modelled. The smallest biological unit of interest in population ecology is the individual; Individual Based Models (IBM; DeAngelis & Gross, 1991) are a class of models that overlap with SEPM. However, IBM do not necessarily represent space; sometimes the age structure of individuals in the population is the only rationale for following individuals. Likewise, SEPM do not necessarily follow the fate of individual organisms. Metapopulation models generally take a population to be the basic unit. These models also vary in the degree of detail that is modelled within each unit. Some models (eg. Possingham & Davies, 1995) track the number of individuals in each population or sub-population. Others (eg. Day & Possingham, 1995) only record the presence or absence of the species in a particular habitat patch. This extreme version, variously called a patch occupancy model, or presence/absence model, assumes that very strong density dependence is operating within each habitat patch (Diekmann et al., 1988). To a certain extent, this "biological unit" axis is not independent of the "spatial representation" axis described above, because one will never find fine grained models where the population is the basic unit of study, by definition. However, a coarse grained model that tracks individuals is possible (eg. Hilborn, 1990).

Finally, one can distinguish between models that represent single species (eg. Hochberg et al., 1994b), and multiple species models (eg. Halley et al., 1994). Multispecies models are necessary to address the role of ecological interactions such as competition and predation on the distribution of populations across landscapes.

Given the degree of overlap between some of the axes above, I will concentrate on classifying models along only three: General/Species Specific, Scale, and Number of species. The raw data for this comparison comes from a computer search of Biological Abstracts from 1990 to 1996. Papers from concept categories in the "ecology-environmental biology" tree containing the words "population", "model", and "spatial*", where the "*" indicates all possible endings, were selected, giving over 600 references. The abstracts of these were examined to find the papers pertaining directly to spatially explicit population models, resulting in a final dataset of 174 references (Table 1.1; Appendix A) to be classified along the three axes described above. This by no means is all spatially explicit models published since 1990, but it is probably a representative sample.

Table 1.1 Summary of SEPM classification ignoring scale. Numbers in the table are counts of references. For detailed citations see Appendix.

		Topic			
Type	# Species	Persistence	Spread	Stability	Other
General	Multi	4		23	16
General	Single	9	4	8	17
Specific	Multi	2	8	2	20
Specific	Single	21	12	2	26

During the classification process, 3 areas of ecological inquiry appeared to dominate the literature on SEPM:

- Rate of spread of invading populations or disease (24 References)
- Stability of interacting populations, especially host-parasitoid (35 References)
- Effect of habitat fragmentation, disturbance, etc. on species persistence (35 References)

The most interesting pattern is the shift from general models of stability to specific models of persistence. Okubo (1980) referred to general models as "educational"; that is, they were useful as tools to learn about the methods, and to explore logical possibilities. The topic of stability is the exploration of long term, asymptotic behaviours of dynamical models. The shift away from this issue in specific models suggests that stability as a topic of immediate interest to empirical ecologists is not particularly interesting, or possibly intractable. Persistence, or the analysis of times to extinction, is a topic that is simpler to grasp theoretically and empirically, and is also pertinent to problems facing decision makers all over the world.

The remaining 79 references were classified as "other"; Table 1.2 lists a selection of the topics addressed in this category.

f these, the most interesting is the use of spatially explicit models to test statistical methods or sampling protocols. Empirical ecologists frequently need to decide how to sample a population parameter, or how to test a hypothesis on a set of data. By examining the performance of statistical tests on data from spatially explicit simulations, the ability of the test to deal with biologically realistic data can be readily evaluated. I call this method the “virtual ecologist”, and will return to it throughout this thesis. Hartway et al. (1998) describe this approach as the most promising contribution to conservation ecology that can be made by SEPM, given the scarcity of data available.

Conclusions of general SEPM

As mentioned in the previous section, general or "educational" models have not always directly overlapped with the interests of ecologists at large. But have they lead to interesting or useful general conclusions, applicable to a broad range of species? I will consider each of the

Table 1.2 Sample of "other" topics found while classifying SEPMs.

Topic	Example Citation
Community Structure	Fahrig et al. 1994
Ecosystem Dynamics	Baretta et al. 1995
Disturbance pattern	Baker 1993
Evolution of Behaviour	Bernstein et al. 1991
Formation of spatial heterogeneity	Cain et al. 1995
Genetic Structure of Populations	Goldstein and Holsinger 1992
Fisheries, Pest, or Forest Management	Hoy et al. 1990
Testing Statistical Methodology	Thomas 1996

three main topics identified above in turn: Spread of species, Stability of population dynamics, and Persistence of populations.

Spread of species

Measuring the rate of spread of an invading population is one of the earliest uses to which spatially explicit models were put (Skellam, 1951). Introducing an Allee effect into the population dynamics slows down the rate of spread (Lewis & Kareiva, 1993). When the landscape is fragmented into patches, the degree to which they are aggregated, relative to the dispersal ability of the species, influences the likelihood of an empty patch being colonised (Doak et al., 1992). Other efforts to connect readily available empirical data such as maps of disease outbreaks (Gibson & Austin, 1996), and life history traits (Van Den Bosch et al., 1990) with spread models are laudable, and necessary. From the frequency of general versus specific spread models (Table 1.1) it would appear that this group of models has successfully made the shift from "educational" to "practical".

Stability of Population Dynamics

Theoretical ecologists have been fascinated by the question of the stability of population numbers from the earliest attempts to describe population dynamics. This arises from the fact that analytic predictions of long term average population sizes are generally derived via asymptotic stability analysis of the solutions to a set of deterministic equations. If the only stable solution to a set of equations is extinction, then a problem arises if the model is to explain the long term persistence of populations of interacting species. For example, Nicholson and Bailey (1935) derived a set of equations for interacting host and parasitoid populations where rapid extinction was the only outcome. This single paper has sparked more theoretical effort than any other, only to find ways of obtaining stable solutions to the problem. General SEPM models have been at the recent forefront of these efforts. I will review the results of some of these models, starting with single species on homogenous landscapes, and progressing through multiple interacting species and heterogenous landscapes.

Skellam (1951) showed that a logistically growing population in a homogenous, bounded space would tend to a spatially uniform stable abundance. Ruxton (1996) examined the interaction between density dependence in local populations and dispersal rates on the likelihood of persistence. When local density dependence is low, increased dispersal decreases persistence by inducing synchrony amongst subpopulations; this effect disappears at high levels of density dependence because subpopulations fluctuate chaotically. Bascompte and Solé (1994) analysed a system of coupled discrete time population models with dispersal limited to neighbouring populations. They showed that increasing dispersal rates relative to a particular size of spatial domain increased the likelihood of stable equilibria. Molofsky (1994) showed a similar effect with simple cellular automata; low dispersal rates or large spatial domains lead to chaos. Logistically growing populations on heterogenous habitats have also been considered by Andersen (1991) and Cantrell and Cosner (1991); the general conclusion is that chaos is more likely when populations are widely distributed relative to their dispersal rates. However, Solé and Valls (1992) were unable to distinguish such spatially distributed chaos from random fluctuations, suggesting that the practical significance of such results is limited.

There is an extremely interesting simulation model of a predator-prey interaction in homogenous space created by Wilson, de Roos, and McCauley (De Roos et al., 1991; McCauley et al., 1993; Wilson et al., 1993; Wilson et al., 1995). They created an individual based model designed to correspond closely to the biological representation of a diffusive Lotka-Volterra predator-prey model. The diffusive L-V model in a finite space has been shown to be spatially homogenous in the long term (Okubo, 1980); ie. local perturbations die out. Putting this into a fine grain, individual formulation showed that long term spatial inhomogeneity did not die out, but was maintained. The greater the prey dispersal relative to the predator dispersal, the "patchier" the spatial distribution of prey becomes. They suggest that such a phenomenon could have been expected for individual dynamics in ecology; similar scale-dependent changes in theoretical constructs occur in physics as one changes from averaging behaviour of many objects to describing the behaviour of individuals (Thermodynamics becomes statistical mechanics becomes quantum mechanics). This effect appears in the simulation model used in Chapter 7 of this thesis.

Spontaneous spatial heterogeneity in interacting populations in the absence of environmental heterogeneity has also occurred in other models. Hassell et al. (1991; 1994) and Comins et al. (Comins et al., 1992) have demonstrated considerable structural complexity can arise in maps of host-parasitoid populations when movement between neighbouring populations is density independent. As for single species populations, when host dispersal rates are low, chaos is the result. Malchow (1995) demonstrates diffusive instabilities for 3-dimensional uniform space when the habitat is flowing (ie. for planktonic organisms) or when the consumers can move in relation to prey density. Lewis (1994) shows a similar result for terrestrial herbivores that respond to herbivory induced changes in plant quality. Making the landscape heterogenous only enhances the effect of spatial interactions (McLaughlin & Roughgarden, 1991; McLaughlin & Roughgarden, 1992).

Competitive interactions are also qualitatively affected by putting the populations on a heterogenous environment. In general, the ability of species to co-exist is increased by landscape heterogeneity (eg. Czaran, 1989; Goldwasser et al., 1994). Bowers and Harris (1994) examined the effect of fragmenting habitat, and showed that it could shift the competitive balance from locally adapted specialist species to generalists. For plants at least, the effect of spatial heterogeneity may disappear when competition is asymmetrical (Hara & Wyszomirski, 1994).

Persistence

Persistence is really a subcategory of stability; the question is how long before the population goes extinct, rather than the long term average dynamic behaviour. The question of extinction really arises only when one considers that population dynamics is fundamentally a stochastic process. Deterministic models are misleading in this regard, as the long term average behaviour predicted from such a model may never approach extinction. Under the corresponding stochastic model however, the long term probability of extinction is always greater than 0, regardless of the population growth rate (Mangel & Tier, 1994).

As can be seen in Table 1.1, persistence has primarily been an applied question. There are a few general models that have provided some useful insights. For example, Adler and Nuernberger (1994) find that if dispersal is costly, persistence is enhanced if otherwise identical patches are clumped together. Scale is important here, as the distance at which patches are "clumped together" depends on a species' mean dispersal distance (Fahrig & Paloheimo, 1988). In the temporal dimension, Fahrig (1992) tested the effect of variation in the duration and size of ephemeral patches on the global size of a simulated population. Increased temporal duration of patches had a bigger effect on population size than patch size.

Durrett and Levin (1994) review some general mathematical results of "interacting particle systems" with an eye towards understanding the persistence of populations distributed in space. They show how some analytical results can be obtained for stochastic models with strictly local interactions on a homogenous landscape and other restrictive assumptions. These analytical results are a potential source of shortcuts for simulation models, and useful as baseline comparisons for simulation models.

Applied Spatially Explicit Population Models

Having described the sorts of conclusions reached by general SEPM I will now turn to their practical counterparts. The focus here will be on comparing their results with those of the general models, to determine if the general models can provide insight.

Spread of species

Models of the spread of individuals have been parameterised to address questions of biological control for specific species such as balsam wooly adelgid (Dale et al., 1991), bovine Tb (Barlow, 1993; White & Harris, 1995), crown of thorns starfish (Black & Moran, 1991), grey squirrel (Okubo et al., 1989), mountain pine beetle (Polymenopoulos & Long, 1990), old world screwworm (Atzeni et al., 1994), rabies in foxes (Smith & Harris, 1991; Murray & Seward, 1992), and russian wheat aphid (Schotzk & Knudsen, 1992). Fisheries modellers are also interested in questions of spread, and in understanding how fish stocks move between areas with different control measures. Examples include demersal fishes in Europe (Arnold & Holford, 1995), estuarine fishes in Mexico (Reyes et al., 1994), and yellowfin tuna (Mullen, 1989; Deriso et al., 1991). It can only be concluded that spread models have reached the point at which they can and are applied in a wide range of practical settings. Many of these models rely on diffusion approximations, often discretised to some particular grid scale. One fruitful avenue for future "educational" models is the examination of conditions under which diffusion approximations may break down for individual organisms.

Stability of Population Dynamics

The few models classified in this category can at best be described as models of population dynamics incorporating a large amount of detail on a specific species with no apparent purpose (see Chapter 5 for a paradigmatic example).

Persistence

Persistence models of specific species are probably the only example of a growth industry in theoretical ecology. There are even commercial software packages for the analysis of persistence on spatially explicit landscapes (Lindenmayer et al., 1995a). These models do not lend themselves to generalisations, because of the specific assumptions contained therein. However, these models are being used in decision making at the government level, a distinction achieved by none of the general models.

Conclusions

Spatially explicit models are in their relative infancy in the fields of stability and persistence. Nonetheless, at least in the study of persistence times they are widely used for practical applications. In the field of population spread or invasion, spatially explicit models seem to have matured and are being widely used in practical applications. Comparisons of general and specific models in all of these fields indicates a need to understand the conditions under which averaging over individuals, or averaging over space, or both will not lead to qualitatively different conclusions.

In this thesis I will use spatially explicit models and computer intensive analysis for two main purposes. First, I seek to understand how processes acting at the individual level scale up to population dynamics when processes are variable in space. Second, I am interested in how ecologists sampling this variability will perceive it, and what that means for drawing conclusions from the often limited data available to ecologists.

In chapter 2, I develop an individual based model of arboreal marsupials, and consider how different natal dispersal strategies influence the long term population dynamics. In chapter 3 I use this arboreal marsupial model to evaluate the common practice of correlating presence/absence data for a species with habitat characteristics in order to identify “good” habitat. In chapter 4, I explore a spatially and temporally extensive data set of infestations of an ectoparasitic tick on large lizards for evidence of density dependent population regulation at a variety of scales. In chapter 5, I develop an individual based simulation of the tick population to see if “emergent” properties of the complex spatiotemporal interaction between ticks and their host lizards can lead to population regulation in the absence of obvious mechanisms. In chapter 6 I make a series of predictions for a proposed landscape scale experiment designed to test the model of chapter 5 in the field. Finally, chapter 7 returns to the data set of chapter 4, and looks at the change in population variability with observation scale for the host lizards.

The quote from Peter Kareiva and Uno Wennergren that begins this chapter is easily the best one line summary of half my motivation for the papers in this thesis. The other half stems from an interest in questions of scale, and how the scale of observation interacts with scales of heterogeneity and dynamics to produce observed patterns. These are broad questions, on which entire books have been written. I cannot hope to cover these topics adequately within this thesis, but I hope that it represents a beginning.

Chapter 2 Modelling dispersal behaviour on a fractal landscape

Introduction

Many organisms do not move far as adults (Wolfenbarger, 1946). In the extreme, entirely sessile animals, like barnacles, are permanently fixed to their substrate. Many mobile animals also limit their movements as adults, restricting long range dispersal to new habitats to the juvenile phase of life. Natal dispersal is crucial to the lifetime reproductive success of an individual, because the location juveniles choose determines, at least in part, how well they can grow and reproduce for the rest of their lives. Despite the importance of this behaviour for population persistence, very little is known about how juvenile organisms disperse and choose new habitats (Stenseth & Lidicker Jr., 1992; Haas, 1995). Knowledge of dispersal performance is crucial to understanding biological invasions (Shigesada et al., 1995), and population responses to disturbances (Green, 1989), especially on structured landscapes.

I construct a spatially explicit population model to explore the population consequences of different dispersal strategies on landscapes with continuous variability in habitat quality. The central focus of this chapter is on variation in the total abundance of individuals on a landscape. On a heterogenous landscape some regions provide above average survival or fecundity, and others below average. Does this variation influence population size, and does it matter how the different regions are arranged in space? Does the strategy used by individuals during natal dispersal influence population size? And finally, what are the individual level consequences in terms of mortality and fecundity that lead to variations in population size?

It is important to distinguish between movements at different temporal and spatial scales. At the finest scales, mobile species move on a daily basis to forage, avoid predators, defend territories, find mates, and care for offspring. This sort of movement has been modelled as a diffusion process (Skellam, 1951), correlated random walks (Kareiva & Shigesada, 1983; Marsh & Jones, 1988), and by detailed simulation (eg. Jones, 1977). At larger scales, many species undertake large periodic migrations between seasonal habitats that can best meet their needs at different times (Keast, 1968; Stenseth & Lidicker Jr., 1992). Migrations generally occur along well-defined routes between large regions, and the modelling of the development of such routes is primarily an evolutionary question over very long time scales. This paper is concerned with natal dispersal, defined as dispersal from the natal home range to a new location which forms the adult home range. Such movements are not incompatible with migration or daily movements, but occur at intermediate temporal and spatial scales. However, because natal dispersal occurs infrequently (ie. once in a lifetime), and is relatively large in scale, empirical data are scarce. Lubchenco et al. (1991) list dispersal as one of the "intellectual frontiers" of ecology, highlighting the need for further analytical and empirical work in this area. Furthermore, Hartway et al. (1998) have demonstrated that errors in estimating dispersal parameters propagate through the predictions of a spatially explicit model to a greater extent that nearly any other parameter.

From the point of view of a juvenile terrestrial vertebrate about to disperse from a natal territory, the location of good quality, unoccupied habitat is unknown. There are two key decisions a dispersing individual must make: in which direction to disperse, and, upon finding an unoccupied site, should the search stop, or is there better quality habitat available? This is a particular instance of a more general problem in operations research, the "job search problem" (Lippman & McCall, 1977). In ecology, the job search problem has also been used as a model of mate choice (Real, 1991). Most work on the job search problem has ignored the first question, which direction to search in, by assuming that the quality of each job, mate, or home range is independent of the quality of previously encountered possibilities. However, the quality of real landscapes is spatially correlated; if the current territory is good, the neighbouring territories are more likely to be good than bad. When a disperser moves across such a landscape step-by-step, as in the model described in this chapter, the quality of subsequent encounters with home ranges is not independent. Furthermore, the direction of movement may influence whether the next unoccupied territory encountered is better or worse than the previous one. Therefore, in the model I construct here I assume a simple stopping rule, and concentrate on the problem of choosing the direction to search in.

Determining the direction a dispersing individual searches depends on the scale at which it can perceive information about the landscape. At one extreme, individuals may know nothing about the landscape beyond their immediate location (eg. Baur & Baur, 1993). In this case, any direction is as good a place to start as any other. At the other extreme, an animal may be able to perceive large areas of the landscape (eg. large, wide ranging raptors). For the purposes of this paper, the analysis is restricted to terrestrial vertebrates who move step-by-step across a landscape. The ecological neighbourhood (Addicott et al., 1987) that determines the scale of this model is a large fraction (say 95%) of the area within which daily resource needs are met; I refer to this as the home range size. I assume that the model individuals can only obtain information about the quality of home ranges immediately next to their current location.

Previous empirical work on dispersal in terrestrial vertebrates (Wolfenbarger, 1946; McCarthy, 1997) has generally assumed that dispersal occurs in a straight line. If dispersal terminates at the first vacancy, and vacancies are randomly distributed, this leads to a negative exponential distribution of dispersal distances. Straight-line dispersal is frequently implemented in patch based metapopulation models (Possingham et al., 1994a; McCarthy, 1996). The opposite extreme is to assume that individuals have perfect knowledge of the nearest vacancy. This is also unrealistic.

A dispersal strategy will have ecological consequences at two different levels. First, it will influence the lifetime reproductive output of each individual, because home range quality determines fecundity and survival as a reproductive adult. Second, it will influence the distribution of the population across the landscape, and consequently the total size of the population. The life history of a species may influence the consequences of different dispersal strategies. Therefore, I parameterise the model for two species of Australian arboreal marsupials, the greater glider (*Petauroides volans*), and the mountain brushtail possum (*Trichosurus caninus*), which differ in their reproductive and survival rates.

The purpose of this chapter is to explore the interaction between individual level dispersal strategies and continuously variable landscapes. First, I look at the long term population sizes ("quasi-equilibrium") that result from a range of possible dispersal strategies, on landscapes with two different levels of heterogeneity. Then I explore the individual level causes of variation in quasi-equilibrium population size under different dispersal strategies.

The Species and their ecosystem

To explore the central questions of this chapter I use two different mammal species as "model" species. Here the life-history of the species is briefly described along with the ecosystem in which they live. Tall eucalypt forests in south eastern Australia are inhabited by several arboreal marsupial species. Many of these are of conservation concern, because their habitats are threatened by timber harvesting. I chose to model two species, the greater glider (GG, *Petauroides volans*), and the mountain brushtail possum (MBP, *Trichosurus caninus*), because I have access to life history data, habitat requirements, and model parameters from other studies (Table 2.1). MBP are omnivorous, may sometimes forage on the ground (How, 1983), and prefer wet forests. GG are entirely folivorous, consuming predominantly eucalypt leaves (Hume et al., 1984), and prefer tall open forest. Both species have patchy distributions in otherwise contiguous forest (Lindenmayer et al., 1990), indicative of habitat quality variation and/or demographic stochasticity. Females of both species are solitary occupants of their territory, although female MBP may share their territory with a male (Lindenmayer, 1997). GG have higher 1st year survival and greater fecundity, while MBP have higher juvenile and adult survival. GG mature after one year as a juvenile, while MBP spend 3 years as juveniles after dispersing.

Table 2.1 Baseline life history parameters for the greater glider (Possingham et al., 1994a) and mountain brushtail possum (D.B. Lindenmayer, Personal Communication). Parameters for each species are presented as stage-structured projection matrices (Caswell, 1989). Fecundity is in the top row, and is the probability that a given stage produces a female offspring each year. Survival is in the subdiagonal entries, and is the probabilities of surviving to the next year. The value in the bottom right corner is the probability of surviving from year to year as an adult. D is the probability of surviving dispersal, and is given in the text. For GG the exponential population growth rate, calculated as the leading eigenvalue of the matrix, is 1.057, and for MBP it is 1.027, assuming $D = 1.0$.

GG	**N**	**J1**	**A**
	0	**0**	**0.49**
	0.55D		
		0.85	**0.85**

MBP	**N**	**J1**	**J2**	**J3**	**A**
	0	**0**	**0**	**0**	**0.4**
	0.3D				
		0.85			
			0.9		
				0.95	**0.95**

The Model

The model was individual based, tracking the location and life history state of all females in the population at one year intervals. I ignored males in this implementation for simplicity and because they do not contribute individually to population growth in these species. The basic spatial unit was a female home range. All runs of the model were performed on a 33 x 33 grid of home ranges, using a 6-cell hexagonal neighbourhood. There were 4 important components to the model: the landscape of continuously variable habitat quality, the population of individuals, the connection between habitat quality and vital rates (survival and fecundity) of individuals, and the dispersal rules used by individuals to move around on the landscape. I describe each of these components in turn.

In cellular automata models, the cells that can be influenced by the state of a particular cell are referred to as the neighbourhood. In this model, the neighbourhood was defined as the cells which an individual could reach in a single dispersal step. In theory, the geometry of the neighbourhood does not influence the outcome of cellular automata models (Durrett & Levin, 1994), as long as suitable weighting functions are chosen for the probabilities of movement between cells. I chose a hexagonal neighbourhood to provide the widest range of directional choices with equal intercell distances, obviating the need for weighting movement probabilities. I tested 4-cell von Neumann (Tyre et al., 1997), and 8-cell Moore neighbourhoods, and the results are not significantly different. The landscape was implemented as a single dimensional array, with offset kernels constructed in advance to allow the landscape to be accessed as either an orthogonal or hexagonal grid. Each offset kernel was an array containing information about how far to move up or down the array to move in a given direction. Moving up one row of the landscape translated to moving up the array by the width of the landscape and so on. For hexagonal grids, whether the current row was odd or even affects the kind of shift required for between row movement. Retrieving information about a neighbouring territory involved three steps: 1) determining whether the current territory is on an edge and whether the row is odd or even, 2) choosing a direction, and 3) using the offset kernel to determine how far up or down the array the desired territory occurs.

Each home range on the landscape has an associated habitat quality. I wanted random landscapes with controllable amounts of spatial autocorrelation. Fractal surfaces can be constructed with a mid-point displacement algorithm (Saupe, 1988). This creates a surface with a specific fractal dimension, H. I used either $H = 2.9$ or 2.5. The higher the fractal dimension, the more "fragmented" the landscape, with high quality home ranges split into a larger number of smaller patches, and increased interspersion of poor quality habitat with high quality habitat (Figure 2.1). This corresponds to less spatial autocorrelation. An example of a high dimension habitat variable is the number of hollow bearing trees (Lindenmayer et al., 1990). Landscape processes lead to trees occurring in clusters. Slope or soil type are examples of lower dimensional habitat variables. The range of floating point values output by the fractal algorithm were linearly scaled to the integer range 0-100. Distributions of habitat quality generated with higher fractal dimensions are compressed more under this transformation. This is because the range of floating point values is larger at larger fractal dimensions. I ignored the slight error on odd rows of the landscape grid resulting from converting the square grid output by the fractal algorithm to the hexagonal grid used in the model. This shift is unlikely to substantially influence the results.

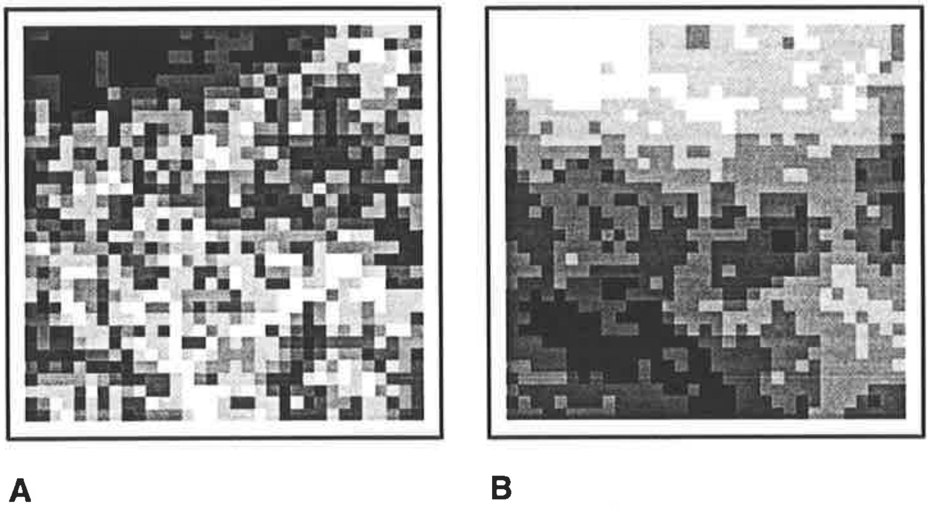


Figure 2.1 Example fractal landscapes. Each cell is a territory. White cells are the 10% poorest cells, Black the 10% best (ie. the portion of the landscape above Q). Other contour breaks are at 30%,50%, and 70%. A) $H = 2.9$. B) $H = 2.5$.

The population was implemented as a singly linked list of individuals. There were three different processes occurring within a year: birth, natal dispersal, and death (Figure 2.2). Within a year, all individuals were checked sequentially to determine if they gave birth. Newborn animals were placed in a dispersal queue. The order of newborns in the queue was the same as the order of their mothers in the population list. The dispersal step followed birth, with individuals being removed from the queue and allowed to move until they settled. After settling, every individual in the population was aged by one year, and checked for normal mortality.

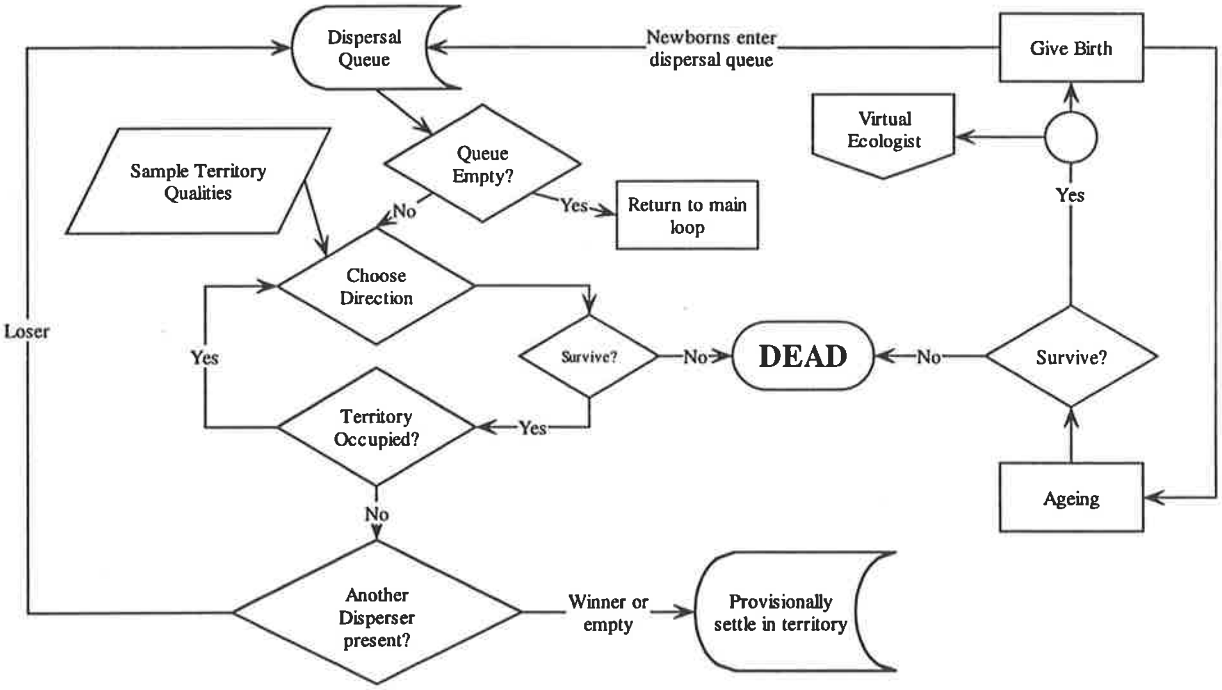


Figure 2.2 Flowchart of basic model processes. The main loop is on the right, with the dispersal loop on the left.

During dispersal there was a per step probability of dying, which means that the probability of surviving dispersal was:

$$D = (1 - d)^n \tag{2.1}$$

where d was the per step probability of mortality ($d = 0.01$ for all runs), and n was the number of steps taken before settling. Note that n will be different for every individual. It will also depend on the local density of individuals, because in crowded conditions unoccupied territories will be rarer (McCarthy, 1997). This was the only point at which density dependence entered the model. There is empirical evidence that dispersing or translocated individuals suffer higher rates of mortality (Pietsch, 1995). The specific movement algorithms I used are described below. Dispersing individuals settle only in unoccupied territories under the assumption that older individuals (ie. dispersers from previous years) were able to repel inexperienced territorial invaders without significant cost to themselves. If a cell was occupied by a disperser from an earlier position in the queue, the resulting territorial dispute was settled randomly, with neither individual having an advantage (50% win/loss). The loser goes back into the dispersal queue to continue dispersing from the disputed location.

It was possible that resolving birth, dispersal, and mortality events sequentially, rather than simultaneously, introduced a bias towards individuals at either end of the queue. The initial order of individuals in the linked list was not important, because individuals were distributed at random on the landscape. Individuals only interact with each other during the dispersal phase. I tested the effect of initial position within the dispersal queue, and found no systematic bias in the final quality of habitat located, or the number of times a territorial dispute occurred. Bias would only occur if the first individual to settle in an unoccupied territory had an advantage over later arriving individuals. This may occur in real animals, but I ignored this possibility in the current model.

The variable landscape influenced individuals through either their probability of surviving from one age class to the next, or their probability of giving birth to a daughter. Both of these vital rates are probabilities, and are bounded between 0 and 1. The logistic, or log-odds transformation scales a probability onto the real number line (bounded by $\pm\infty$). I assumed that habitat quality has a linear effect on the log-odds of survival or reproduction. The annual probability of giving birth to a daughter in each home range $p_{x,i}$ is modified by the local habitat quality, Q_x according to

$$\ln\left(\frac{2p_{x,i}}{1-2p_{x,i}}\right) = b\left(\frac{Q_x}{\tilde{Q}}-1\right)+\ln\left(\frac{2p_i}{1-2p_i}\right) \qquad (2.2)$$

where b was the effect of habitat quality on fecundity, Q_x was the habitat quality value in home range x, $\tilde{Q}$ was the 90th percentile habitat quality, and p_i was the annual fecundity of age class i in a territory of quality $\tilde{Q}$. The two in the denominator and numerator of the log-odds transformation is a correction for ignoring males. I assumed the sex ratio was 50/50. Therefore, when the probability of reproduction in a year was one, the maximum probability of having a female offspring is 0.5. The exact distribution of habitat quality values differed between replicate landscapes. $\tilde{Q}$, which was an average of 72 ($H = 2.9$) or 70 ($H = 2.5$), scales habitat quality to remove any bias between different random landscapes. It ensures that regardless of the exact details of the landscape, only 10% of home ranges have fecundity (or survival) rates greater than p_i. When $b > 0$, individuals have increased fecundity when $Q_x > \tilde{Q}$, and decreased fecundity when $Q_x < \tilde{Q}$. I use a similar transformation for the effect of habitat quality on survival:

$$\ln\left(\frac{s_{x,i}}{1-s_{x,i}}\right) = a\left(\frac{Q_x}{\tilde{Q}}-1\right)+\ln\left(\frac{s_i}{1-s_i}\right) \qquad (2.3)$$

where $s_{x,i}$ is the probability of surviving to the end of age class *i* in territory *x*, and *a* is the

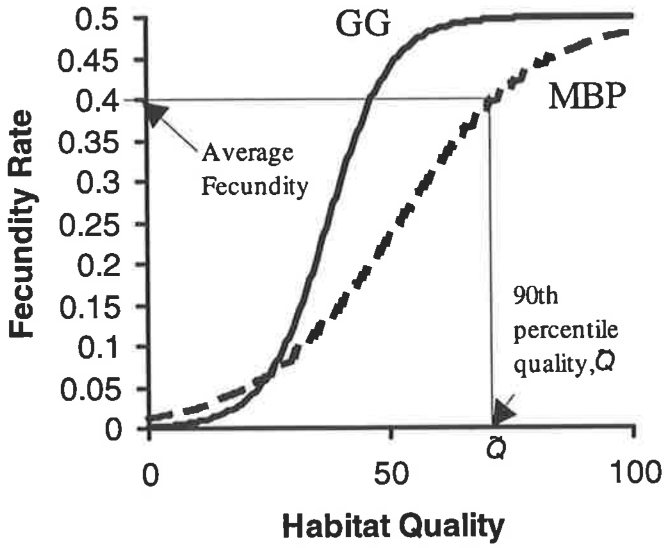


Figure 2.3 Plot of Eq. (2.2) using parameters for MBP ($b = 5$) and GG ($b = 11$). Thin solid lines show the relationship between $\tilde{Q}$ and the fecundity parameter for MBP. In the absence of spatial variation all territories would have $p = 0.4$. When spatial variation in habitat quality influences fecundity, most territories (90%) will have fecundities lower than 0.4.

effect of habitat quality on survival. I chose a, b and $\tilde{Q}$ to ensure that approximately half of the landscape was occupied at equilibrium, based on preliminary runs. I refer to runs where variation in quality is attributed to survival as "survival scenarios" ($a = 0.6$, $b = 0$ for both species), and runs where fecundity is spatially variable as "fecundity scenarios" ($a = 0$, $b = 11$ for GG, 5 for MBP). The fecundity effect parameter b for GG is approximately double that for MBP, because p_{adult} is so close to 0.5 for GG; smaller slopes did not introduce enough variation in fecundity. A smaller amount of variation in survival leads to the same population level response because the sensitivity (sensu Caswell, 1989) of the population growth rate to the survival parameters, particularly adult survival, is much higher than to fecundity.

The effect of habitat quality on population level parameters can be quantified by calculating the intrinsic rate of population growth from a projection matrix, with the values in the matrix modified according to (2.2) and/or (2.3) (Figure 2.4). In the results, I refer to habitat where the intrinsic population growth rate is less than one as "marginal habitat" (Stenseth & Lidicker Jr., 1992), and territories with intrinsic population growth rates of greater than one as "high quality habitat". Essentially, individuals in marginal habitat do not produce enough offspring to replace themselves, on average.

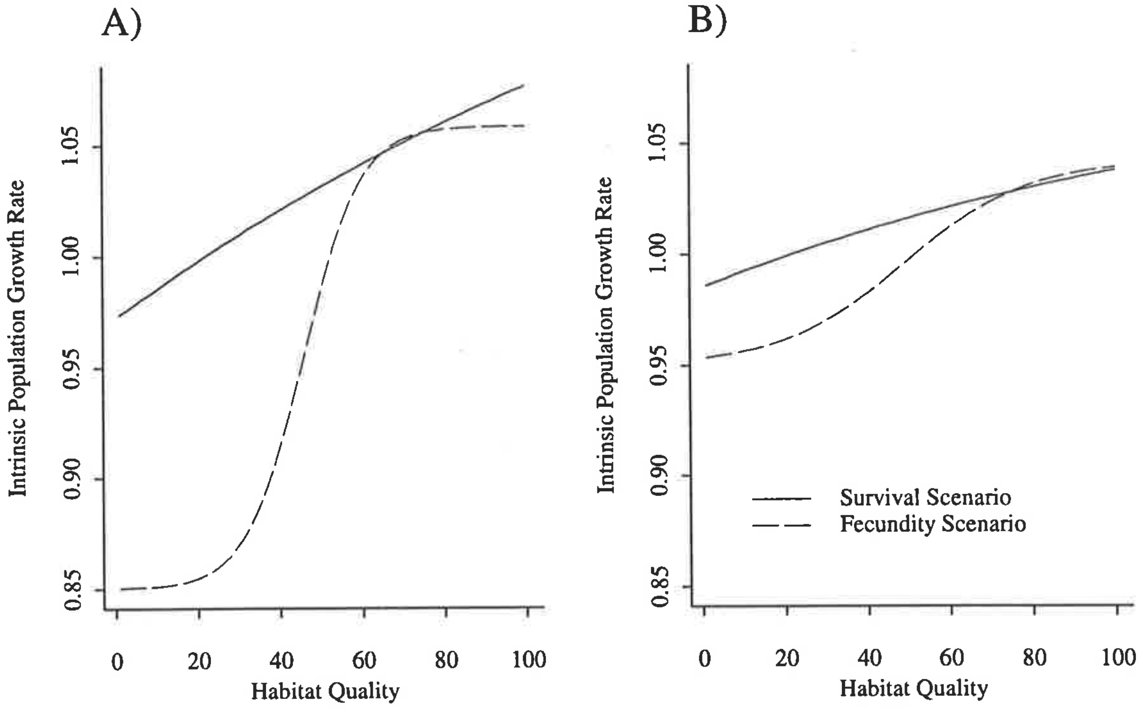


Figure 2.4 Effect of Habitat Quality on intrinsic population growth rates for all four scenarios, assuming a landscape with $\tilde{Q}_{90} = 75$. A) Greater Glider parameters. B) Mountain Brushtail Possum parameters. For both species, the annual probability of birth at quality 0 is ≈ 0 when fecundity is strongly influenced by habitat quality (Dashed lines).

I assumed habitat quality can be represented as a single, continuous, bounded variable with a linear effect on the log odds of either mortality or fecundity. This is obviously only one of an infinite range of possible connections between habitat quality and individual life history parameters. There is no empirical data to support a more complex effect, and the consequences of simpler connections (ie. binary source/sink quality) have been worked out elsewhere (eg. Keitt & Johnson, 1995; With et al., 1997). Furthermore, it is likely that any more complex relationship could be reduced to a combination of variables with a linear effect (Meents et al., 1983; Austin et al., 1990). I also assume animals can detect fine differences in this habitat quality variable. The consequences of coarse quality detection will not be explored here.

Very little is known about how individuals make choices about where to move on a heterogenous landscape during dispersal (Wolfenbarger, 1946; Gustafson & Gardner, 1996). I need a rule that tells the model animals which of the neighbouring territories to go to next. It seems reasonable that individuals would be more likely to move towards territories with higher habitat quality. I define the direction selection rule by "wrapping" a symmetrical beta distribution with a parameter α onto a circle:

$$P(x) = \int_0^x \frac{\Gamma(2\alpha)}{2\Gamma(\alpha)} x^{\alpha-1}(1-x)^{\alpha-1}\,dx \qquad (2.4)$$

where $x = 0.5$ was the direction in which the greatest increase in territory quality occurred, and $x = 0$ or $x = 1.0$ were the opposite direction. The range $0 \le x \le 1$ is then divided up among the 6 neighbouring cells to provide a table from which a direction can be picked with a uniform random number. When $\alpha = 1$, this rule mimics a uniform random walk, with all directions equally likely. As α increases, the probability of moving "uphill" on the quality landscape increases (Figure 2.5). I refer to strategies with $\alpha = 1$ as "random walkers" (RW) and strategies with $\alpha \approx \infty$ as "hill climbers" (HC). Hill climbers do not use (2.4) to choose a direction; they always move towards the home range with the greatest increase in quality. Intermediate strategies are referred to using the value of α, or in general as "biased random walkers". Individuals stop moving when they encounter a vacant territory, or a territory occupied by another dispersing individual. On average, this strategy will lead dispersers to remain in high quality habitat during dispersal. Field studies indicate that some species stay

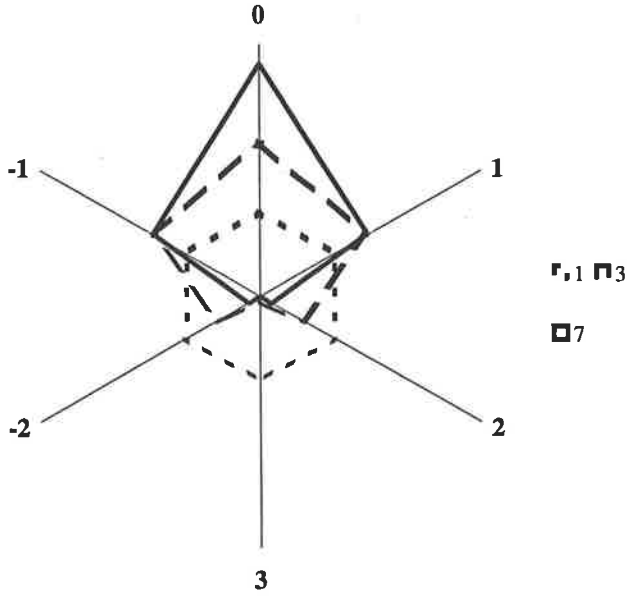


Figure 2.5 Effect of the parameter α on the turning distribution. Direction 0 is always in the direction of greatest increase in habitat quality. The dotted line is $\alpha = 1$ (random walkers, RW), the dashed line $\alpha = 3$, and the solid line $\alpha = 7$. Values of $\alpha >> 7$ are effectively hill climbers. For comparison, the probability of moving in direction 0 when $\alpha = 7$ is 0.46, and when $\alpha = 1$ the probability of moving in any direction is 1/6 or 0.167.

within favourable habitat during dispersal (eg. Wolfenbarger, 1946; Holekamp, 1984; Merriam & Lanoue, 1990; Kindvall & Ahlen, 1992a; Nelson, 1993; Haas, 1995).

In addition to picking a direction to move in, and defining when to stop, a complete dispersal strategy specifies what to do in case of ties in quality improvement between two or more directions, what to do on edges, and what to do if all directions are worse than the current location. If two or more directions yield equal increases in habitat quality, the best direction was chosen randomly from among the tied directions. Once a direction has been chosen from the beta distribution, if it would take the individual off the edge of the landscape, a new direction was chosen randomly. A random direction was also chosen if all surrounding territories were lower in quality than the current territory.

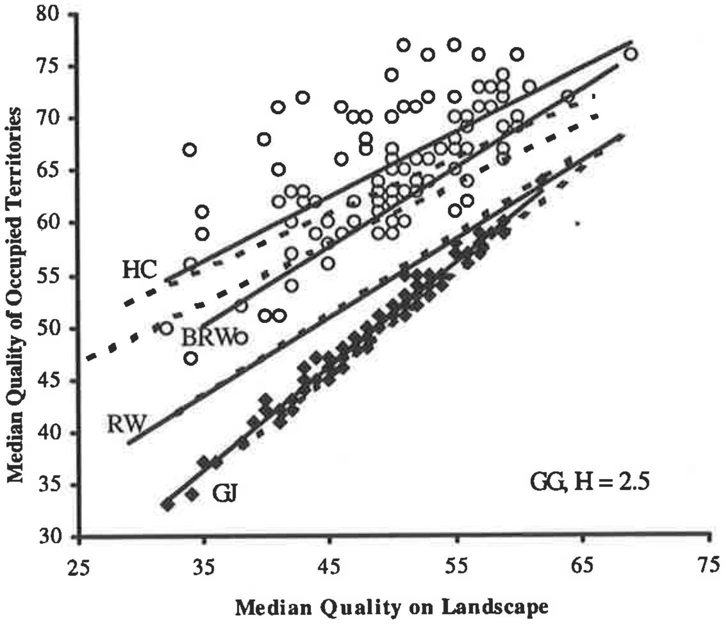
The final component of the general strategy was a rule that applies an increasing penalty to moving into already occupied territories. Individuals keep track of the number of steps they have taken since leaving their natal territory. They subtract the number of steps they have taken from the quality of occupied territories when they sample the neighbouring territories (ie. a territory quality of 72 is reduced to 67 after 5 steps). Therefore, the longer individuals spent unsuccessfully looking for good, unoccupied habitat, the less likely they were to move towards occupied territories. In the extreme, this means that hill climbers and biased random walkers acted like random walkers when surrounded by occupied territories, because the decremented quality of all surrounding territories was less than the quality of the current territory. This assumption reflects a simplistic kind of updating of an individuals information about the world in which it is dispersing. Dispersers begin optimistically looking for the best habitat, but as time progresses without finding good and unoccupied habitat, they become less optimistic and begin to broaden their search criteria. This updating mechanism is particularly critical to dispersal strategies with strong habitat selection (high α and hill climbers). In preliminary runs without updating, these strategies went extinct with very high frequency because individuals would climb to local peaks of habitat quality and persist in attempting to occupy those sites until they died.

The biased random walker is quite distinct from a "correlated random walk" (eg. Kareiva & Shigesada, 1983), where the direction chosen is correlated with the previous direction, but has nothing to do with variation in the underlying landscape. Gustafson and Gardner (1996) have analysed the between-patch dispersal rates generated by a dispersal rule similar to ours on a heterogenous landscape. Their model did not include population dynamics, and their "self-avoiding random walkers" only terminated dispersal (ie. settled) in one of seven possible habitat types. Furthermore, their model did not include competition for limited territory space as a component leading to increased dispersal distances. Brooker et al. (1999) have performed a similar simulation using landscapes classified from remotely sensed images of real landscapes.

My biased random walker strategy relies on local correlations in habitat quality. To determine what happens when there are no local correlations in habitat quality, I examine a strategy referred to as "global jumpers" (GJ). Global jumpers take steps by randomly choosing a territory from the landscape as a whole. This means that the quality of the territory they finally select is a function only of the frequency distribution of habitat quality, and not influenced by the spatial distribution of habitat quality on the landscape. This strategy also removes correlations in occupancy from localised dispersal.

Results

As a first step, I confirmed that the different strategies lead to differing degrees of habitat selection on all landscapes and under all life history scenarios. The median (50th percentile) quality of occupied territories should increase when habitat selection is stronger. When there is no habitat selection or spatial autocorrelation in habitat quality, the median of occupied habitat should be equal to the median quality on the entire landscape, and the slope of the relationship should be one. This is the case for Global Jumpers (Figure 2.6). By comparison, all other strategies generally led to increased median quality of occupied home ranges (HC > BRW > RW > GJ). The maximum possible quality is 100, because of the scaling applied to habitat quality values (ie. 0 - 100). When the median quality on the landscape was high, the distribution above the median was compressed, and the slope is less than 1.0 (compare Hill



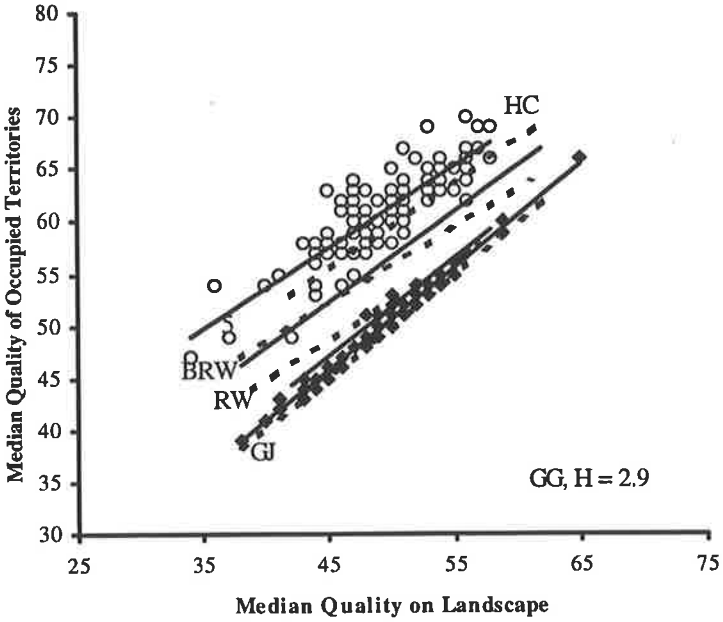


Figure 2.6 Effect of different dispersal strategies on the median quality of occupied territories. For clarity, symbols are only plotted for Global Jumpers (GJ) and Hill Climbers (HC) in the survival effect scenario, for GG on both types of landscapes. Other strategies shown are Random Walkers (RW) and biased random walkers with $\alpha = 5$ (BRW). Lines are independent least-squares fitted to each scenario/dispersal strategy combination. Dashed lines are fecundity effect scenarios, solid lines are survival effect scenarios.

Climbers with Global Jumpers). This effect was especially noticeable on landscapes with *H* = 2.5, where the amount of variability in the median landscape quality was higher than on landscapes with *H* = 2.9. Variation between life history scenarios within a particular strategy had no consistent effect on the median quality of occupied habitat.

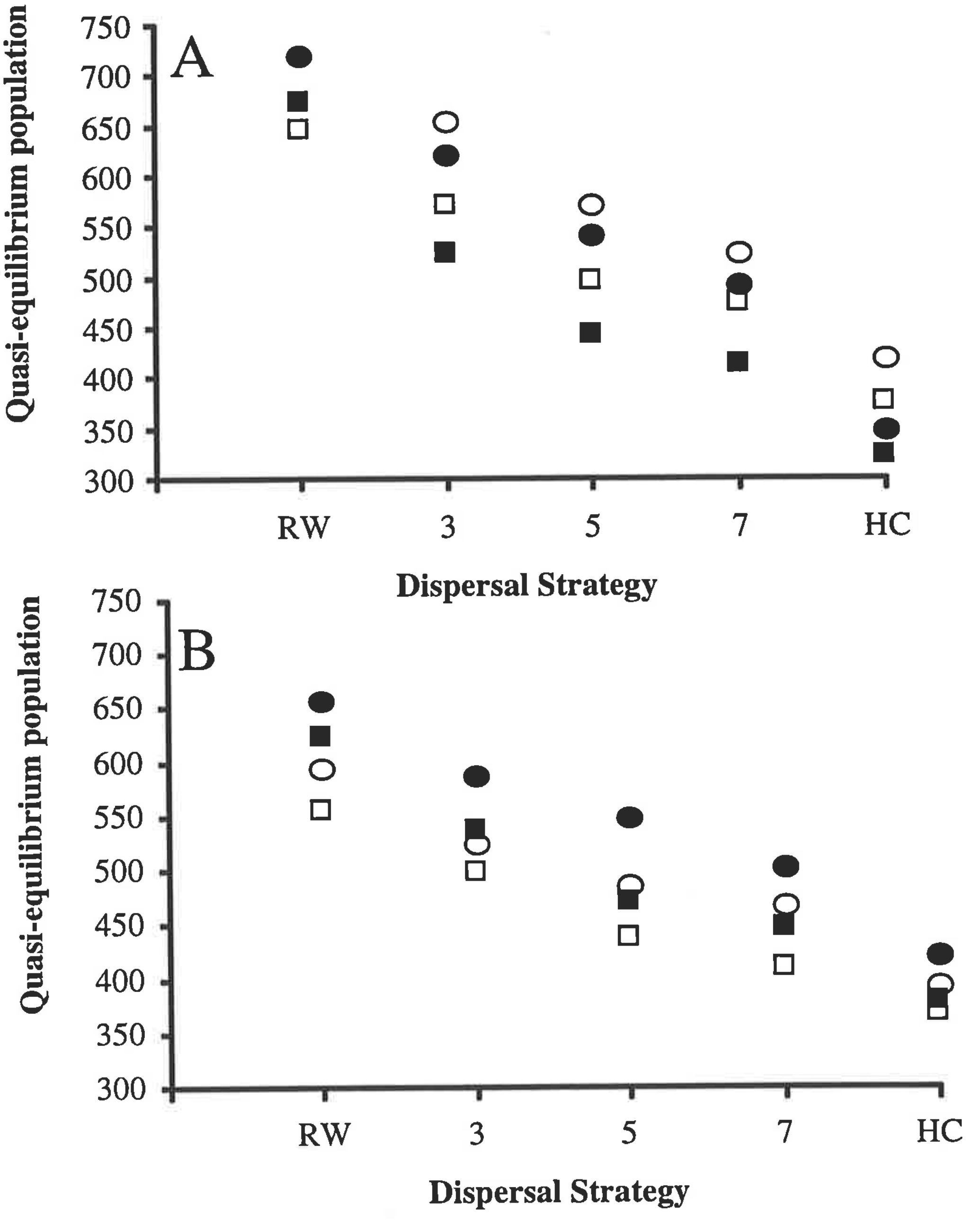


Figure 2.7 Effect of habitat selection on quasi-equilibrium population size (ie. population size at 200 years). Each point is the average of 100 replicate landscapes with H = 2.5 (squares) or 2.9 (circles); standard errors are smaller than the points. Survival scenarios are indicated with filled symbols, and fecundity scenarios with open symbols. A) greater gliders. B) mountain brushtail possum. Note the x-axis scale is not linear; HC (hill climbers) represent an infinite α. RW = Random Walkers, n = 3, 5, or 7 = Biased random walkers with α = n. The point for *H* = 2.9, fecundity effect for GG is obscured beneath that for *H* = 2.9, survival effect.

For all parameter values, populations reach a quasi-equilibrium within 100 years. None of the simulated populations went extinct, indicating that the probability of extinction is low. There were substantial differences between dispersal strategies in the long term equilibrium population sizes (Figure 2.7). In general, there were higher populations in the absence of habitat selection behaviour (smaller α). Landscape structure and life history values also influence population size, but the magnitude of these effects was much smaller. For both species, and all life history scenarios, fragmented landscapes ($H = 2.9$) had larger populations. The mechanism by which landscape quality influences individuals, either through fecundity or survival, affected population size differently for the different species. MBP had higher population sizes when survival varied across the landscape, and fecundity was constant. GG had higher population sizes when fecundity varied across the landscape, and survival was constant. Random walking GG had either no or reversed differences. These differences within dispersal strategies between different kinds of landscapes, could have arisen either from the interaction between the spatial structure of the landscape and the particular dispersal strategy, or simply from small changes in the distribution of habitat quality under different scenarios and landscapes. I can tease these effects apart by examining the life history performance of individuals at the equilibrium population size.

Dispersal strategy influenced long term reproductive success at two points in the model. Individuals that searched more intensively for better habitat should have tended to end up in higher quality habitat with better survival or reproduction once settled. However, the process of searching for that habitat may have led to increased mortality during dispersal. Figure 2.8 shows average fecundity and juvenile survival as a function of dispersal strategy and life history scenario for greater gliders on fragmented landscapes ($H = 2.9$). Mortality during the first year includes both dispersal mortality and aging mortality. Overall, the stronger the habitat selection behaviour was, the less likely individuals were to survive during dispersal (Figure 2.8A). This was true under both life history scenarios. Dispersal mortality introduced density dependence into the model. When individuals sought high quality territory, dispersers competed for a smaller number of territories, and dispersal mortality increased at smaller population sizes.

Habitat selection reduced post-dispersal mortality when survival varied across the landscape (Figure 2.8B). However, the magnitude of the increase did not offset the decrease in survival during dispersal. HC cut the effect of spatial variability on first year survival in half, while decreasing survival during dispersal by > 10% (compare HC with GJ in Figure 2.8A,B). For both species, the average fecundity was reduced when there was spatial variation in the probability of reproduction. The variation in population size as a function of dispersal strategy was primarily a result of increased density dependence in dispersal mortality.

Conclusions

This chapter uses a spatially explicit ecological model to examine whether or not the type of dispersal rule used by individuals influences population dynamics. This work is novel because it examines continuous variation in habitat quality, as opposed to "patchy" variation where habitat is either available or not (Keitt & Johnson, 1995; Gustafson & Gardner, 1996). It also explores strategies that make use of information about the environment to decide where to look for habitat. I have formed a 'neutral landscape model' (With & King, 1997) to test the effects of a typical span of dispersal strategies on population dynamics. There are many variations on the strategies used here. The point is not that these strategies are the only ones, but rather that the choice of strategy, *any* strategy, is one that should be made carefully. To the best of my knowledge, the interaction between a continuously heterogenous landscape and simple dispersal rules has not been explored before, and leads to counter-intuitive results.

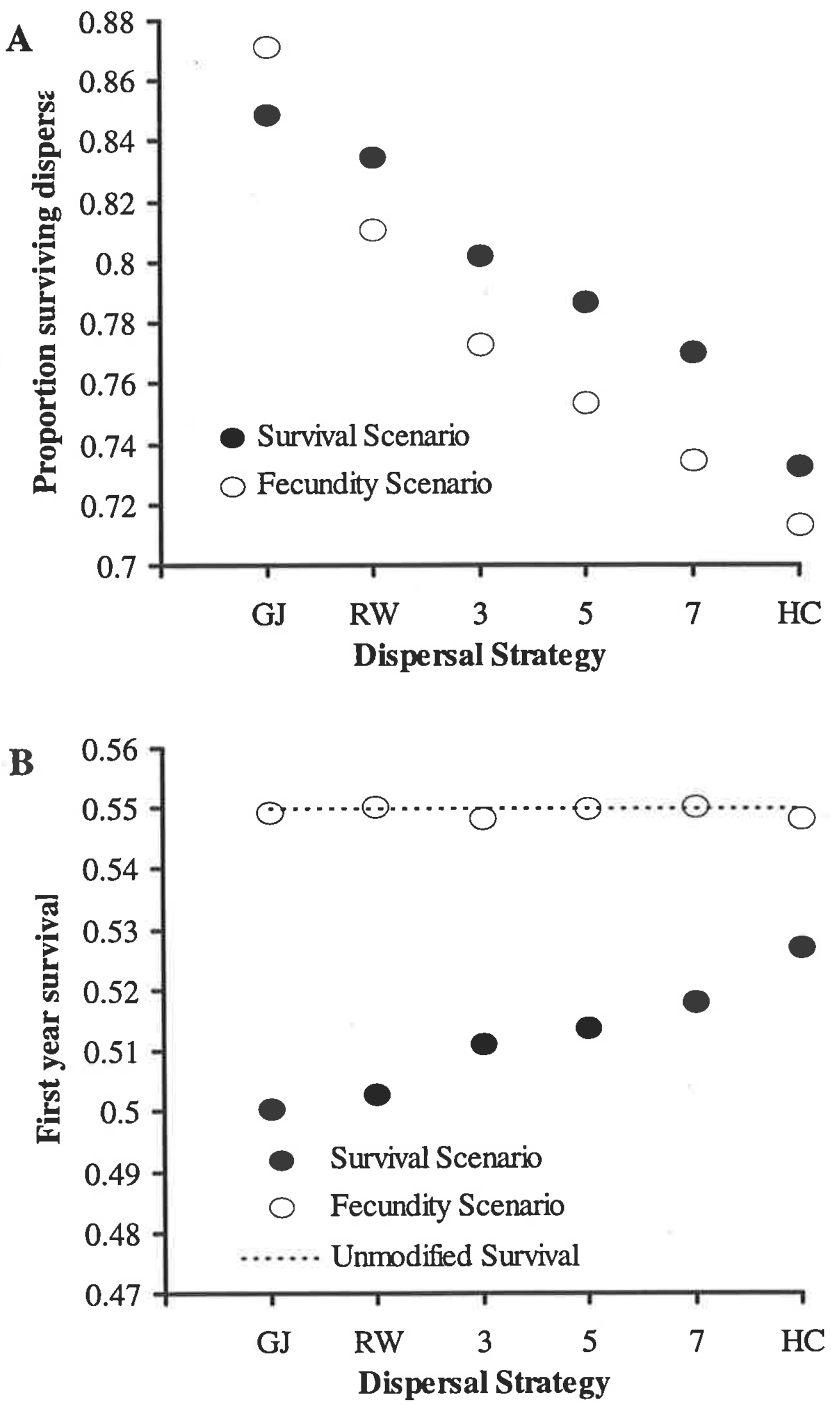


Figure 2.8 Life history parameters determined by recording the fate of all individuals born between year 160 and 180. Only results for GG, H = 2.9 are shown for clarity. A) Dispersal mortality. B) First year survival. C) Adult fecundity. Dashed lines indicate the value input to the model in the absence of spatial variability (Table 2.1). Each point is the average of 100 replicate runs, and standard errors are smaller than the points.

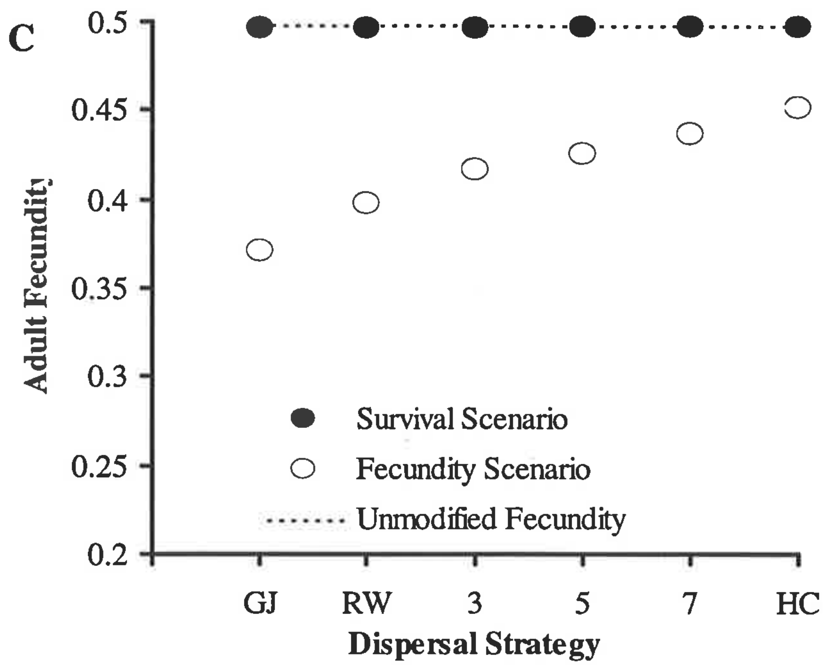


Figure 2.8 continued.

The primary conclusion is that strong habitat selection behaviour leads to reduced population sizes. This occurs because of density-dependent mortality while searching for high quality habitat. Individuals that are more selective about their habitat requirements tend to move farther, and suffer greater mortality during dispersal. As a result, when all individuals seek the best habitat, and good habitat is finite, density-dependence in dispersal mortality arises at smaller population sizes. The stronger the bias in the random walk, the more individuals tend to remain clustered around local centres of high habitat quality, and not venture into poorer quality habitat. Some empirical work has demonstrated that dispersing individuals do tend to remain within high quality habitat during dispersal (Holekamp, 1984; Merriam & Lanoue, 1990; Haas, 1995). Other work has shown that dispersers do compete for limited high quality habitat (Smith & Peacock, 1990).

A second important conclusion from this work is that it is not necessary to have any form of active habitat selection in order to obtain a relationship between habitat quality and occupancy. The random walking strategy does not use information about the landscape to make decisions about where to move. Animals end up in better quality habitat than if they were randomly distributed because they do better in the neighbourhood of areas that favour individual survival or fecundity, and they do not disperse rapidly away from such areas. Nonetheless, the relationship between habitat quality and occupancy is weaker for random walkers than for hill climbers (Figure 2.6).

The reduction in life history parameters in the presence of spatial variation is a consequence of averaging a non-linear function (Chesson, 1981; Chesson, 1990). There are two ways in which the average of a function of a random variable can be calculated. If $g()$ is the function, and Z is the random variable, then the first possibility is to average the random variable, and then apply the function, or $g(E(Z))$. The alternative is to take the function of each instance of the random variable, and average the results, or $E(g(Z))$. These two quantities will not be identical. The magnitude of the change can be approximated by looking at the expectation of a Taylor expansion of a function at the mean of a random variable (Hilborn & Mangel, 1997, p. 58):

$$E\left(g(Z)\right) = g(\mu) + \frac{1}{2} g''(\mu) VAR(Z) \qquad (2.5)$$

where Z is a random variable with mean μ, E is the expectation operator, and $g(Z)$ is the function (or its derivative) evaluated at Z. Clearly, if g'' is negative, then $E(g(Z)) < g(E(Z)) = g(\mu)$. In this case, habitat quality is a random variable. When habitat quality does not influence fecundity, I am using an "average" fecundity for all individuals. When fecundity varies spatially, variation above the average quality increases fecundity less than variation below the average quality (Figure 2.3). As a result, the average fecundity of the population in the presence of spatial variation is reduced compared to the fecundity in the absence of spatial variation.

I can also explain the different responses of the two species' equilibrium population size to variation in fecundity (Figure 2.7) using (2.5). The second derivative of (2.2), the response of fecundity to habitat quality, is:

$$\frac{\partial^2 p_{x,i}}{\partial Q_x} = \frac{-1}{2e^{\beta}\left[(\beta\tilde{b})^2 + \tilde{b}^2\right]} \qquad (2.6)$$

where

$$\beta = \tilde{b} Q_x - b + \ln\left(\frac{2p_i}{1-2p_i}\right) \qquad and \qquad \tilde{b} = \frac{b}{\tilde{Q}}$$

and (2.6) is always negative when evaluated at $\tilde{Q}$. Furthermore, the larger b is, the smaller (2.6) is in absolute magnitude, and the less effect variability in habitat quality will have on average fecundity. As shown in Figure 2.3, the value of b used for GG is larger than for MBP. Therefore, landscape variability will decrease the average fecundity of MBP more. The magnitude of the effect of landscape variability under the survival scenario is equivalent, because a is the same for both species. Under the fecundity scenario, GG have higher population sizes than under the survival scenario, and MBP lower than under the survival scenario, because the impact of variability on average fecundity is greater for MBP.

A final point from this analysis is that behaviour can reduce or eliminate the effects of spatial variation on individual performance. Individuals that use habitat selecting rules tend to obtain higher quality territories, and therefore their populations do not suffer the penalties of non-linear averaging to the same extent as populations of non-selective individuals. This improved individual performance comes at a cost; the density dependent ceiling that arises through increased dispersal mortality is lower. Determining the dispersal strategy that is optimal in an evolutionarily stable sense (Maynard-Smith, 1982) is difficult in this model because of the complexity in the landscape, and individual and population level responses to that complexity. The interaction between individually optimal behaviour and spatially variable landscapes is only beginning to be studied (Roitberg & Mangel, 1997), and promises to be interesting.

Although this model has included fine scale spatial variability in habitat quality, I ignored variation in individual phenotypic quality. While this is not an uncommon assumption in population modelling, it is potentially important in the context of the optimal behaviour patterns discussed above. Verhulst et al. (1997) showed that phenotypic variation among great tits (*Parus major*) interacts with the quality of their natal habitat to determine the distance they disperse. High quality birds born in low quality habitat are more likely to disperse long distances. In the context of the current model, this indicates that the assumption of equal competitive ability among new dispersers is false for some species, and will have an influence on the optimal strategy to follow during dispersal. High quality individuals may be better off with a biased or hill climbing strategy, because they will be able to displace other individuals from high quality home ranges. In contrast, low quality individuals may be better off searching for unoccupied territories without regard for their quality.

Recent years have witnessed an explosion of individual based, spatially explicit population models (see review in With & King, 1997). Most have utilised homogenous landscapes without variability (Kareiva & Wennergren, 1995). The variability that is introduced is generally binary source/sink variation with patches of useable habitat in an unusable matrix (eg. Keitt & Johnson, 1995). The effects of this kind of spatial structure are well understood in the context of patch-based metapopulation models (Kareiva, 1990; Day & Possingham, 1995). What has not been addressed is the effect of variable habitat quality within otherwise contiguous patches of habitat. Such variability is assumed to have little or no effect on population dynamics. It does have an influence because of non-linear averaging (Chesson & Warner, 1981; Chesson, 1990). Analytical approaches to understanding the effects of spatial variability are limited because they have difficulty accounting for spatial autocorrelation in habitat quality (but see Possingham et al., 1994b), and including the effect of individual behaviour. This model has demonstrated that behaviour and spatial variability interact in interesting and sometimes non-intuitive ways, and that ignoring the interaction may lead to misinterpretations of observations of population dynamics.

Chapter 3 Matching observed pattern with model process: can territory occupancy provide information about life history parameters?

> *"Low sensitivity is to be expected when modelling habitat selection, as only a very small proportion of important variables will be measured. Many variables will be subtle, impossible to quantify, or be involved in complex interactions with other variables that may not have been identified."*
>
> *J.L. Pearce et al. (1994)*

Introduction

A fundamental question posed by wildlife managers is which habitats to conserve and put management effort into (Morrison et al., 1992; Block & Brennan, 1993). This question often arises during reserve design, when choices must be made about which habitats to include in a reserve system (Pressey et al., 1996). Clearly, the answer involves identifying the characteristics of "good" habitat for a species. At the simplest level, good habitat is simply habitat that allows birth rates to exceed death rates (source habitat), as opposed to habitat where death rates exceed birth rates (sink habitat; Pulliam, 1988). Therefore, rational decision-making about population management requires information about how birth and death rates vary with changes in habitat characteristics such as vegetation structure and topography (Possingham et al., 1993). Furthermore, populations occur on fragmented or spatially complex landscapes. In such situations, information about the ability of a species to disperse between different patches of habitat is crucial to understanding the responses of populations to managed or stochastic changes (Fahrig & Merriam, 1994; Sutcliffe et al., 1997).

It is costly in both time and money to get quantitative information about key population processes: birth, death, and dispersal rates, often requiring years of sampling to acquire small amounts of information (Stacey & Taper, 1992). Paradis and Croset (1995) estimated survival rates for only 2 different kinds of habitat for Mediterranean Pine Voles (*Microtus duodecimcostatus*), requiring substantial trapping effort over 3 years. Measuring dispersal by juveniles away from natal habitat is particularly difficult (Kareiva, 1990). For example, Nelson (1993) needed 14 years of weekly airborne radio-tracking to measure natal dispersal distances in only 86 juvenile white-tailed deer (*Odocoileus virginianus*) from a single population. Relating these dispersal distances to characteristics of the source population or home ranges would require a dramatic increase in the amount of sampling effort required. Decisions about habitat reservation or management are generally made on much shorter time scales. An extreme case in point is the negotiation of Regional Forest Agreements in Australia over the last five years (Commonwealth of Australia, 1992). In the North East Forests region of New South Wales alone it was necessary to obtain information about habitat requirements for 2211 species of plant (NPWS, 1994b) and 405 species of vertebrates (NPWS, 1994a). Often the only information available is the intuition of what constitutes good habitat by an ecologist who has spent years studying the species in the wild, or inferences from similar species. However, failing to act because of a lack of accurate information is also a management action with associated costs (Parma et al., 1998).

The combination of few resources and a pressing need for information leads to increased reliance on observations of the presence or absence of a species in different kinds of habitat (habitat occupancy). When sites with certain characteristics are more likely to be occupied, or have higher population abundances, it is commonly assumed that these sites are better quality habitat (Van Horne, 1983; Davey, 1989). This approach uses the probability of occupancy as a surrogate for habitat quality. Presence/absence observations can be collected in single surveys without waiting for population processes to occur. There are two stochastic processes at work when an ecologist collects a sequence of observations of habitat occupancy. The essential, but hidden, process is population dynamics. The population may be increasing in an area, decreasing, or extinct. The second process is that of observation; it is a stochastic process because even if the species is present at a site it may not be detected. This is especially important if the population is present in low numbers, or if each site is surveyed briefly in order to increase the number of sites sampled. The key problem in interpreting the results of survey data is extrapolating to population dynamics parameters from observations of habitat occupancy.

Many statistical methods exist for estimating the probability of occurrence from a set of observed characteristics. Logistic regression, a type of Generalised Linear Model (GLM) which estimates the log-odds of occupancy as a linear function of some habitat variables, is widely used (Austin et al., 1990; Lindenmayer et al., 1990; Lindenmayer et al., 1991; Buckland & Elston, 1993; Allaine et al., 1994; Pearce et al., 1994; Lindenmayer et al., 1995b; Buckland et al., 1996; Marquez et al., 1997; Mysterud & Ims, 1998). Recent advances such as autologistic regressions have also incorporated spatial dependency (Augustin et al., 1996), a key feature of population distributions. Other approaches for identifying good habitat include linear optimisation (Biggins et al., 1993), other types of generalised linear models (Pedlar et al., 1997), generalised additive models (NPWS, 1994b), univariate descriptive statistics and correlations (Collins & Lichvar, 1986; Hayward et al., 1993; Merendino & Ankney, 1994; Donald et al., 1996), canonical correspondence analysis (Fiedler & Reilly, 1994; Anderson & Gribble, 1998), indexes based on expert opinion (Houston et al., 1986), regression combined with multivariate discriminant functions or principle components analysis (Braithwaite et al., 1983; Prescott & Collister, 1993; Rotenberry & Wiens, 1998), and other methods (Hogle et al., 1993; Homer et al., 1993; Brandt et al., 1995; Neave et al., 1996). This list is not exhaustive. The point is that many methods are being used to identify good habitat from either static or repeated surveys of occupancy or abundance.

Combining static survey data with measurements of habitat occupancy can be done at a range of spatial scales, from day to day microhabitat selection within a home range (eg. Mysterud & Ims, 1998; Rotenberry & Wiens, 1998), to measurements of home range occupancy (eg. Lindenmayer et al., 1990; Lindenmayer et al., 1991; Lindenmayer et al., 1994; Lindenmayer et al., 1995b), up to abundance at population scales (eg. Braithwaite et al., 1983; Buckland et al., 1996). A few studies have also examined habitat-abundance correlations at a range of scales (Wiens et al., 1987; Pedlar et al., 1997). If the goal of habitat modelling is to provide information about spatial variation in population processes like survival or reproduction, then the most logical scale is one that identifies individual patterns of habitat selection while integrating over time scales appropriate to survival and reproduction. For this reason, in this chapter I concentrate on sampling at the scale of a single home range with an annual time step, matching the scale of the arboreal marsupial model outlined in Chapter 2. I also limit myself to using logistic regressions, as these are increasingly employed in habitat modelling, and have the simplest data requirements for the response variable (presence/absence; Austin et al., 1994). Furthermore, single home ranges will be either occupied or not for solitary, territorial species such as those considered in this chapter.

The assumption that an increased probability of occupancy or abundance indicates high habitat quality or positive population growth is plausible (see Temple & Cary, 1988), but a variety of processes could obscure the relationship, decreasing the power of these statistical tests to detect habitat occupancy patterns, and consequently habitat quality. Simple metapopulation models (eg. Levin, 1974) show that even good habitat is sometimes unoccupied when colonisation and extinction processes are at equilibrium. This general conclusion is widely supported by population subdivision models (see review in Kareiva, 1990). More sophisticated metapopulation models (eg. Day & Possingham, 1995) and empirical results (Fritz, 1979; Kindvall & Ahlen, 1992a) show that the proximity of good habitat patches to each other also influences the likelihood that a patch is occupied. In other words, bad habitat close to good habitat could be more often occupied than good habitat far from any other good patch. When demographic stochasticity is considered (McCarthy et al., 1994), the amount of variation interfering with the detection of a relationship between habitat characteristics and occupancy is enormous. Finally, Van Horne (1983) highlighted several examples in which correlations failed to adequately identify high quality habitat defined on the basis of population processes. The conclusion was that density or occupancy is particularly likely to fail as a predictor of habitat quality when population densities are high. This is because increased competition for high quality habitat leads to increased numbers in lower quality habitat (ie. the losers).

There are four quantitative measures of the quality of a habitat model: percentage of deviance or variance explained, error rate, specificity, and sensitivity (Table 3.1). The last three are unique to habitat models based on occupancy (presence/absence). The percentage of deviance explained can measure quality for models based on abundance as well. The deviance of a generalised linear model is roughly equivalent to the residual variance of a regression; the higher the proportion of deviance "explained" by including a variable in the model, the better the model. The error rate is simply the proportion of errors made by the model; how many sites were predicted to be occupied and were not, and vice versa. A low error rate is better. Specificity and sensitivity are the two sides of the error rate coin. A model is more "specific" if most sites that are actually unoccupied are predicted to be unoccupied. A high specificity means that the model is doing a good job of predicting where the animal does not occur. Conversely, a model is more "sensitive" if most sites that are actually occupied are predicted to be occupied. A high sensitivity means that the model is doing a good job of predicting where the animal does occur. It is not uncommon for empirical habitat models to have low explanatory power, and be more specific than sensitive (eg. Figure 3.1).

Table 3.1 Calculation of error rate, sensitivity, and specificity (Lindenmayer et al., 1991; Pearce et al., 1994). a = occupied sites predicted to be occupied. b = false negatives, or occupied sites predicted to be unoccupied. c = false positives, or unoccupied sites predicted to be occupied. d = unoccupied sites predicted to be unoccupied. N is the total number of sampled sites. A site is predicted to be occupied if the probability of occupancy is greater than or equal to 0.5.

		Predicted occurrence		
		yes	no	
Actual occurrence	yes	a	b	a+b
	no	c	d	c+d
				N

Error Rate = (b+c) / N;
Sensitivity = a / (a+b);
Specificity = d / (c + d).

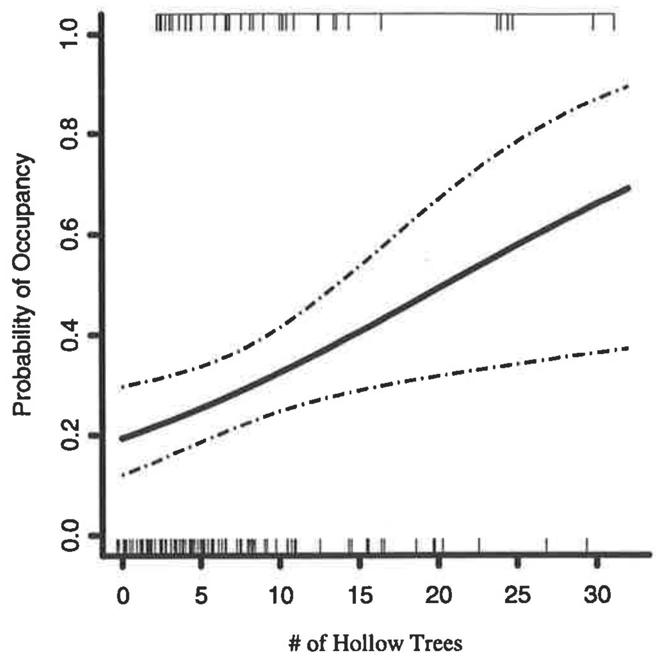


Figure 3.1 Predicted probability of occurrence for Greater Gliders (*Petauroides volans*) in Mountain Ash Stands (modified from Lindenmayer et al., 1995b). Rug plots indicate the frequency of sites observed with (top) and without (bottom) greater gliders. Dotted lines are 95% confidence intervals on the predicted probability. The model explains 3.9% of the deviance, with an error rate of 0.27, sensitivity of 0.13, and specificity of 0.97.

In one case where a statistical habitat model (linear regression of density on habitat variables) was tested for its ability to predict density in an independent data set (Maurer, 1986), its performance was notable for what it didn't predict, rather than what it did. Maurer sampled two grassland areas in western North America, recording the abundance of a suite of grassland birds and a group of structural characteristics of the vegetation. Maurer fitted a linear multiple regression model to data from one area, and then used that model to predict the density of each species in the other area. The model performed dismally, with positive predictions at sites where a species was entirely absent. Maurer gave two main reasons for the failure of the regression model. First, in many cases the model was "extrapolating" to regions of the habitat variable space not included in the original dataset. This occurrence is likely, and in a multivariate dataset may be very difficult to detect. The second reason given was that "limiting factors" may have been present at the second site that were not present at the first. The implication of this statement is that if more variables, for example the density of possible competitors, had been included, the models would have performed better.

That sampling more variables is better is a common implicit assumption of habitat models (D. B. Lindenmayer, Personal Communication). It is important to note that this assumption is quite distinct from the more usual problem of deciding which variables to include in a statistical model. This problem arises in habitat modelling once the set of variables to be sampled has been decided upon, and can be dealt with in a wide range of methods a complete discussion of which is beyond the scope of this thesis. The problem I am discussing here comes one step sooner, in the design of a survey. Clearly, only a limited number of variables can be measured. Once these have been selected, the data collected, and an analysis conducted, it is common to attribute the unexplained variance to variables that were not measured in the first instance. The clearest statement of this assumption that I have seen is quoted at the beginning of this chapter.

The extent to which occupancy data can be relied on to provide information about population processes is unknown. However, there is an increasing need for rapid acquisition of information for decision making in environmental management. As a result, "snapshot" surveys will increase in frequency and importance because they can be performed quickly with limited resources. There are three problems to be addressed in this chapter. First, to what extent does demographic stochasticity interfere with the accurate detection of habitat quality-occupancy relationships, when all other possible sources of error are eliminated? Second, how does sample size and population density relate to the accuracy of a habitat model? Third, what can a positive relationship between habitat quality and occupancy tell us about the fundamental population processes of birth, death, and dispersal?

I address these problems by sampling a spatially explicit simulation model with a "virtual ecologist". The virtual ecologist will sample the model landscape and then use classical statistical modelling to define the driving forces behind habitat quality. I will make the problem as easy as possible for the virtual ecologist and see how she goes.

The Model

I use the model and general parameter values from Chapter 2, with one exception. In Chapter 2 the "Global Jumper" dispersal strategy was used to identify what happened when spatial autocorrelation due to landscape heterogeneity and dispersal was removed. In this chapter I use a random landscape, and use only local dispersal rules. By "random" here I mean uncorrelated in space, as all the simulated landscapes are generated with randomisation algorithms. On random landscapes I assume that territory quality is normally distributed with a mean of 50 and a standard deviation of 17.6. This variance generates a 90th percentile of the distribution at 72, which is the same as the average 90th percentile on the fractal landscapes with $H = 2.9$. This is the value used to scale the habitat quality effect on survival or fecundity [see (2.2) and (2.3)].

The Virtual Ecologist

The "virtual ecologist" is a method for testing both the power of statistical analyses, and for relating the output of the analysis to underlying population processes. The relationship between habitat characteristics and population processes is completely known in the model. Therefore, by sampling the model output in a manner similar to a real ecologist, and utilising standard statistical methods, the output of the statistical tests can be related to the original processes. The virtual ecologist uses one of three different methods for choosing the sites to be sampled: random, extensive random, and regular (Figure 3.2). Random selection is just that: n sites are selected without replacement from all possible territories across the landscape. Regular sites are selected along a rectangular grid, without choosing sites on the edge, and ignoring the effect of the hexagonal bias on odd rows. Extensive random sites are chosen by categorising all territories into 10 groups based on the variable that determines habitat quality, 0-9, 10-19, ...90-100, and then choosing $n/10$ territories randomly from each category. If there are less than $n/10$ sites in a category, then all sites are chosen, and the remainder are randomly chosen from other categories, one per category starting with the lowest category. Superficially, this might appear to be better described as a "stratified random" sample, but in fact this is incorrect. A stratified random sample is taken from strata defined in such a way as to increase the precision of a parameter estimate (Stuart, 1984). My extensive sampling method merely ensures that the full range of habitat quality values are represented in the sample.

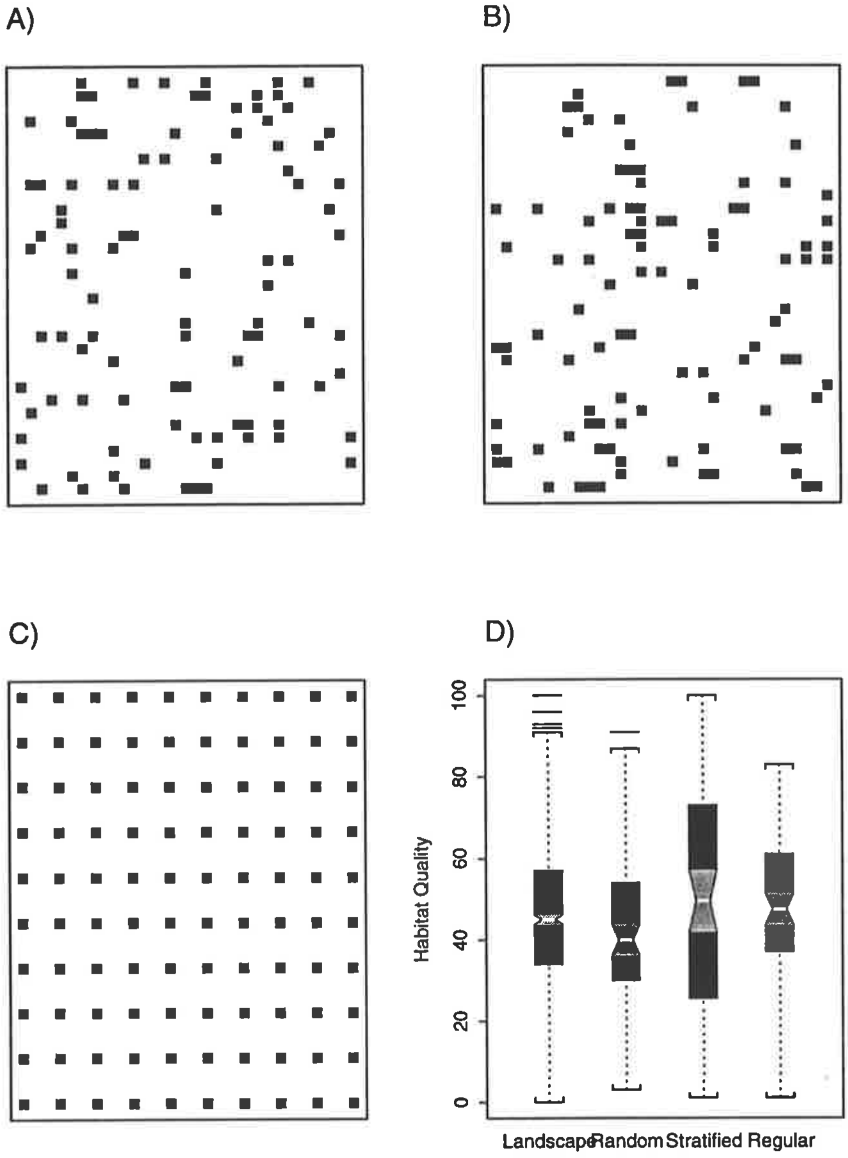


Figure 3.2 The three different sampling regimes used by the virtual ecologist, A) Random sampling, B) Extensive random sampling, C) Regular sampling, and D) a boxplot of the resulting distribution of habitat qualities in sampled sites for a landscape with $H = 2.9$. "Landscape" is the actual distribution of habitat quality, for comparison. The median is given by the central line, with the notch indicating 95% confidence limits of the median. The black box is the interquartile range (IQR), and the whiskers show the total range of the data, excluding outliers, which are shown with a line. Outliers are defined as points more than 1.5 times the IQR from the central box.

The virtual ecologist virtuously sampled 100 sites in the last year of the baseline runs, which is 9.2% (100 / 1089) of the total available habitat. This compares favourably with actual empirical studies of this nature, and is well above sample sizes of 35-70 recommended in the literature (Morrison et al., 1992). Lindenmayer et al. (1991) only sampled 0.27% of the total available habitat for Leadbeater's possum (*Gymnobedelius leadbeateri*) in 3600 person hours. Sampling by the virtual ecologist takes place after juvenile dispersal, but before annual mortality. The sites sampled by the virtual ecologist coincide exactly with the home range grid, a happenstance unlikely to occur in reality. Furthermore, the virtual ecologist makes no errors in detection; if the species is present she records it. The only contributions to unexplained deviance in the models are the limited number of observations, and demographic stochasticity.

The virtual ecologist performs all statistical analyses in S-Plus 4.0 for Windows. The logistic regression model predicts the probability that a site is occupied. She uses the percent of deviance explained as a measure of the "fit" of a particular logistic regression model by calculating the percentage decrease in deviance when habitat quality is included in the model:

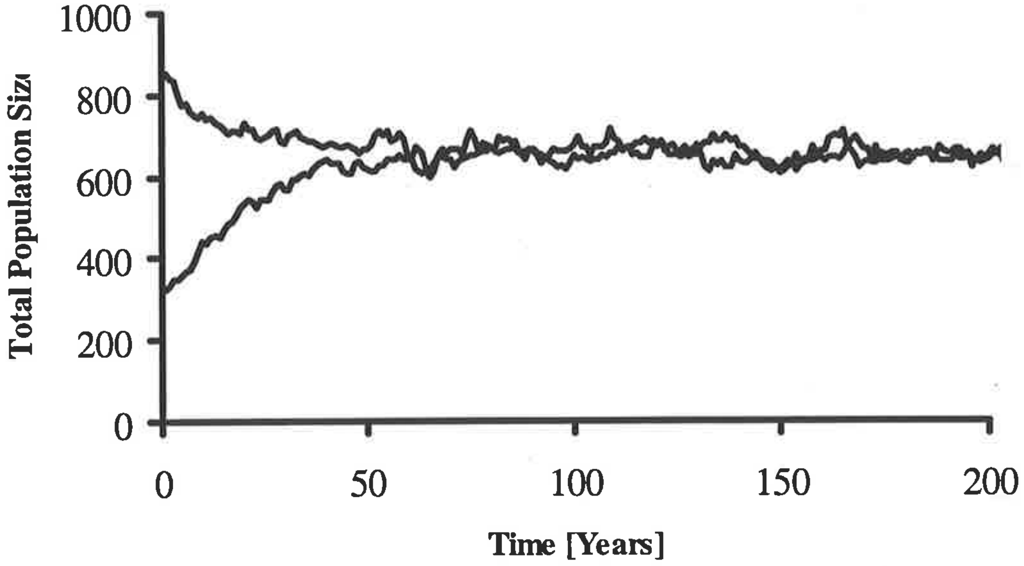
$$\%D = \frac{D_0 - D_Q}{D_0} \qquad (3.1)$$

where D_0 is the null deviance with no covariates included in the model, and D_Q is the residual deviance when habitat quality is included in the model (NPWS, 1994b; NPWS, 1994a; Venables & Ripley, 1994). Deviance is roughly comparable to the sum of squares in a linear model with gaussian errors and an identity link. She also calculates the error rate, sensitivity, and specificity of her habitat models (Table 3.1). Error rate is a measure of the total number of incorrect predictions made by the model, where the model is said to predict a "presence" if the probability of occupancy is ≥ 0.5. This is not the only possible choice for a prediction threshold. Values higher than 0.5 increase the likelihood of false negative predictions, while lower prediction thresholds increase the likelihood of false positive predictions. Sensitivity is the accuracy of the model in sites where the species is actually present. Sensitivity is 0 if all sites where the species is found are predicted to be unoccupied, and 1 if all occupied sites are predicted to be occupied. Specificity is the accuracy of the model to in sites where the species is actually absent, and is otherwise similar to sensitivity. She reports these statistics for all regressions, regardless of whether habitat quality makes a significant contribution to the model or not.

I ran 100 replicate simulations of 200 years in length for each species/life history scenario combination. The population size reaches a quasi-stationary state well within this time (Figure 3.3A). The population dynamics of both species follow exponential growth to a ceiling. The density dependent effect that sets the ceiling is dispersal mortality; dispersal mortality reaches 40-50% at the ceiling (Chapter 2; Tyre et al., 1998). Although the fecundity scenarios appear to have a much stronger negative effect on population growth rates (Figure 2.4), this does not translate into a corresponding effect on the size of the population at quasi-equilibrium. Figure 3.3B shows the distribution of population sizes for one dispersal rule of greater gliders. Landscape structure has a larger impact on population size than life history scenario.

Assume that the virtual ecologist has provided the four example habitat occupancy analyses for Greater Gliders shown in Figure 3.4. The same parameters were used for all four analyses; they are shown here to provide an indication of the range of data collected by the virtual ecologist. There are three important observations to make. First, individual gliders were observed in marginal habitat, or areas where the birth rate cannot compensate for mortality losses. Individuals end up in these areas by chance when better habitat is occupied. Second, territories in high quality areas are sometimes unoccupied, because individuals die and replacement does not necessarily happen instantaneously. Third, habitat quality can influence the probability of occupancy even when active habitat selection behaviour is weak. The $\alpha = 3$ dispersal rule is close to a random walk (Figure 2.5), and yet there is still a significant effect of habitat quality on occupancy. This arises because of the localised nature of the random walk and spatial correlations in habitat quality; individuals search nearby territories first.

In the following sections I present the results pertinent to each of the three questions raised in the introduction, followed by a brief discussion and interpretation. I define "better" predictions as a higher median percentage of deviance explained, with no overlap in 95% confidence limits of the median.



B)

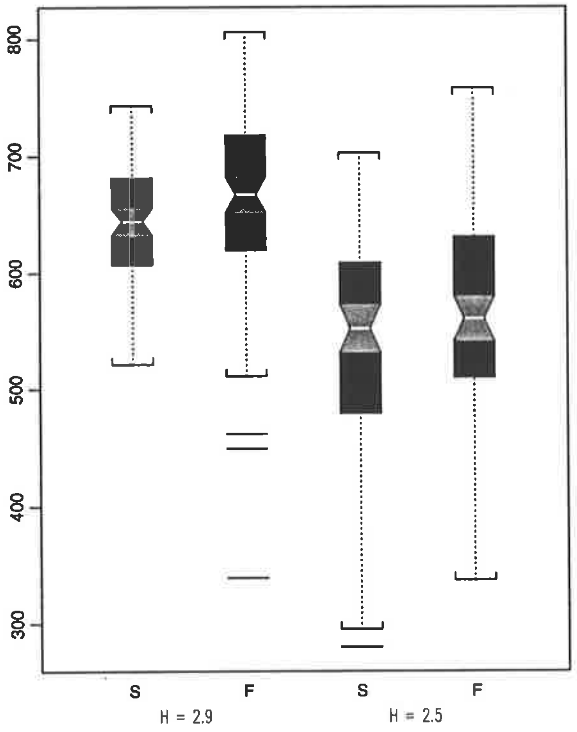


Figure 3.3 A) Population dynamics for Greater Gliders, *b* = 10.0, $\tilde{Q}$ = 90. The total population size converges to a quasi-equilibrium within 50 years from most initial population sizes. The maximum possible population size is 1089 (33^2). B) Boxplots of population size at 200 years from 100 replicate runs for greater gliders with $\alpha = 3$ under the 4 different life history / landscape structure combinations. S = survival scenario, F = fecundity scenario.

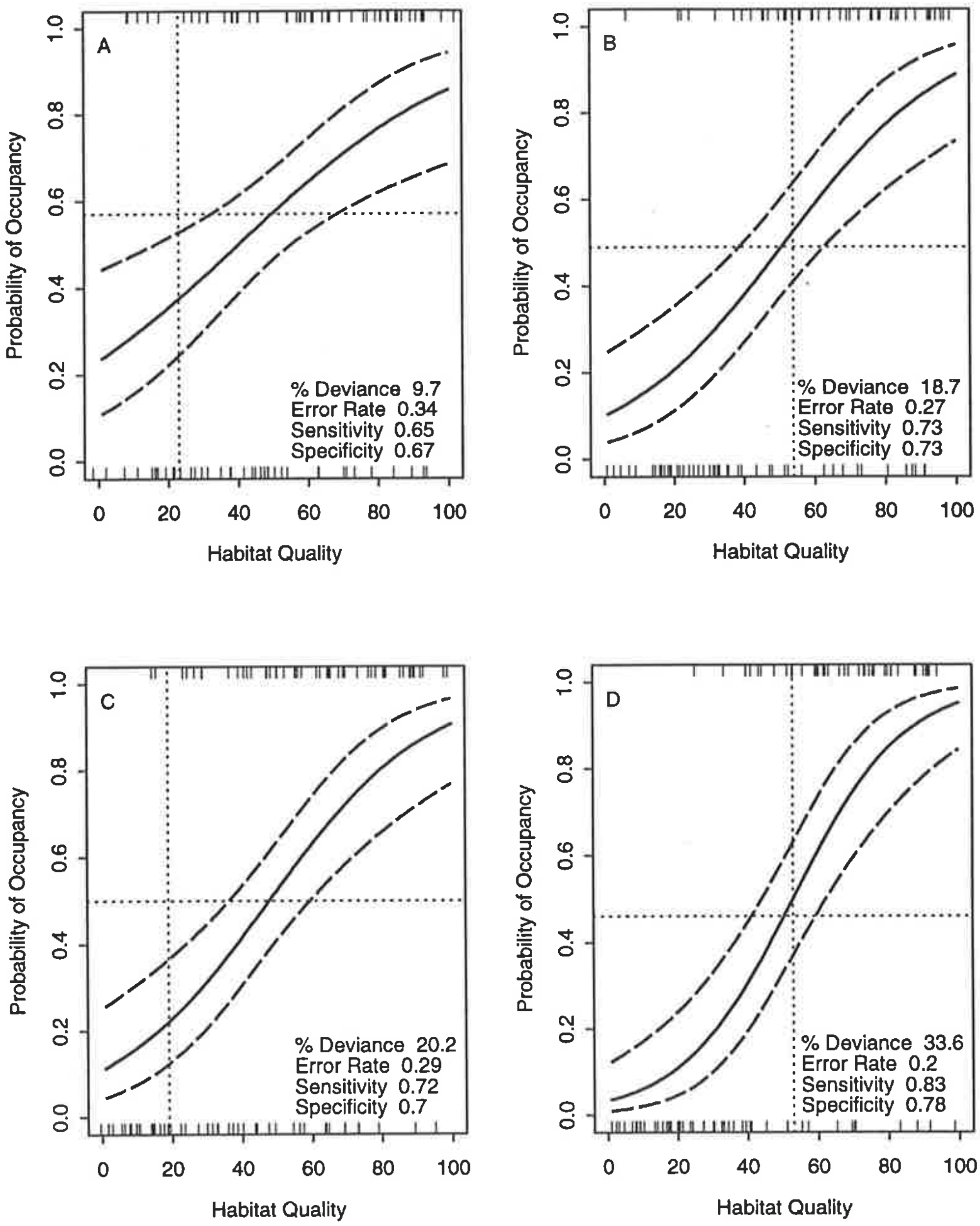


Figure 3.4 Four example logistic regressions for habitat occupancy by Greater Gliders, $\tilde{Q} = 90$, $\alpha = 3$, when the virtual ecologist is using extensive sampling. The solid line is the predicted probability of occurrence, and the dashed lines are 95% confidence limits. Rugs indicate the frequency distribution of observed occupied (top) and unoccupied (bottom) home ranges. The vertical dotted line indicates the boundary between marginal and high quality habitat (ie. where the intrinsic rate of population growth is 1.0), and the horizontal dotted line is the proportion of sampled sites that were occupied. A) Survival Scenario, $H = 2.9$, B) Fecundity Scenario, $H = 2.9$, C) Survival Scenario, $H = 2.5$, and D) Fecundity Scenario, $H = 2.5$.

Explanatory power

Results

Figure 3.5 and Figure 3.9 summarise the performance of logistic regression models for the two species for extensive sampling with $\alpha = 3$. Table 3.2 and Table 3.3 provide median values for all combinations of sampling plan and dispersal rule. Conclusions about the relative performance of the models by comparing the percentage of explained deviance are generally backed up by examining the overall error rates (Figure 3.5 and Figure 3.9, Table 3.2 and Table 3.3); lower error rates correspond to higher percentage deviance explained, but the relative change in error rate tends to be smaller. There are no consistent patterns within landscape types between life history scenarios. Variation between fecundity and survival scenarios in the median error rate and percentage deviance explained is generally much smaller than differences between landscape types or sampling plans. There are three broad and consistent conclusions. Logistic regressions generate better predictions 1) when sampling is extensive across the full range of habitat variables, 2) on smoother, more predictable landscapes (smaller H), and 3) when individuals are strong habitat selectors. In addition, sensitivity varies much less than specificity, and models seem to be more accurate when fecundity varies. I will consider each of these in detail.

Extensive sampling roughly doubles the amount of deviance explained compared to random or regular sampling. There is little or no difference between random or regular sampling plans. Both of these plans are “random”, in the sense that the distribution of habitat values sampled is determined by the distribution actually present (Figure 3.2). In contrast, extensive sampling ensures that extreme habitat values are represented in the model. This is accompanied by a sharp increase in the specificity of the models (fewer false positives), especially on rough landscapes ($H = 2.9$). Specificity of models with random or regular sampling on rough landscapes is also much more variable than in other cases. The sensitivity of the models either does not change, or actually decreases when sampling is extensive (ie. more false negatives).

Logistic regressions explain nearly twice as much deviance on smooth landscapes compared with rough landscapes. This improvement comes about primarily through an improvement in the specificity, with few consistent changes in sensitivity. When habitat selection behaviour is strong ($\alpha = 10$), the improvement in model accuracy on smooth landscapes is not as great. The sensitivity and specificity are meaningless measures on the random landscapes. The slopes for most of these models are very small, and consequently the predicted probability of occupancy is above or below the prediction threshold for the entire range of habitat qualities. If the predicted probabilities are all below 0.5, then sensitivity is 0 (all occupied territories predicted to be unoccupied), and specificity is 1 (all unoccupied territories predicted to be unoccupied). Whereas more than 95% of replicate habitat models are significant by an analysis of deviance on both types of fractal landscapes, generally much less than half of the replicate habitat models on random landscapes actually include a significant effect of habitat quality on occupancy.

Strong habitat selection behaviour also increases the accuracy of the models. Increasing the bias towards good habitat for the biased random walker increases both the percentage deviance explained the specificity to the highest levels for both species under all landscape/life history scenarios. Some of the other differences that are observed (ie. higher specificity on smoother landscapes) disappear when habitat selection is strong.

For MBP, logistic regressions predict occupancy better when fecundity is variable, For GG, the life history scenario only matters when the dispersal rule is $\alpha = 10$, and then the models are more accurate when survival is variable. This is also generally true on random landscapes for both species, although obviously the trend is much weaker.

Table 3.2 Medians and 95% confidence limits for the percentage deviance explained, error rate, sensitivity, and specificity for all combinations of sampling plan and dispersal rule for greater gliders. Confidence limits cannot be calculated for the sensitivity and specificity under the global jumper dispersal rule, because the values are nearly all one or zero. SS is survival scenario, and FS is fecundity scenario. Values in brackets are lower and upper 95% confidence limits on the medians.

	% Deviance	Error Rate	Sensitivity	Specificity
Random Sampling, $\alpha = 3$				
SS, Random	1.4 (1.1, 1.8)	0.36 (0.35, 0.37)	0.98 (0.97, 1)	0.03 (0.01, 0.06)
FS, Random	1 (0.6, 1.4)	0.2 (0.18, 0.22)	0 (0, 0)	1 (1, 1)
SS, H = 2.9	7.2 (6.2, 8.2)	0.33 (0.32, 0.34)	0.84 (0.81, 0.87)	0.41 (0.37, 0.46)
FS, H = 2.9	8.3 (6.4, 10.2)	0.31 (0.3, 0.32)	0.78 (0.74, 0.81)	0.5 (0.43, 0.57)
SS, H = 2.5	18.6 (16.6, 20.6)	0.27 (0.26, 0.28)	0.75 (0.72, 0.78)	0.7 (0.66, 0.73)
FS, H = 2.5	20.5 (18.3, 22.6)	0.25 (0.24, 0.26)	0.77 (0.75, 0.8)	0.7 (0.66, 0.74)
Extensive Sampling, $\alpha = 3$				
SS, Random	3.3 (2.7, 3.9)	0.34 (0.33, 0.35)	0.93 (0.91, 0.96)	0.14 (0.09, 0.2)
FS, Random	1.6 (1.1, 2.1)	0.23 (0.21, 0.26)	0 (0, 0)	1 (1, 1)
SS, H = 2.9	16.8 (15, 18.5)	0.29 (0.28, 0.3)	0.75 (0.74, 0.77)	0.66 (0.64, 0.68)
FS, H = 2.9	16.1 (14.2, 18.1)	0.28 (0.27, 0.29)	0.78 (0.76, 0.79)	0.66 (0.63, 0.69)
SS, H = 2.5	32 (30, 34.1)	0.21 (0.2, 0.22)	0.77 (0.76, 0.78)	0.8 (0.79, 0.82)
FS, H = 2.5	32 (30.1, 33.9)	0.22 (0.21, 0.23)	0.74 (0.73, 0.76)	0.81 (0.8, 0.82)
Extensive Sampling, $\alpha = 10$				
SS, Random	8.1 (7.1, 9.2)	0.34 (0.33, 0.35)	0.56 (0.54, 0.59)	0.75 (0.72, 0.77)
FS, Random	3.5 (2.6, 4.4)	0.15 (0.14, 0.16)	0 (0, 0)	1 (1, 1)
SS, H = 2.9	35.1 (33.3, 36.8)	0.2 (0.19, 0.21)	0.74 (0.73, 0.76)	0.84 (0.84, 0.85)
FS, H = 2.9	29.4 (27.6, 31.2)	0.23 (0.22, 0.24)	0.72 (0.71, 0.74)	0.82 (0.81, 0.83)
SS, H = 2.5	42.8 (41, 44.6)	0.17 (0.16, 0.18)	0.74 (0.73, 0.76)	0.88 (0.87, 0.88)
FS, H = 2.5	39.2 (37.6, 40.8)	0.2 (0.19, 0.21)	0.74 (0.73, 0.76)	0.85 (0.84, 0.86)
Regular Sampling, $\alpha = 3$				
SS, Random	1.7 (1.3, 2.2)	0.34 (0.32, 0.35)	1 (0.99, 1.0)	0 (0.0, 0.02)
FS, Random	0.8 (0.5, 1.1)	0.23 (0.21, 0.25)	0 (0, 0)	1 (1, 1)
SS, H = 2.9	7.7 (6.6, 8.9)	0.32 (0.31, 0.33)	0.86 (0.84, 0.89)	0.37 (0.33, 0.42)
FS, H = 2.9	8.6 (7.3, 9.9)	0.31 (0.3, 0.32)	0.86 (0.83, 0.89)	0.43 (0.38, 0.48)
SS, H = 2.5	16 (14, 18)	0.29 (0.28, 0.3)	0.75 (0.73, 0.78)	0.67 (0.64, 0.71)
FS, H = 2.5	19.5 (16.7, 22.3)	0.26 (0.25, 0.27)	0.78 (0.75, 0.81)	0.71 (0.67, 0.74)

Table 3.3 Same as for Table 3.2, but for mountain brushtail possums.

	% Deviance	Error Rate	Sensitivity	Specificity
Random Sampling, $\alpha = 3$				
SS, Random	1.9 (1.4, 2.4)	0.3 (0.29, 0.31)	0.99 (0.98, 0.99)	0.03 (0.01, 0.04)
FS, Random	0.9 (0.6, 1.3)	0.32 (0.31, 0.33)	0 (0.0, 0.01)	1 (0.99, 1.0)
SS, H = 2.9	11.4 (10, 12.8)	0.29 (0.28, 0.3)	0.85 (0.83, 0.88)	0.44 (0.38, 0.49)
FS, H = 2.9	14.3 (12.7, 15.9)	0.31 (0.3, 0.32)	0.71 (0.68, 0.73)	0.69 (0.66, 0.73)
SS, H = 2.5	23.4 (21.2, 25.6)	0.24 (0.23, 0.25)	0.79 (0.77, 0.82)	0.71 (0.68, 0.74)
FS, H = 2.5	33.8 (31.5, 36.1)	0.19 (0.18, 0.2)	0.74 (0.72, 0.77)	0.84 (0.82, 0.86)
Extensive Sampling, $\alpha = 3$				
SS, Random	3.8 (3, 4.5)	0.31 (0.3, 0.32)	0.98 (0.97, 1)	0.06 (0.03, 0.1)
FS, Random	1.7 (1.2, 2.2)	0.35 (0.34, 0.36)	0.05 (0.0, 0.1)	0.99 (0.95, 1.0)
SS, H = 2.9	24.1 (22, 26.2)	0.23 (0.22, 0.24)	0.81 (0.8, 0.82)	0.71 (0.69, 0.74)
FS, H = 2.9	30.2 (27.9, 32.5)	0.22 (0.21, 0.24)	0.76 (0.74, 0.77)	0.79 (0.78, 0.81)
SS, H = 2.5	39.8 (37.8, 41.7)	0.18 (0.17, 0.19)	0.82 (0.81, 0.83)	0.83 (0.82, 0.84)
FS, H = 2.5	40.6 (39, 42.3)	0.17 (0.16, 0.18)	0.8 (0.79, 0.81)	0.86 (0.85, 0.87)
Extensive Sampling, $\alpha = 10$				
SS, Random	9.9 (9, 10.9)	0.33 (0.32, 0.34)	0.68 (0.67, 0.69)	0.67 (0.66, 0.69)
FS, Random	3.9 (3.1, 4.8)	0.31 (0.29, 0.32)	0.06 (0.02, 0.11)	0.97 (0.95, 0.99)
SS, H = 2.9	36.7 (34.5, 38.9)	0.2 (0.19, 0.21)	0.78 (0.77, 0.79)	0.83 (0.82, 0.84)
FS, H = 2.9	37.5 (35.5, 39.5)	0.19 (0.18, 0.2)	0.74 (0.72, 0.75)	0.85 (0.85, 0.86)
SS, H = 2.5	45.4 (44, 46.7)	0.16 (0.15, 0.17)	0.8 (0.79, 0.82)	0.86 (0.85, 0.87)
FS, H = 2.5	49.6 (47.5, 51.7)	0.14 (0.13, 0.15)	0.81 (0.8, 0.83)	0.89 (0.88, 0.9)
Regular Sampling, $\alpha = 3$				
SS, Random	2.1 (1.6, 2.7)	0.31 (0.3, 0.32)	0.99 (0.98, 1)	0.03 (0.01, 0.05)
FS, Random	1 (0.6, 1.3)	0.34 (0.32, 0.36)	0.03 (0.01, 0.06)	1 (0.99, 1.01)
SS, H = 2.9	12.1 (10.6, 13.6)	0.29 (0.28, 0.3)	0.88 (0.86, 0.91)	0.43 (0.37, 0.48)
FS, H = 2.9	14.8 (13.3, 16.2)	0.3 (0.28, 0.31)	0.72 (0.69, 0.75)	0.69 (0.66, 0.72)
SS, H = 2.5	22.1 (20.3, 23.9)	0.25 (0.24, 0.26)	0.79 (0.77, 0.82)	0.7 (0.66, 0.74)
FS, H = 2.5	30.4 (27.7, 33.1)	0.2 (0.19, 0.21)	0.77 (0.75, 0.79)	0.82 (0.79, 0.84)

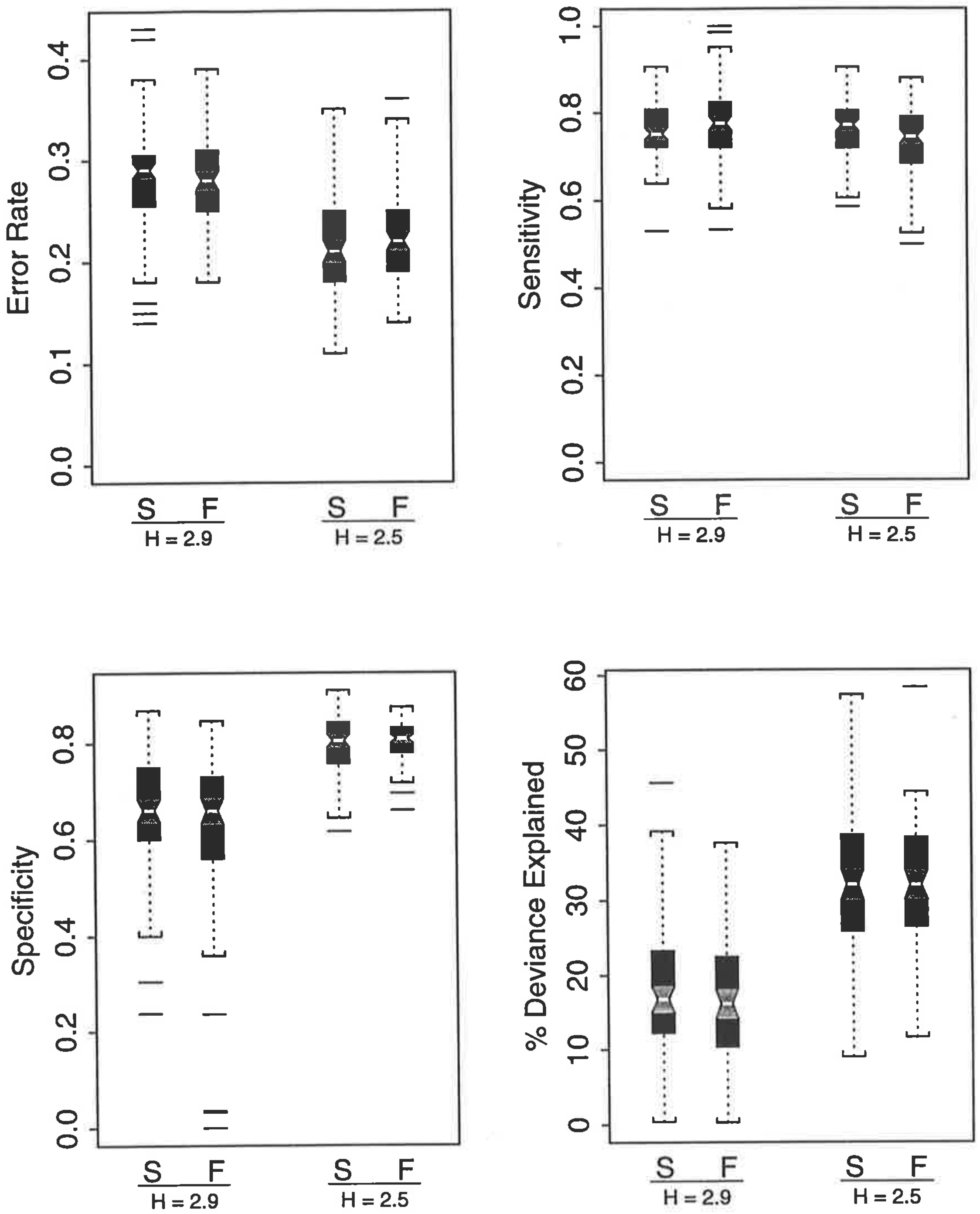


Figure 3.5 Boxplots of error rate, sensitivity, specificity, and the percent deviance explained for greater gliders with $\alpha = 3$ and extensive sampling. S = survival scenario and F = fecundity scenario. Boxplots as for Figure 3.2.

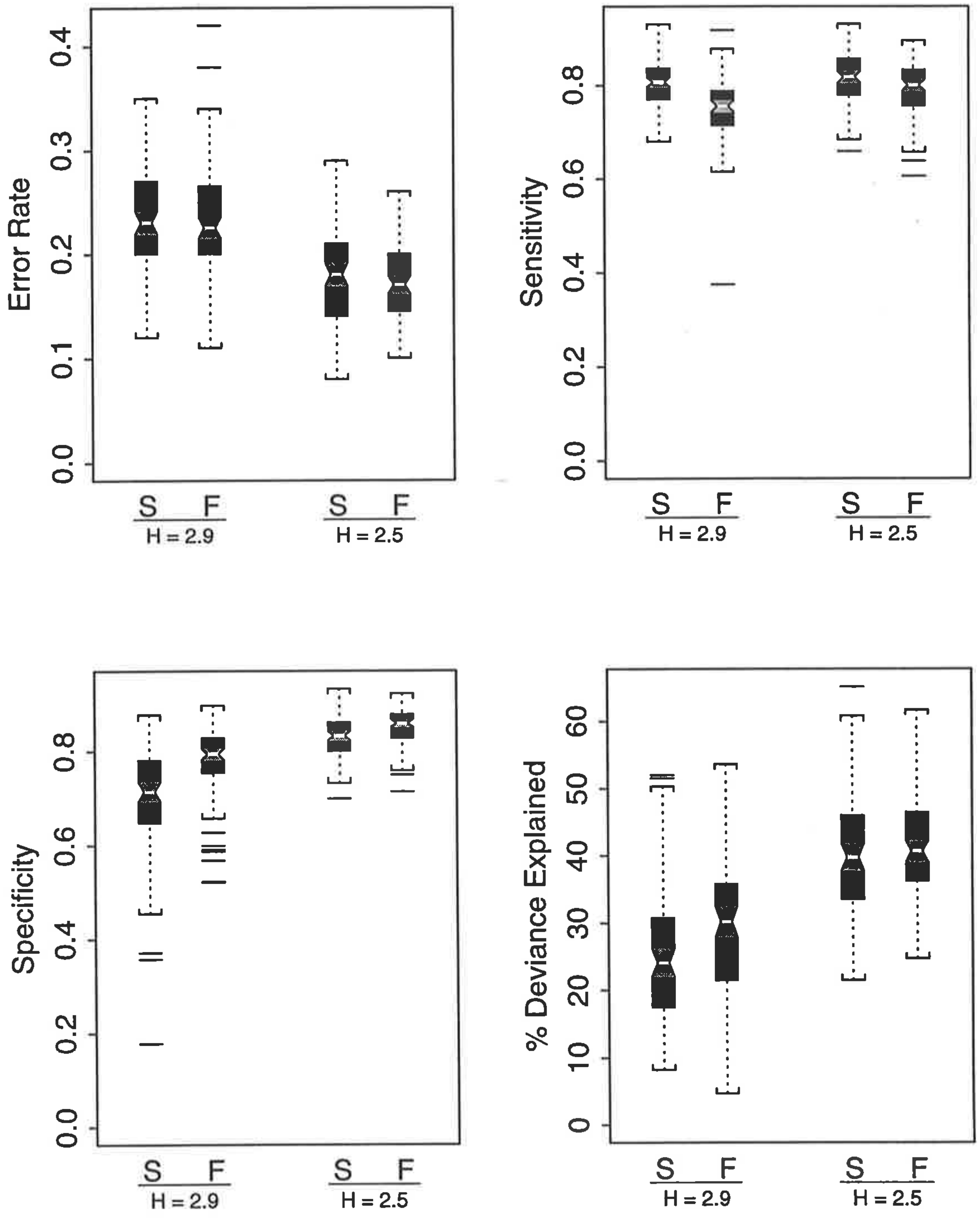


Figure 3.6 Boxplots of error rate, sensitivity, specificity and percent deviance explained for mountain brushtail possums with $\alpha = 3$ using extensive sampling. Boxplots as for Figure 3.2.

Discussion

Unexplained deviance arises from two kinds of errors: unoccupied territories predicted to be occupied (false positives), and occupied sites predicted to be unoccupied (false negatives). The ability of the model to avoid false positives is measured by the specificity, while the avoidance of false negatives is measured by the sensitivity (Table 3.1). The changes in the model output described above have to be understood in the context of processes leading to these two kinds of errors. For pedantic purposes, consider an "ideal landscape" that varies perfectly smoothly, from the best territory in the top left corner, to the worst territory in the bottom right (Figure 3.7). All territories above the predicted threshold (0.5) are occupied, and all territories below the predicted threshold are unoccupied. Such a situation would lead to a model with both the sensitivity and specificity equal to one. The key to understanding the diversity in the model output is to recognise that specificity is generally related to processes in the unoccupied, lower right hand corner, while sensitivity is related to processes in the occupied, upper left corner.

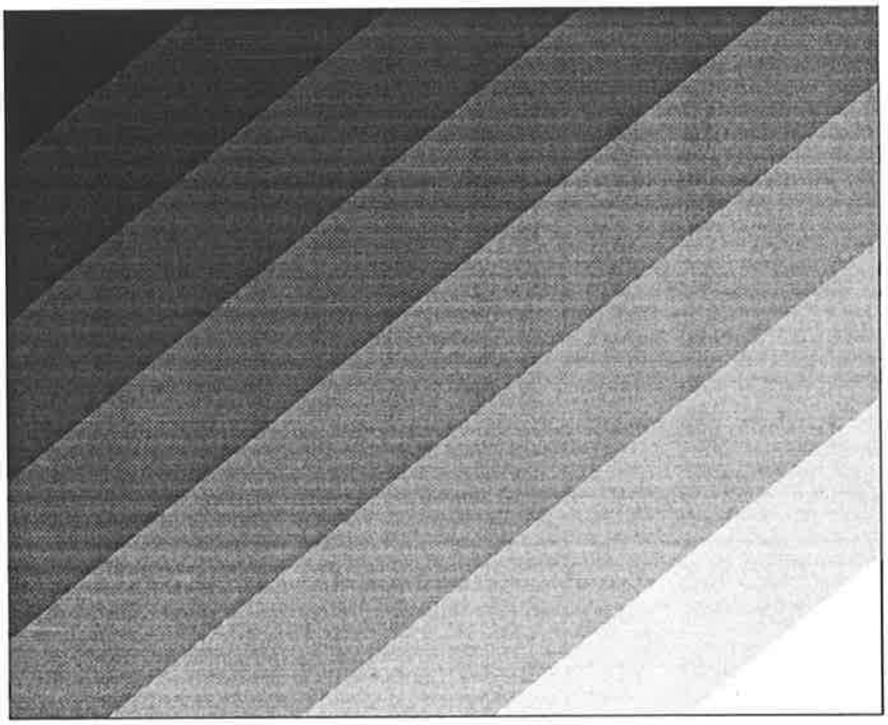


Figure 3.7 An idealised landscape, where the contours represent different predicted probabilities of occurrence. The x=y diagonal has a predicted probability $p = 0.5$, while in the bottom right corner $p = 0$, and in the top left $p = 1$.

When an individual dies in a high quality territory, that territory is a potential false positive prediction. When adult mortality is relatively high, as with the Greater Gliders, the probability that an otherwise good territory is observed to be vacant is higher than if mortality was relatively lower. If survival is the only component that contributes to errors of this kind, then the specificity of the models should be highest when survival is high, and not variable. This is generally true for MBP, and for random or regular sampling with GG. MBP also have higher specificity than GG when survival is not variable.

The likelihood that an otherwise high quality territory is found to be empty is not just a function of the average survival. It is also increased if the lag between the site becoming unoccupied and being recolonised is greater. This lag is a function of imperfect information on the part of individuals inhabiting the landscape; they do not know the location of unoccupied, high quality habitat. In the extreme, if habitat patches had boundaries, the biased random walkers would not cross them before exhausting the possibilities within the current patch. This helps to explain why predictions made on smoother landscapes have higher specificity. As the idealised landscape becomes rough, sites in the unoccupied lower right hand corner will exceed the prediction threshold, and be predicted to be occupied. However, they remain unlikely to be occupied, because all the individuals are searching in the upper left corner, and are unlikely to cross the poorer habitat separating the new high quality sites from the occupied, and generally high quality, region. These isolated territories become false positive predictions, and decrease a model's specificity.

The other source of unexplained deviance is territories predicted to be empty that are in fact occupied, or false negatives (Figure 3.5). This type of error is measured by the sensitivity of the model. The main population process responsible for these errors is local competition for space. If a dispersing individual cannot locate unoccupied habitat by looking "uphill" on the quality gradient, they gradually switch over to looking anywhere. The likelihood of encountering a marginal site near a good site is increased on landscapes with $H = 2.9$, because of increased "interdigitation" (eg. Figure 2.1). Increased use of marginal habitats in the vicinity of high quality habitat has been found in other theoretical work incorporating continuous variation in habitat quality (Milne et al., 1989; Gustafson & Gardner, 1996). However, individuals that are selecting habitat will tend to avoid the occasional poor quality territory interspersed among otherwise good territories. Thus, sensitivity actually increases slightly on rougher landscapes, because there is more likely to be an alternative high quality territory nearby. This effect is reduced with increasing habitat selectivity, which generally improves the avoidance of poor quality territories across all landscape types.

The general magnitude of variation in sensitivity is quite low across all scenarios and landscapes when compared with variation in specificity (Figure 3.5 and Figure 3.9, Table 3.2 and Table 3.3). The sensitivities measured in this model are also generally much higher than those reported in empirical examples. The example for greater gliders in Figure 3.1 has a sensitivity of 13%, while Pearce et al. (1994) reported sensitivities of 38% and 40.6% for helmeted honeyeaters (*Lichenostomus melanops cassidix*). As suggested in the quote at the beginning of the chapter, the discrepancy could be due to unmeasured variables in the real empirical system that are important components of good quality habitat. However, it is clear from the model that even when all important variables are measured accurately the sensitivity will never be 100%.

The relationship between specificity and overall quality of the statistical model might permit a general statement of how different life history characteristics influence the amount of variation that can be explained. As described above, high survival reduces false positives. However, it increases false negatives, because once a home range is occupied it is more likely to remain so. If regression models are more influenced by false positive errors than false negatives, then species with higher survival should be predicted better by logistic regression models. MBP have higher adult survival, longer time to maturation, lower newborn survival, and lower fecundity when compared with GG. In many cases the models explain more deviance for MBP than GG, as expected if false positive errors (specificity) have a bigger impact on overall error rates.

Effect of sample size and population density

From a practical standpoint, an important question to be resolved is how many sites must be sampled to achieve a certain goal. I evaluated this for the current model by examining how the error rate changes with sample size for GG using extensive sampling.

Paradoxically, the error rate actually increases with sample size on high dimensional landscapes (Figure 3.8). For the smallest sample size considered (20), nearly a quarter of replicates suffered numerical instability during the model fit. I postulate that this odd result arises because the model is too simple. Very few points are actually needed to determine that habitat quality is influencing territory occupancy. The more points that are sampled, the higher

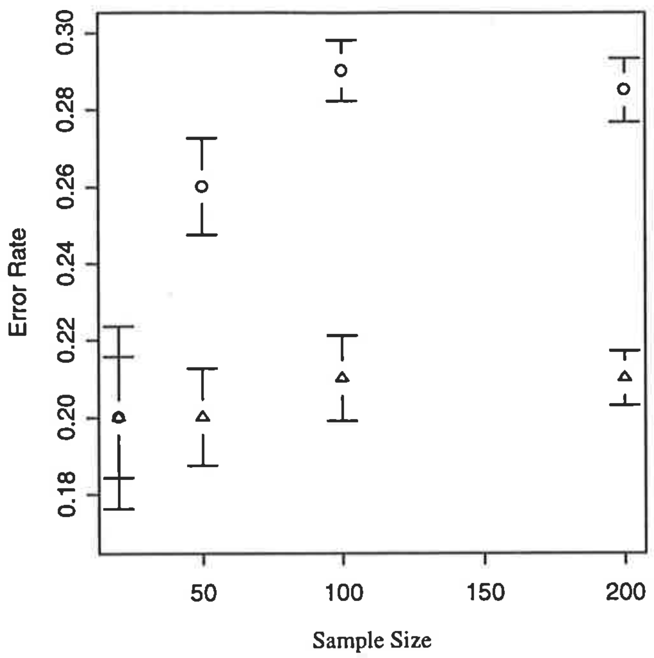


Figure 3.8 Effect of sample size on error rate for both landscape types (circles: $H = 2.9$, triangles: $H = 2.5$). Points are medians of 100 replicate runs. Error bars are 95% confidence intervals.

the likelihood of getting a relatively rare false positive or false negative, and this leads to the increased error rate.

This effect is even clearer if a regression is calculated on the data from the entire landscape, rather than sampling. Even in the absence of sampling variation, a logistic regression model does not predict perfectly or explain all the deviance (Figure 3.9).

Van Horne (1983) was one of the earliest critics of density or habitat occupancy as a surrogate for habitat quality. She highlighted several examples in which correlations failed to adequately identify high quality habitat defined on the basis of population processes. The conclusion was that density or occupancy is particularly likely to fail as a predictor of habitat quality when population densities are high. This is because increased competition for high quality habitat leads to increased numbers in lower quality habitat (ie. the losers). The conceptual background for this conclusion is the Ideal Free Distribution model of Fretwell and Lucas (1970). The IFD carries many assumptions that are difficult to meet, and it would be interesting to see if population density does in fact have an impact on the relationship between habitat variables and territory occupancy.

I considered the relationship between density and several measures of model success for some of the data presented in the previous section with a sample size of 50. The percentage deviance explained is negatively correlated with total population size in the sample year on both landscape types (Figure 3.10). The overall error rate and sensitivity are not correlated with density. The specificity is correlated with density on high dimension landscapes ($H = 2.9$, $r = -0.34$, $p < 0.001$), but only marginally on smoother landscapes ($H = 2.5$, $r = -0.18$, $p = 0.08$). The significance tests in all cases have to be treated with caution because the distributions of error rate, sensitivity, and specificity are quite skewed. The coefficient of habitat quality in the logistic regression models is also marginally negatively correlated with population size.

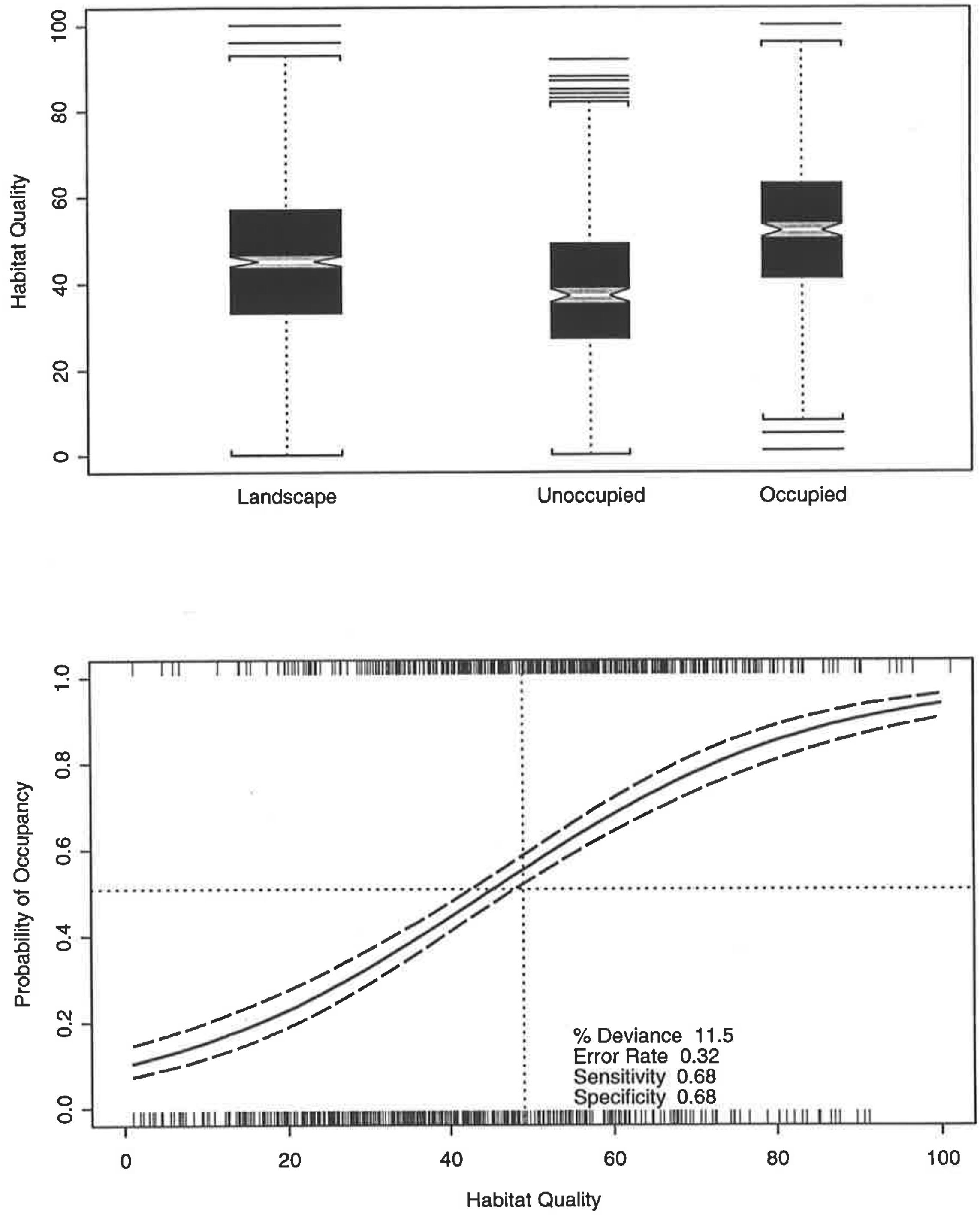


Figure 3.9 A) Boxplot of habitat quality on the landscape, and in occupied and unoccupied territories, for all 1089 territories. Data from greater gliders with $\alpha = 3$, fecundity scenario, and $H = 2.9$. B) Same data as A) with the logistic regression plotted as for Figure 3.4.

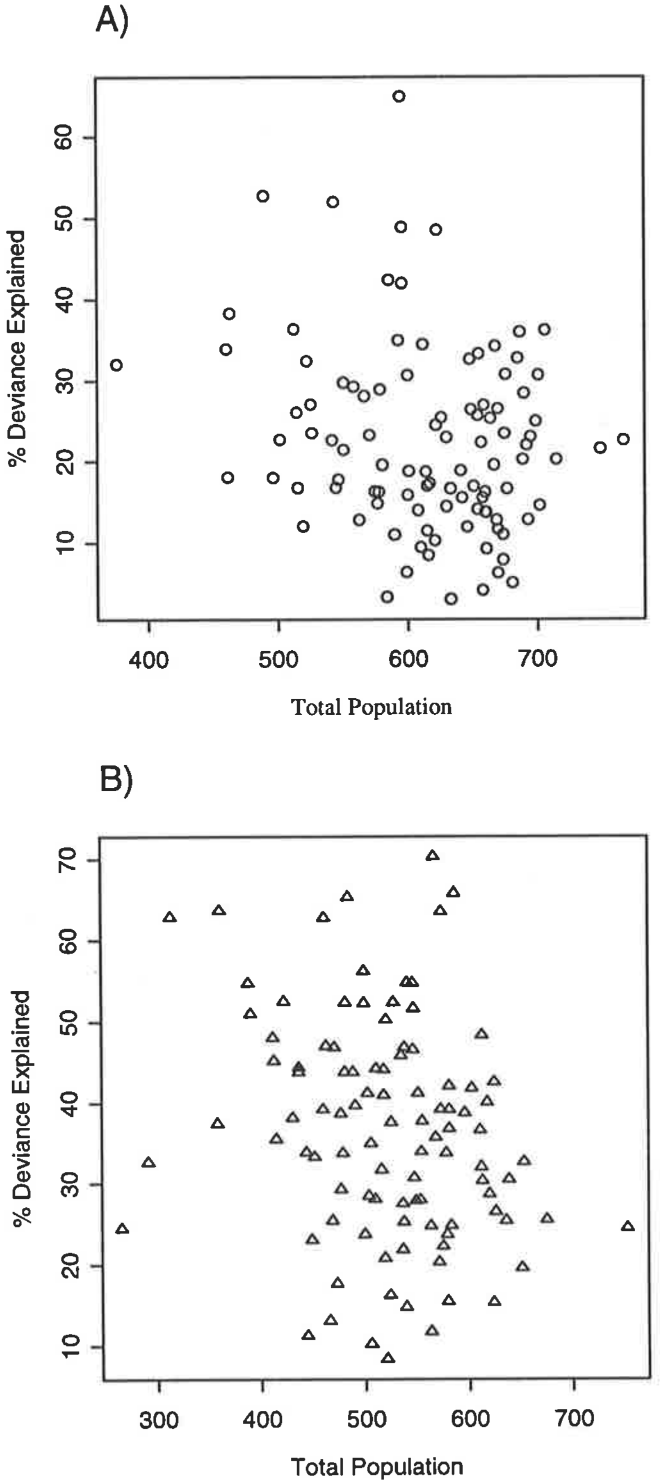


Figure 3.10 Percentage deviance explained vs. total population size on landscapes with A) $H = 2.9$, and B) $H = 2.5$. Pearson correlation coefficients are -0.224 and -0.227 respectively with $p < 0.025$ for both.

In conclusion, the size of the population at the time of sampling does influence the quality of the model. High density leads to poorer models by increasing the number of false positive errors, and this reduces the accuracy of the regression model. The difference between good and marginal habitat will be detected as smaller than it actually is. The relationships are quite variable (small *r*) and not consistent across landscape types. Part of this problem arises because the population size I have used here is the population size at the time of sampling, whereas the population size prior to dispersal may have a larger influence on the number of individuals forced into poorer quality habitat.

What can pattern tell us about process?

The ultimate test of a static habitat model is whether or not it recovers information about population processes. In this case, the processes that are of interest are birth and death rates of individuals in the population. The question to be resolved is whether or not there is a simple relationship between birth and death rates and the effect a habitat quality variable has on the probability of territory occupancy. If I examine the rate at which occupied territories remain occupied, p_{11}, as a function of habitat quality for any particular territory, I should be able to determine if this relationship looks like the one for probability of occupancy. This rate is related to the average survival rate, but because the virtual ecologist is sampling after dispersal, it also includes the possibility that an adult dies and the territory is immediately recolonised by a dispersing juvenile. I will call p_{11} the "survival probability". Likewise, I can determine the rate at which empty territories become occupied, p_{01}. This is a combination of both the number and fecundity of other individuals in the local area, and the probability of mortality during dispersal. I will refer to this as the "recolonisation probability".

For a single run of the model with GG (Figure 3.11), the survival probability does not have a similar functional form to the probability of occupancy, regardless of which life history scenario I consider. The recolonisation probability does increase similarly to the probability of occupancy. Furthermore, the regression slopes over 100 replicate runs for each species, life history scenario, and landscape type, the regression of habitat occupancy on habitat quality provides much more information about the recolonisation probability than the survival probability (ie. higher *r*, Figure 3.12, Figure 3.13, and Table 3.4). The random landscape runs can be generally discounted here, because the occupancy models for many replicates are in fact not significant. In this case the regression slope is randomly varying around zero. For GG, and ignoring the random landscape runs, only three of sixteen correlations between retention probability and occupancy slopes are significant at the 0.05 level, compared with all correlations with colonisation probability. Four of sixteen occupancy vs. survival probability correlations are significant for MBP.

Conclusions

The first main point of this chapter is that habitat occupancy analysis can never explain 100% of the variability in habitat occupancy. Residual variance will persist, irrespective of the number of habitat variables that are measured, the accuracy of wildlife surveys, or the number of samples taken. In the current model the single source of variability in population process rates is perfectly measured, and there is no error in occupancy measurement. The virtual ecologist still struggled to explain more the 50% of the deviance under these ideal conditions. If real wildlife ecologists think they explain more deviance by doing survey work and measuring more habitat variables then they are clearly wrong.

The second main point of this chapter is that habitat occupancy models do provide some information about population process rates, but not about all process rates. The main information provided is an upper bound on the probability that an unoccupied site becomes occupied. This probability is a combination of natal dispersal ability and the proximity of occupied good habitat. This recolonisation probability varies substantially across the landscape regardless of what population process is influenced by habitat quality. It is probably more accurate to interpret a significant effect of habitat on occupancy as indicating a high probability that the species occurs in the vicinity of sites with those characteristics, and is able

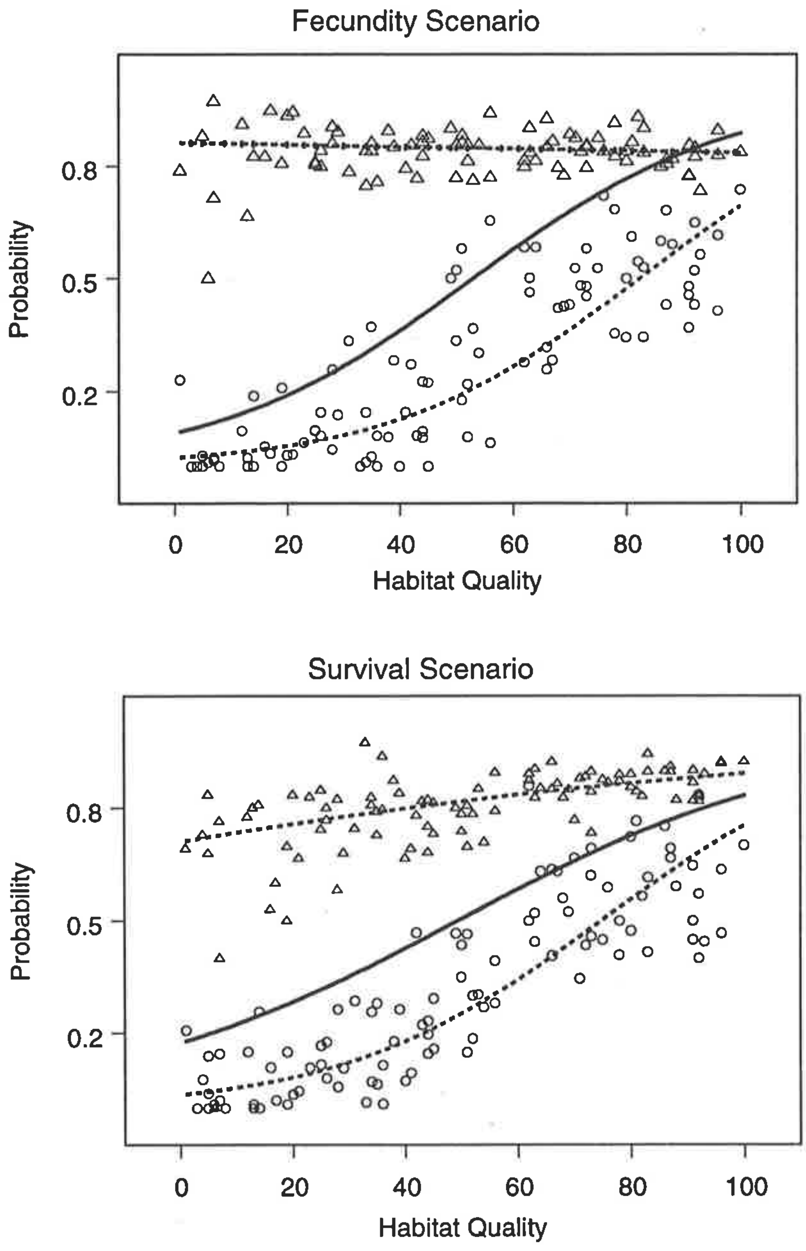
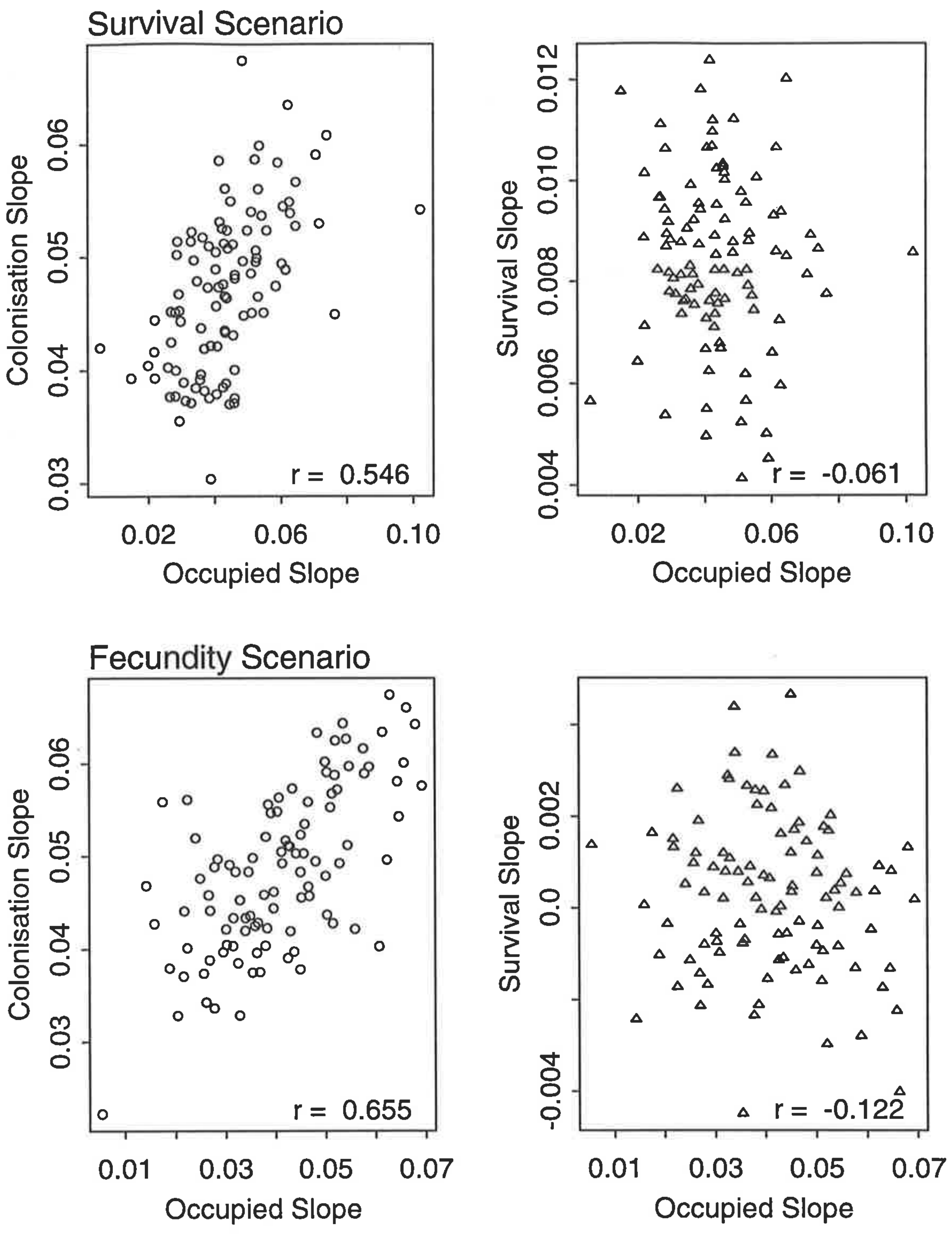


Figure 3.11 Examples of the relationship between p_{11} or p_{01} and habitat quality for greater gliders on landscapes with H=2.9. For both life history scenarios, the solid line is a logistic regression of occupancy at t=200 on habitat quality, open triangles are p_{11}, the probability that an occupied territory remains occupied, and open circles are p_{01}, the probability that an unoccupied territory becomes occupied. The dashed lines are logistic regressions through each of those sets of points.



Survival Scenario

Fecundity Scenario

Figure 3.12 Scatterplots of the regression slopes for habitat occupancy at *t*=200 on habitat quality vs. slopes of either colonisation or survival probabilities measured over 100 years for greater gliders, $\alpha = 3$, extensive sampling on landscapes with $H = 2.9$. Parametric correlation coefficients are given for each pair in the lower right corner.

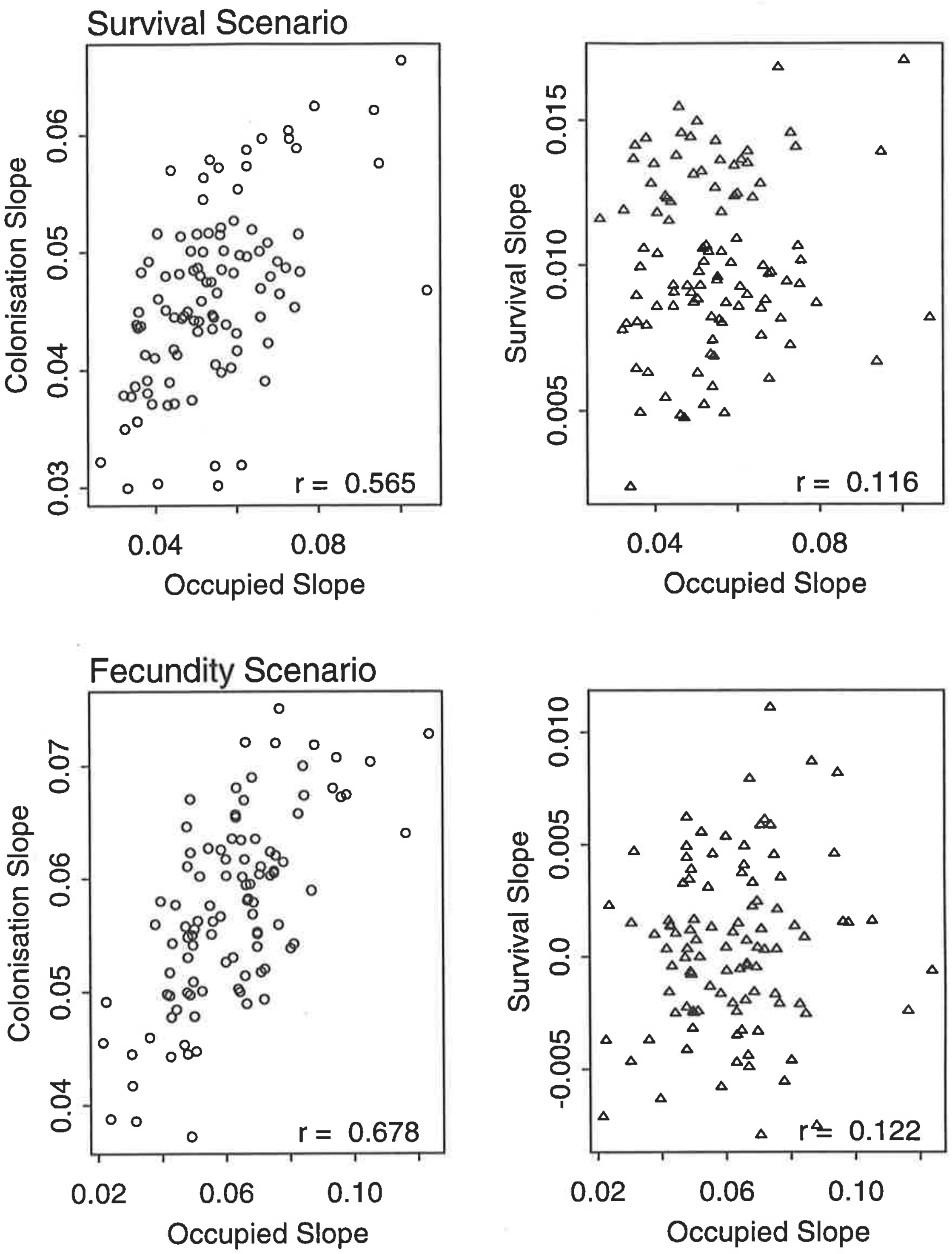


Figure 3.13 As for Figure 3.12, but for mountain brushtail possums.

Table 3.4 Relationships between survival or recolonisation rates and predicted occupancy probabilities. Pearson product-moment correlation coefficients are given for the regression slopes of either Colonisation probability (p_{01}) or survival probability (p_{11}) vs. occupancy. SS is survival scenario, FS is fecundity scenario. Values in brackets are p values from a parametric test of the hypothesis that $r = 0$.

	Mountain Brushtail Possum		Greater Glider	
	Col. vs. Occ.	Surv. vs. Occ.	Col. vs. Occ.	Surv. vs. Occ.
Random Sampling, α = 3				
SS, Random	0.131 (0.195)	0.076 (0.455)	0.164 (0.103)	0.2 (0.046)
FS, Random	0.584 (< 0.001)	0.483 (< 0.001)	0.595 (< 0.001)	0.245 (0.014)
SS, H = 2.9	0.566 (< 0.001)	0.245 (0.014)	0.473 (< 0.001)	0.303 (0.002)
FS, H = 2.9	0.561 (< 0.001)	0.247 (0.013)	0.645 (< 0.001)	0.051 (0.611)
SS, H = 2.5	0.535 (< 0.001)	0.102 (0.314)	0.613 (< 0.001)	0.008 (0.936)
FS, H = 2.5	0.386 (< 0.001)	0.047 (0.64)	0.697 (< 0.001)	0.019 (0.851)
Extensive Sampling, α = 3				
SS, Random	0.236 (0.018)	0.239 (0.017)	0.121 (0.232)	-0.056 (0.581)
FS, Random	0.506 (< 0.001)	0.415 (< 0.001)	0.346 (< 0.001)	0.267 (0.007)
SS, H = 2.9	0.565 (< 0.001)	0.116 (0.25)	0.546 (< 0.001)	-0.061 (0.545)
FS, H = 2.9	0.678 (< 0.001)	0.122 (0.228)	0.655 (< 0.001)	-0.122 (0.226)
SS, H = 2.5	0.564 (< 0.001)	0.216 (0.031)	0.516 (< 0.001)	0.303 (0.002)
FS, H = 2.5	0.35 (< 0.001)	0.138 (0.17)	0.536 (< 0.001)	0.044 (0.662)
Extensive Sampling, α = 10				
SS, Random	0.302 (0.002)	0.01 (0.919)	0.279 (0.005)	0.099 (0.325)
FS, Random	0.515 (< 0.001)	0.29 (0.003)	0.452 (< 0.001)	0.139 (0.167)
SS, H = 2.9	0.523 (< 0.001)	0.168 (0.095)	0.568 (< 0.001)	0.027 (0.793)
FS, H = 2.9	0.561 (< 0.001)	0.116 (0.252)	0.367 (< 0.001)	0.194 (0.053)
SS, H = 2.5	0.379 (< 0.001)	-0.018 (0.858)	0.414 (< 0.001)	0.033 (0.741)
FS, H = 2.5	0.38 (< 0.001)	0.261 (0.009)	0.416 (< 0.001)	0.206 (0.04)
Regular Sampling, α = 3				
SS, Random	0.191 (0.057)	0.134 (0.183)	0.164 (0.103)	0.204 (0.042)
FS, Random	0.494 (< 0.001)	0.331 (< 0.001)	0.515 (< 0.001)	0.062 (0.537)
SS, H = 2.9	0.552 (< 0.001)	0.335 (< 0.001)	0.329 (< 0.001)	0.122 (0.227)
FS, H = 2.9	0.58 (< 0.001)	0.046 (0.649)	0.587 (< 0.001)	0.15 (0.136)
SS, H = 2.5	0.606 (< 0.001)	0.012 (0.909)	0.599 (< 0.001)	0.049 (0.629)
FS, H = 2.5	0.536 (< 0.001)	0.157 (0.119)	0.608 (< 0.001)	0.187 (0.063)

to disperse there. There is no information about survival rates. This lack of information about survival and fecundity rates is unfortunate, because spatial variation in these rates influences the probability of extinction of populations. Population extinction or quasi-extinction risk is especially sensitive to variation in survival (McCarthy et al., 1994; Letcher et al., 1998), and it is this rate that habitat occupancy models provide the least information about.

The third point is that the model has not included everything that might have an impact on whether or not spatial variability has a detectable effect on habitat occupancy, and most of these omissions would make the relationship harder to quantify, not easier. For example, the landscape is static. Real landscapes shift and change according to the natural processes of succession and disturbance, and in response to human manipulations. If such processes mean that the landscape changes slowly at spatial scales related to dispersal distance, then temporal variation in habitat quality should not influence the relationship between occupancy and quality, because populations will be able to track the changes. Problems will arise when succession or disturbance, particularly human generated disturbances, occur faster on larger scales. Essentially, this leads to fragmentation of the landscape, blocking dispersal to other patches of suitable habitat. Wiens and Rotenberry (1987) observed this failure to track habitat changes in the course of their regional scale study of bird responses to habitat structure. At their Fort Rock site the habitat structure shifted over a three year period in a direction that their statistical models predicted decreased density or complete absence of Horned Larks (*Eremophila alpestris*). Lark density did not decrease significantly over the same period at this site.

The second important feature of real populations that is missing from the model are dispersal barriers that make movement between habitat "patches" difficult and rare. The model landscape is essentially a single "patch", in the metapopulation sense of the word. Whether or not a patch has good habitat is less important that the proximity of that patch to other occupied patches (Gustafson & Gardner, 1996). Predicting occupancy of patches from a set of snapshot observations within a continuous region will tend to overpredict the presence of a species in isolated patches.

The third thing that I have not attempted to do here is directly model the spatial distribution by including information about location or occupancy in neighbouring territories in the habitat models (eg. Augustin et al., 1996). Such information will generally not be available at the home range scale because it requires sampling effort of a much greater magnitude than point estimates of occupancy.

Direct estimation of extinction and colonisation rates from occupancy data (Hanski, 1994) is a relatively new idea that has not yet been widely applied (for eg. see Quintana-Ascencio & Menges, 1995). The basic idea of this "incidence function estimation" is to treat extinction and recolonisation of subpopulations as a markov chain process at equilibrium. Under this assumption it is possible to estimate the relationship between these metapopulation process parameters and occupancy, as long as there is a mainland present (ie. a patch immune to extinction). In the absence of a mainland, the only stationary state for a metapopulation is complete extinction. If patches are occupied, the observed state may be quasistationary, but applying the incidence function assumption of stationarity leads to underestimation of extinction rates (Hanski, 1994; Day & Possingham, 1995). Incidence functions have been structured primarily at the metapopulation scale, where the processes of interest are extinction and recolonisation. The distinguishing characteristics of habitats at this scale is generally the size and isolation of patches. However, many management problems are focused at finer scales, within single populations. At this scale, it is probability of death and dispersal of individuals that is being estimated, and the number of relevant habitat characteristics is much larger. The results of this study indicate that applying the incidence function concept at this finer scale is likely to be futile. Variation in survival (extinction) rates has a large impact on population dynamics, but is undetectable by occupancy at the home range scale.

I have developed a new concept of experimenting with models that transcends traditional power analysis: the "virtual ecologist". This concept is increasing in importance for conservation biology and other ecological disciplines where empirical experiments are impossible because of the temporal and spatial scales involved (Turner et al., 1995). In these fields many studies rely on "snapshots" at single points in time to understand processes that cannot be measured easily. This critical assessment of the conditions under which snapshot data can be extrapolated to understand processes is timely. Snapshot data provides little or no information about process rates at individual scales; the rates that are needed to make management decisions.

Chapter 4 Multi-scale analyses of Density Dependence in a parasitic tick

Introduction

The issue of what forces are responsible for regulating the abundance of organisms has been a source of controversy among ecologists for decades (Peet, 1991), and the debate shows no signs of abating (Bonsall et al., 1998). Density dependence must operate at some level of abundance, if only in competition for living space (den Boer, 1991). For example, it is not possible for an ectoparasitic tick to reach densities much higher than the surface area of the host divided by the area of a tick! However, in many systems, density dependent effects on process rates are absent or undetectable at typical densities (eg. Hassell et al., 1987; Roitberg et al., 1990; den Boer, 1991; Stiling et al., 1991).

The controversy over the extent to which density dependence regulates populations extends to parasitology. Two recent books on the ecology of parasites make opposing statements about density dependence, with Smith (1994) asserting that abundant evidence exists for density dependent population regulation, while Esch & Fernández (1993) assert that most parasite populations are regulated in a density independent fashion. It is not an idle question. Calculating the efficacy and cost of parasite control measures in human and agricultural animal populations relies on a detailed knowledge of population regulation at the level of "infrapopulations" (within single hosts, Esch & Fernández, 1993), and metapopulations (among all hosts in a population). Most work on population regulation in parasites has been done on endoparasites such as intestinal nematodes or cestodes (eg. Anderson & Gordon, 1982; Guyatt et al., 1990; Srividya et al., 1991; Goater, 1992), and under laboratory conditions. Often the primary interest in looking for density dependent processes is to evaluate the potential of the parasite to regulate the host population (eg. Lampo & Bayliss, 1996; Vail & Smith, 1997), or of the potential for acquired immune responses over a host's lifetime (eg. Dizij & Kurtenbach, 1995). Density dependence of a process on within host parasite burden has been found in parasite fecundity, survival, development, and host mortality (Smith, 1994), and all of these influence both population regulation, and the observed dispersion of parasites among hosts (Anderson & Gordon, 1982).

This chapter, and the following one, are motivated by an interest in the population regulation of an ectoparasitic tick of reptiles in Australia, *Aponomma hydrosauri*. The processes regulating this species are of interest for a purely ecological reason, as opposed to the practical matters discussed above. The biogeographical distribution of *A. hydrosauri* forms a sharp parapatric boundary with a second tick species, *Amblyomma limbatum*, across south-eastern Australia (Petney & Bull, 1984; Bull et al., 1989; Chilton & Bull, 1996). This boundary is not maintained by predation (Chilton & Bull, 1996), or interspecific competition (Bull et al., 1989). Mating interference may play a role (Andrews et al., 1982), as may climate, but these effects are either weak, or one-sided (ie. low moisture preventing *A. hydrosauri* from moving north). Bull & Possingham (1995) developed a simple landscape model of parapatry and showed that very weak competition (ie. nearly undetectable) could maintain a parapatric boundary if habitat quality fluctuated in space in a wave-like fashion. Neighbouring species could co-exist where habitat was good (on the crest of the wave), but weak competition would prevent them from crossing the neighbouring trough.

Given the lack of obvious competitive mechanisms operating between the two species, it is worth asking what evidence is available for population regulation within *A. hydrosauri*, ie. is there any evidence for intraspecific competition. In this chapter, I examine a spatially and temporally extensive data set of tick abundance (donated by Prof. C. M. Bull) for evidence of density dependent population regulation. In the next chapter, I develop an individual based model of the tick population to explore the extent to which the mechanisms identified in this chapter affect population dynamics.

A fundamental question, of a technical nature, is how one might detect density dependence. This is especially difficult in a spatially complex environment. There are two different, broad approaches to the detection of density dependence in the field. The first is based on key factor analysis of mortality within life history stages of insects (Varley et al., 1973), and the second is based on analysis of abundance time series (Bulmer, 1975). Key factor analysis involves the calculation of mortality rates for individual life history stages, either over time series or within single generations. Hassell (1987) noted that these values could be regressed on density, and significant regressions would indicate the presence of density dependence for that mortality factor. This analysis has been most broadly applied to insect data sets, as entomologists collect substantial information on life stage specific mortalities in the context of pest management. Medical parasitologists have also employed this method. Studies based on this method have drawn conflicting conclusions about the importance of density dependence (Stiling, 1988; Hassell et al., 1989; Strong, 1989). Some of this confusion may be related to the spatial scale of the analysis relative to the spatial scale of population mixing (Ray & Hastings, 1996). I will return to this problem later.

Bulmer's (1975) time series analysis assumes that populations can be adequately represented as random walks. A random walk with density dependent growth tends to have a lower correlation at a time lag of one unit (years, generations or whatever is appropriate), and he designed a test based on detecting significant deviations from the random walk model. This idea has not enjoyed the same wide applicability as key factor analysis, because it relies on the availability of accurate, long time series of abundance data with no trend. Pollard et al. (1987) extended Bulmer's (1975) analysis, relaxing some assumptions by using bootstrapping to perform significance tests. However, these time series methods are heavily dependent on the assumption of no sampling error. The presence of even moderate amounts of sampling error strongly biases these methods towards the detection of density dependence (Bulmer, 1975). Woiwod and Hanski (1992) used these and other time series methods to analyse insect population data from the Rothamstead insect survey, and concluded that both direct and delayed density dependence was widespread in moth and aphid populations in England.

There is a third method of detecting density dependence that appears to be peculiar to the study of parasites. The often extreme overdispersion ($s^2 >> m$) of parasites among hosts has long intrigued ecologists since Crofton (1971) first used the negative binomial distribution to quantify overdispersion. Note that in this chapter I will follow the customary practice of parasitologists by using the term overdispersion to refer to the state in which the variance is *greater* than the mean, while underdispersion refers to the variance being *less* than the mean. This is the opposite to much of the ecological literature (and some other parts of this thesis) concerned with spatial pattern, in which the term overdispersion refers to a pattern that is more regular (ie. s2 < m in a distribution of quadrat counts; Krebs, 1989).

Anderson & Gordon (1982) elucidated the relationship between population dispersion and population dynamic processes of birth, death, immigration, and emigration. They summarised their arguments with a "dispersion spectrum" (Figure 4.1), using the variance/mean ratio as an indication of dispersion. The basis for interpreting changes in dispersion is a simple stochastic model where the number of parasites of a particular stage on a host is a balance between birth, death, immigration, and emigration. Direct reproduction of the parasite within the host or heterogeneity in the rate of emigration off hosts, or the death of parasites on hosts increase dispersion. These processes increase dispersion because they result in some hosts developing much higher parasite populations than others. Parasite induced mortality of hosts, or positive density dependence in immigration onto hosts or mortality rate of parasites on hosts will reduce dispersion. These processes reduce dispersion by preferentially reducing large populations within hosts. Therefore, if dispersion is reduced when density increases, it is at least possible that density dependence in immigration or mortality rates are responsible. This conclusion has been asserted for at least one species (Lampo & Bayliss, 1996).

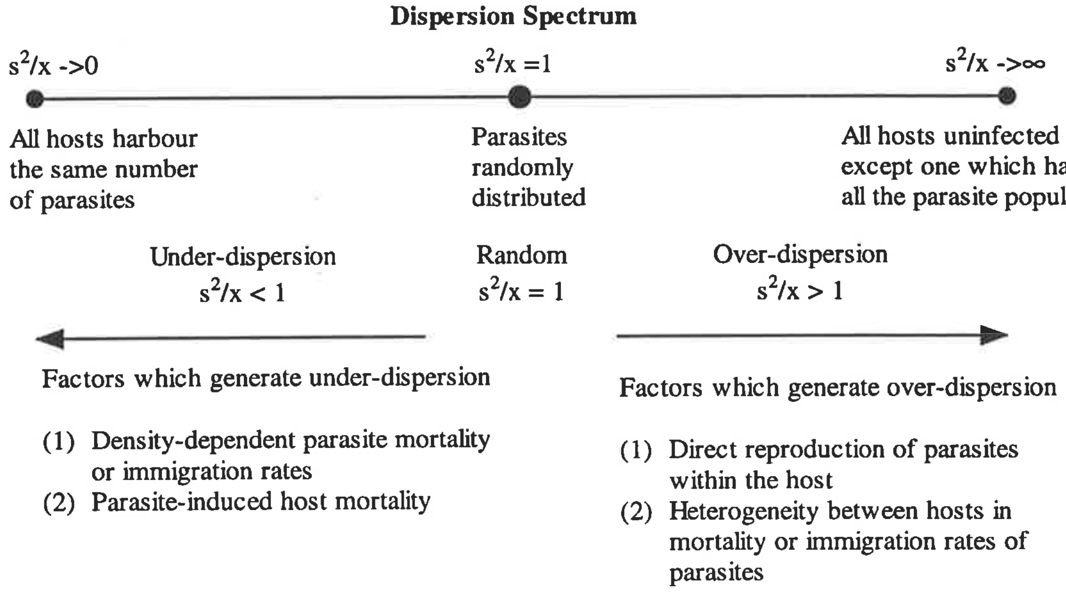


Figure 4.1 The dispersion spectrum for parasite distributions among hosts, indicating the processes that either increase or decrease dispersion. Adapted from Anderson & Gordon (1982).

Density dependent decreases in aggregation or overdispersion have been noted in other host-parasite systems (eg. Scott, 1987). Kretschmar & Adler (1993) developed a general model of host parasite dynamics that incorporates the effects of aggregation, and showed that a positive relationship between the mean density and an aggregation parameter stabilises the population dynamics. However, their model makes one critical assumption that host mortality rates increase linearly with parasite burden. If the effect is truly zero, then the Kretschmar & Adler model predicts that there will be no positive equilibrium, ie., the populations are completely unregulated.

Traditionally, the study of density dependence tends to assume that populations are closed. This assumption can be bypassed by conducting the analysis at multiple scales. For example, analysing the data set in toto for the landscape scale, and then analysing subdivisions of the data independently to "zoom in" on the population processes. The analysis of problems like this one at multiple scales of observation is a major challenge in ecology (Schneider, 1994). I will use a multiple scale approach, starting at the whole landscape scale and zooming down to the individual scale, to try and identify the extent to which spatial and temporal variation in process rates can contribute to population regulation in *Aponomma hydrosauri*.

First, I consider temporal trends in tick abundance across a range of scales. The detection of trends is important for the interpretation of the analysis of density dependence. Second, I look for density dependent signals in the dispersion of ticks among hosts at the landscape scale. Third, I employ two different time series analyses for the detection of density dependence. Finally, I analyse the probability of successful engorgement by larvae to identify possible density dependence at the individual scale. This work is exciting because it brings new methods to bear on parasite population regulation at a range of scales, made possible by a data set unique in its spatial and temporal scope.

Study Species

A. hydrosauri is a parasite of large reptiles in southern Australia. At a site near Mt. Mary, South Australia, the predominant host is the sleepy lizard, *Tiliqua rugosa*. Ticks in this region also infest Bearded Dragons (*Pogona viticeps*), sand goannas (*Varanus gouldii*), and brown snakes (*Pseudonaja textilis*). These alternative hosts are both less common and less commonly infected at the study site, and are hereafter ignored.

The life cycle of *A. hydrosauri* has 4 stages: egg, larva, nymph, and adult (Sharrad, 1979; Chilton, 1989). Only the last 3 stages attach to hosts. There is no requirement for each stage to use a new host, but this may occur by chance. No development occurs in the colder months between May and August, with all engorgement and host attachment activity occurring between September and April. Each host stage begins with attachment to the host, followed by a period of engorgement while the tick feeds on the host (Figure 4.2). When engorgement is complete, the tick detaches from the host when the host enters an overnight refuge site. Detaching is followed by a pre-moulting period of variable duration. Following moulting, a tick waits in the refuge for a new host to attach to, beginning the cycle again. The cycle ends with engorged adult females detaching and laying eggs. Adult males remain on the lizard waiting for several months for potential mates to board.

In any ecological analysis it is important to consider the relationship between the scale of analysis and the scale of appropriate ecological processes in time and space. Individuals take approximately one warm season (September to April) to complete development, so the appropriate temporal scale is annual. Some ticks can complete development faster, and it is important to note that development is not synchronised into cohorts, as it is in some northern hemisphere temperate tick species (eg. Vail et al., 1994). In space, the number of ticks present on a particular lizard will be related to previous numbers in an area from which ticks could recruit to that lizard. Ticks require three hosts to complete development, therefore the greatest distance over which a tick could move during development from egg to adult is three times the host's home range diameter, if it boarded a new host each time, and the host home ranges only just abutted. The probability of boarding a different host will increase with the degree of overlap between host home ranges. Therefore movements of three home range diameters will be rare, because the higher the overlap between home ranges the less extra distance can be gained. Movements over longer distances will be possible, for example on juvenile hosts during natal dispersal, but these will be rarer still. Field observations place the average home range size at around 3 ha (Bull & Baghurst, 1998; Bull et al., 1998; Bull & Freake, in press), or approximately 100 m in radius if home ranges are assumed to be circular. Therefore the "ecological neighbourhood" (Addicott et al., 1987) of recruitment is about 600 m, and it seems reasonable to suppose that tick populations in 1 km^2 regions are likely to be fluctuating largely independently of populations in neighbouring regions. I will present data at this fine scale, but small sample sizes prevent me from performing most analyses. Analyses at the larger scales are likely to be averaging over regions that are responding independently to variation in abiotic and biotic factors affecting population dynamics. This large scale averaging over heterogenous regions may reduce the power of density dependence analyses (Ray & Hastings, 1996).

The second tick species in this region, *Amblyomma limbatum,* has a sharp parapatric boundary with *A. hydrosauri* in the middle of the study site (Petney & Bull, 1984; Bull et al., 1989; Chilton & Bull, 1996). I ignore *A. limbatum* in this work, and exclude captures of lizards from the *A. limbatum* side of the boundary for my analysis of *A. hydrosauri* population dynamics (see below for details).

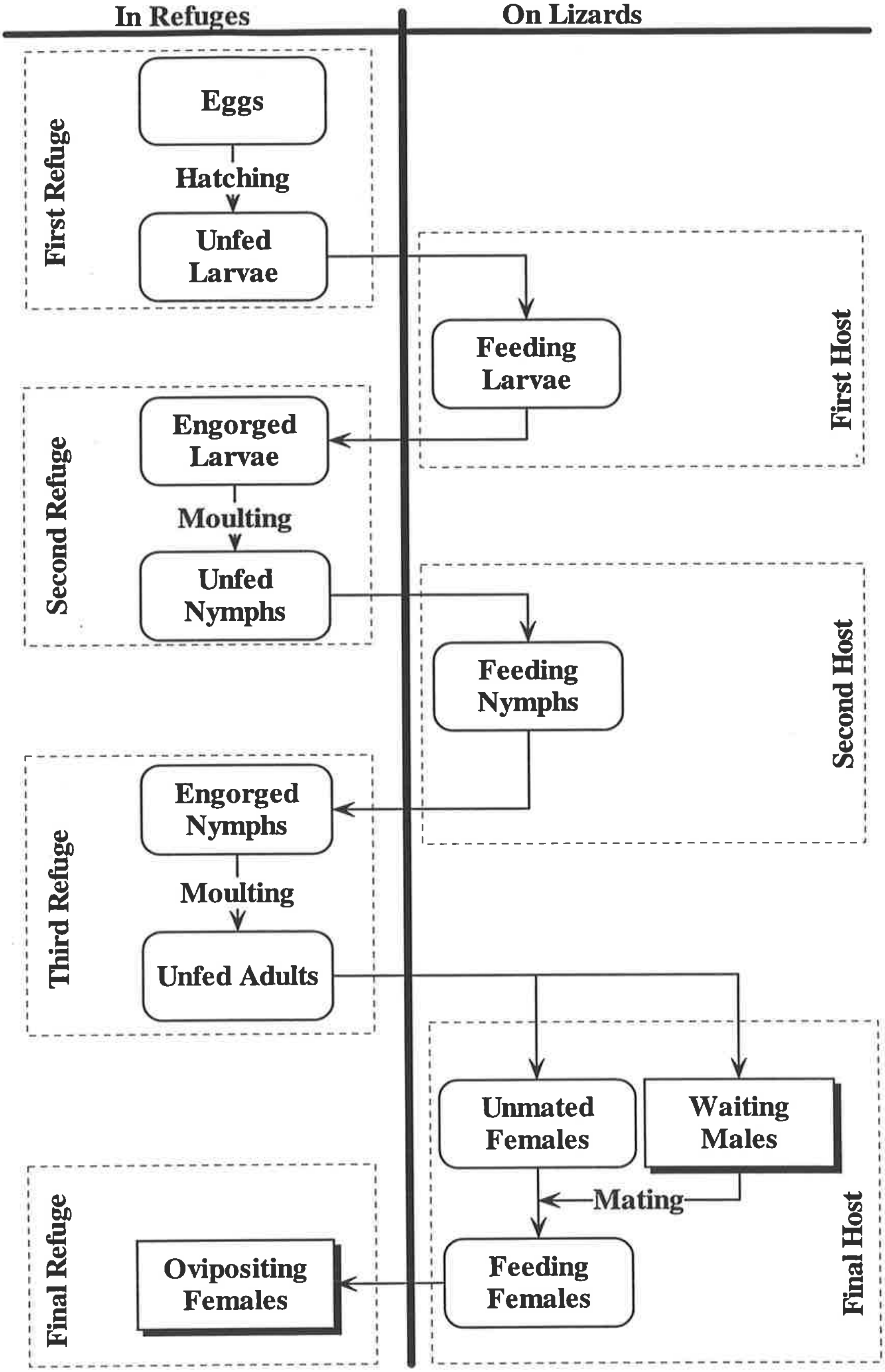


Figure 4.2 Flowchart of the various life history steps a larva goes through. Rounded rectangles indicate each stage, while rectangles with shadows indicate the endpoint of male and female tick life histories.

Data collection, culling, and transformation

The dataset consists of 15 years (1982-1997) of captures of Sleepy Lizards (*Tiliqua rugosa*) along 6 transects in the Mt. Mary region of South Australia (Figure 4.3), at a spatial resolution of 50 m (see Bull, 1995, for further details). Each data point is a count of a number of ticks on a lizard at a point in time and space. I use the year in which the season began to identify the time (ie. all captures in that season are lumped), and lump captures into 1 km segments along each transect. The spatial location is therefore specified by a transect number and a position on that transect, measured in 1 km units. I excluded all captures of lizards that did not occur directly on one of the six transects, to ensure that I am sampling a band of uniform width along all portions of the transect. This resulted in 22952 captures of *T. rugosa* over the 15 years of the study.

Captures of individual lizards occurred at random, and consequently at variable intervals. If a lizard is captured twice in quick succession there is a high likelihood that ticks present at the first capture are also present at the second. These observations of tick abundance are not independent. Therefore, I exclude from the dataset all captures that occurred less than 29 (larvae take 30 days on average to engorge, and most ticks are larvae) days after a previous capture of the same lizard. This applies to 5932 records out of a total of 22952, leaving us with a total record set of 17115.

As an aside, it may seem that it is possible to calculate the proportion of records that will not be independent, given information about the distribution of engorgement times. This calculation could then be used to efficiently choose a cutoff for making the records relatively independent. In practice, this is very difficult, if not impossible. Consider two captures of the same lizard, *t* days apart. The lizard has 10 larvae on board at each capture. Superficially, it would seem that if time to engorgement is normally distributed, then the probability that any one of the ten ticks on the initial capture is still present in the second capture is $1-N(\mu,\sigma^2)$, where N() is the cumulative normal distribution with mean μ and variance σ^2 of the engorgement time for larvae (see Chapter 5). However, the time at which each larva initiated feeding relative to the time of capture is unknown. The simplest assumption is that the initial capture occurs halfway through the distribution, in which case using the mean time as a cutoff will lead to >95% of larvae having dropped off before the next capture occurs (30 days is 2.6 SD of the larval engorgement distribution).

As mentioned above, the site is divided in two by a parapatric boundary between *A. hydrosauri* on the south, and *A. limbatum* on the north side. There are few, if any, *A. hydrosauri* north of the boundary. I eliminated this large scale heterogeneity and further reduced the dataset by dividing each transect into 1 km blocks, and excluding captures from blocks that had either, less than 100 lizard captures over the duration of the study, or less than 0.25 *A. hydrosauri* / lizard over the duration of the study. This ensures that I am concentrating only on lizard captures south of the tick boundary, and that the calculations at all scales are based on a reasonable number of captures. Transect 6 is entirely eliminated under these criteria. This leaves a total of 7774 captures. The final number of captures in all years for each transect is shown in Table 4.1.

Finally, I excluded adult male ticks from all counts of adult ticks on lizards. Male ticks remain attached to hosts for extended periods of time, and therefore have the possibility to bias the numeric results, although their numbers are generally quite low (average less than 1 male / capture). It is possible that average male numbers influence population dynamics through an Allee effect, as adult females do not engorge until mated. I ignore this possibility in the current analysis. For most of the analyses that follow, I use the total number of ticks on a lizard, lumping all life history stages together (except adult males).

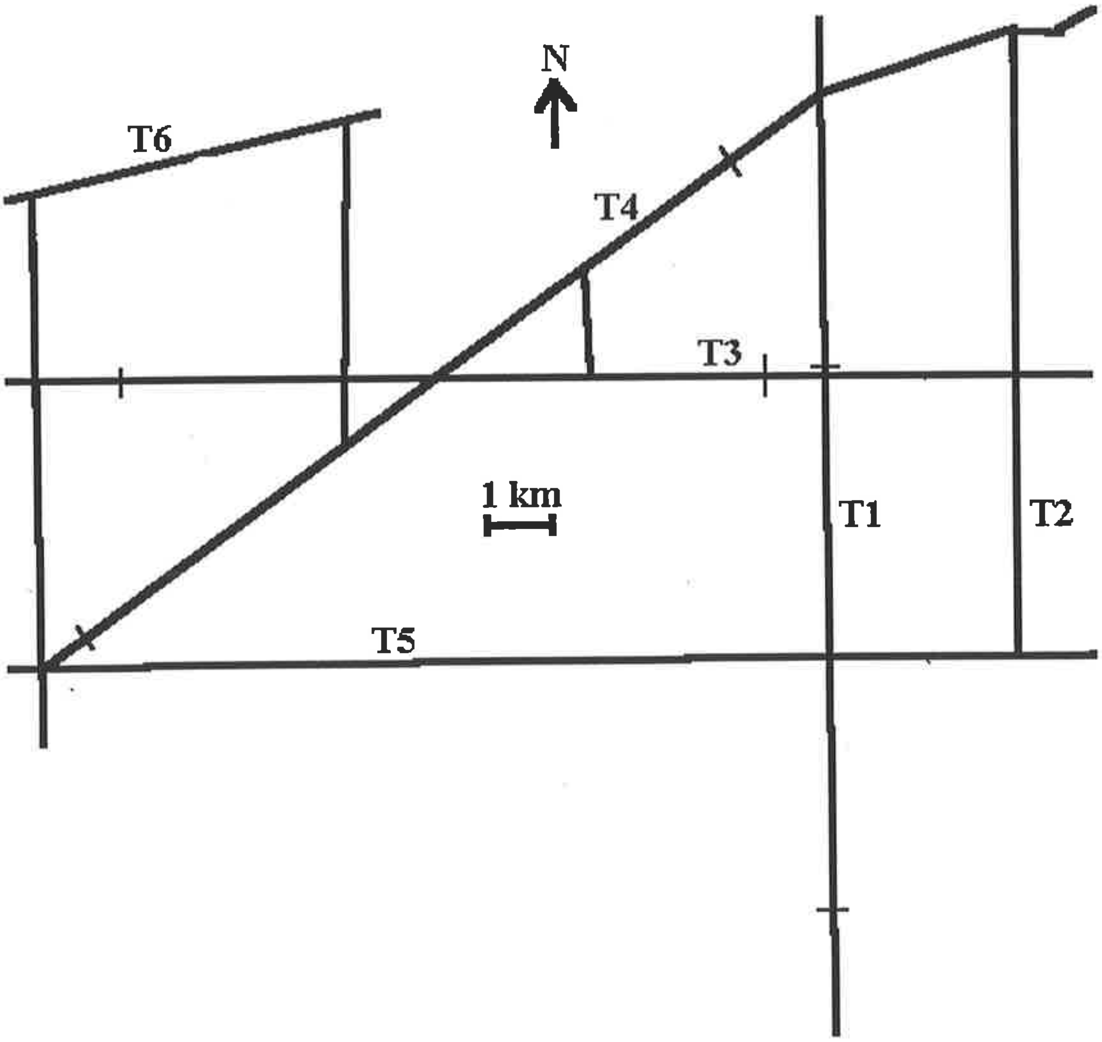


Figure 4.3 Map of the study transects near Mt. Mary, SA (139°40′E, 34°02′S). The number of each transect is indicated. Transects are dirt roads, and the small crosses indicate the ends of the regions included in the analyses.

Temporal dynamics

I consider the dynamics of the system at three scales. First, by looking at the entire study area over all transects. I refer to this as the "landscape" scale. The next scale down is to examine each transect individually. I refer to this as the "transect scale". These two scales are both large, relative to the ecological neighbourhood of recruitment. The smallest scale I consider is to break individual transects into 1 km blocks. I will refer to this as the "population" scale, assuming that neighbouring 1 km blocks have more or less independent populations of ticks. At each scale, I calculate the average number of ticks per lizard in each year from the empirical data.

The absence of a trend with time would be suggestive of population regulation, although a trend does not exclude the possibility of density dependent regulation. A trend does render some time series tests inconclusive, and therefore it is important to identify a trend if it exists.

Table 4.1 Number of lizard captures by year and transect after non-independent captures, and locations with too few captures or no ticks have been eliminated. Bottom row indicates the total sample size, and the number of 1 km blocks retained for each transect.

	Transect					
Year	1	2	3	4	5	Landscape Total
1982	65					65
1983	165	25	33	31		254
1984	151	38	102	55		346
1985	192	35	142	151	43	563
1986	195	36	194	139	39	603
1987	283	17	162	100	60	622
1988	339	30	221	189	80	859
1989	389	19	142	146	105	801
1990	240	17	97	124	106	584
1991	225	16	98	88	77	504
1992	126	16	125	111	63	441
1993	174	5	121	59	64	423
1994	110	13	171	135	41	470
1995	170	31	190	105	40	536
1996	125	48	83	103	32	391
1997	139	17	79	47	30	312
# blocks retained	12	3	6	9	9	7774

I tested for the existence of a temporal trend in tick abundance with a simple linear model applied to the logarithmically transformed data. A logarithmic transformation is appropriate in this instance because tick density cannot decrease below 0. The transformation corresponds to the assumption that tick density is log-normally distributed. Preliminary tests indicated that the 1982 value had an excessive influence on the regression (high leverage), and it was eliminated from the final analysis. 1982 had the smallest number of captures of any year, and was a year of severe drought.

Results & Discussion

The tick population fluctuates in space and time (Figure 4.4). At the landscape scale there appears to be a general trend towards increasing tick density. 1987, 1990, and 1993 stand out as particularly high density years. 1997 may also be a peak density year. These peaks are reflected in the transect scale data as well, although each peak tends to occur predominantly on one transect. There is a suggestion that densities on other transects increase at the same time, although not to the same extent, and not consistently across all transects. For example, from 1993 to 1994 transects 1, 3, and 5 decreased in density, while transect 2 increased.

The apparent temporal variation is even greater at the population scale (Figure 4.5). The peaks in 1987, 1990, and 1993 appear at some locations on some transects. Peaks in other years appear at this scale. The temporal variability also appears to increase in locations nearest to the boundary, particularly on Transect 1.

The unpredictable nature of the peaks in the data is possibly a result of variable sample size. The largest average tick densities tend to be associated with low sample sizes (Figure 4.6). High numbers of ticks do occur occasionally. If a single observation of many ticks is made at a time and place when relatively few other captures are made, then this large observation will tend to skew the mean to a greater extent than if the sample size was larger. This does not have much influence on the general increasing trend in tick density with time, especially at the landscape scale. Most of the excessive peaks observed at the smaller scales occur earlier in the time series, and if anything bias the sequence towards a smaller increase than would be otherwise observed. One possible solution to this problem would be to recalculate the observations with robust statistics such as the median and the median absolute deviation (Venables & Ripley, 1994). This is not as straightforward as it seems at first appearance, because the median number of ticks in most years is zero.

There is a linear increase in log-transformed tick abundance with time at the landscape scale ($F_{1,13} = 20.04$, $p < 0.001$, $x_t = 0.99 + 0.096t$, $R^2 = 0.61$, $t = \{2,\ldots,16\}$). At the transect scale, there is a significant linear trend for transects 1, 3, and 5 (Table 4.2). The trend for transect 5 is the least significant, and also has two large positive residuals in 1993 and 1997. I have not attempted to test for trends in the population scale analysis, because the sample sizes are small and highly variable. There does appear to be a trend on Transect 1, particularly locations -9 to -7.

Table 4.2 Results of linear models fitted to log-transformed tick density at the transect scale. All tests had 1, 13 degrees of freedom, except for transect 5 with 1, 11.

Transect	Intercept	Slope	*F*	*p*
1	2.02	0.82	10.5	0.006
2	1.40	0.43	1.40	0.26
3	0.97	0.73	15.49	0.002
4	1.75	0.21	1.99	0.18
5	-5.6	1.34	6.052	0.03

Given that the overall abundance of ticks appears to be increasing with time, the question arises as to what other parameters of the tick population might be changing with either density or time. In the next section I analyse the distribution of ticks among lizards in more detail, using maximum likelihood methods to fit parametric distributions to the capture data.

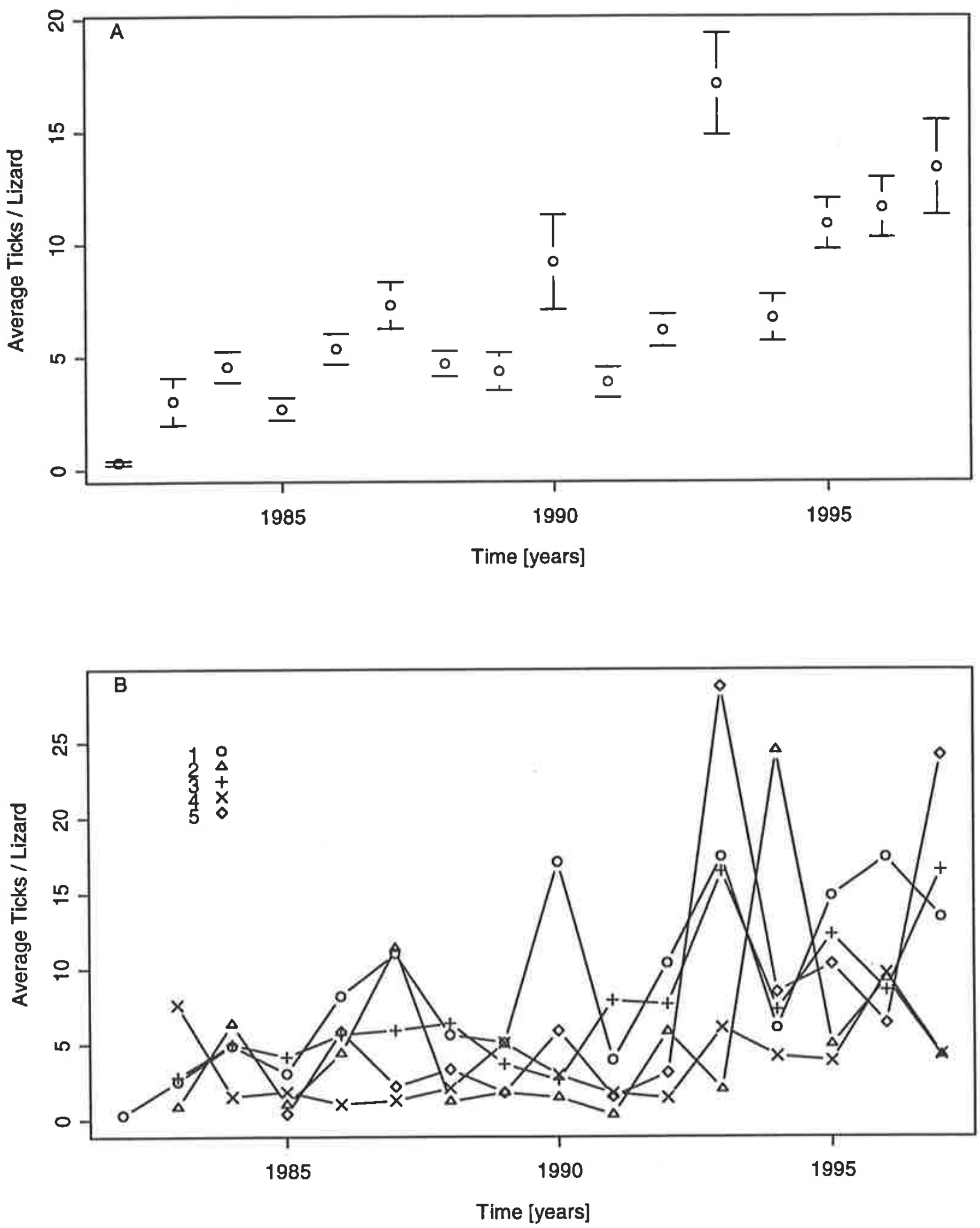


Figure 4.4 Average ticks / lizard from 1982 to 1997 at A) landscape scale, and B) transect scale. Error bars are standard errors of the mean, and are not shown in B for clarity. Only transects 1 and 2 run the entire time. Transects 3 and 4 started in 1983, and transect 5 in 1985.

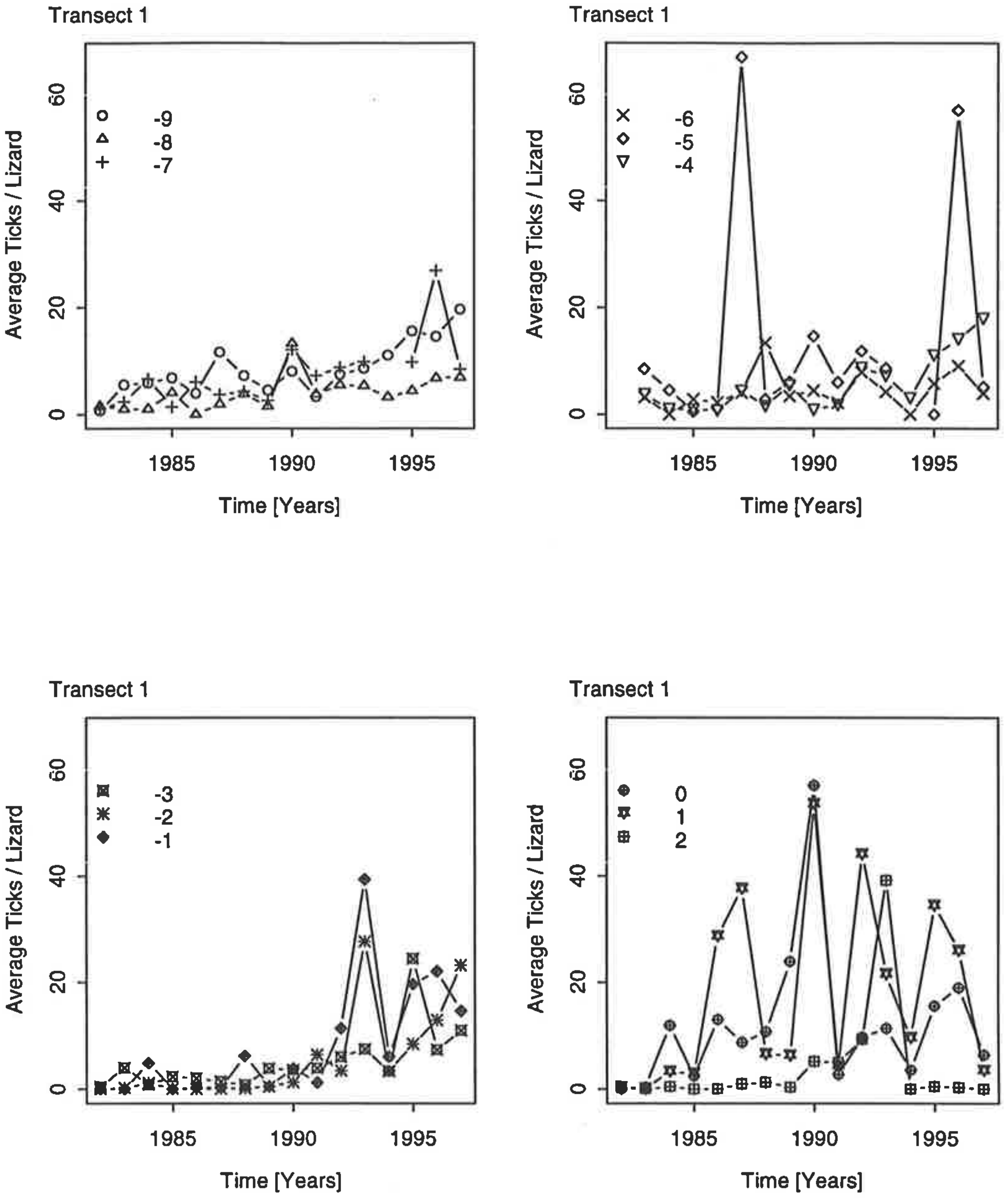


Figure 4.5 Tick abundance with time at the population scale. Each line represents a single 1 km block along the length of the transect. Transects 2 - 5 are shown on separate pages.

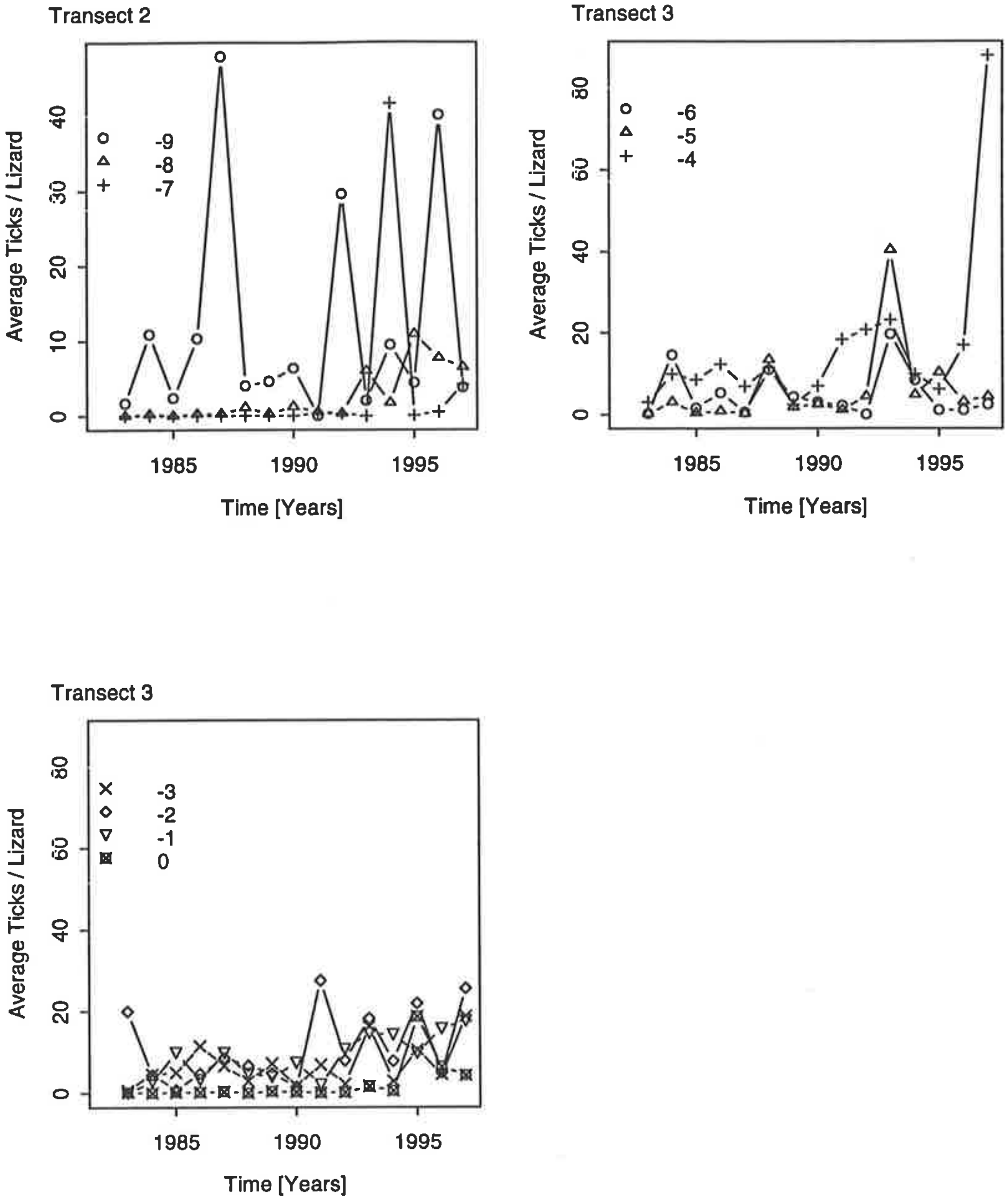
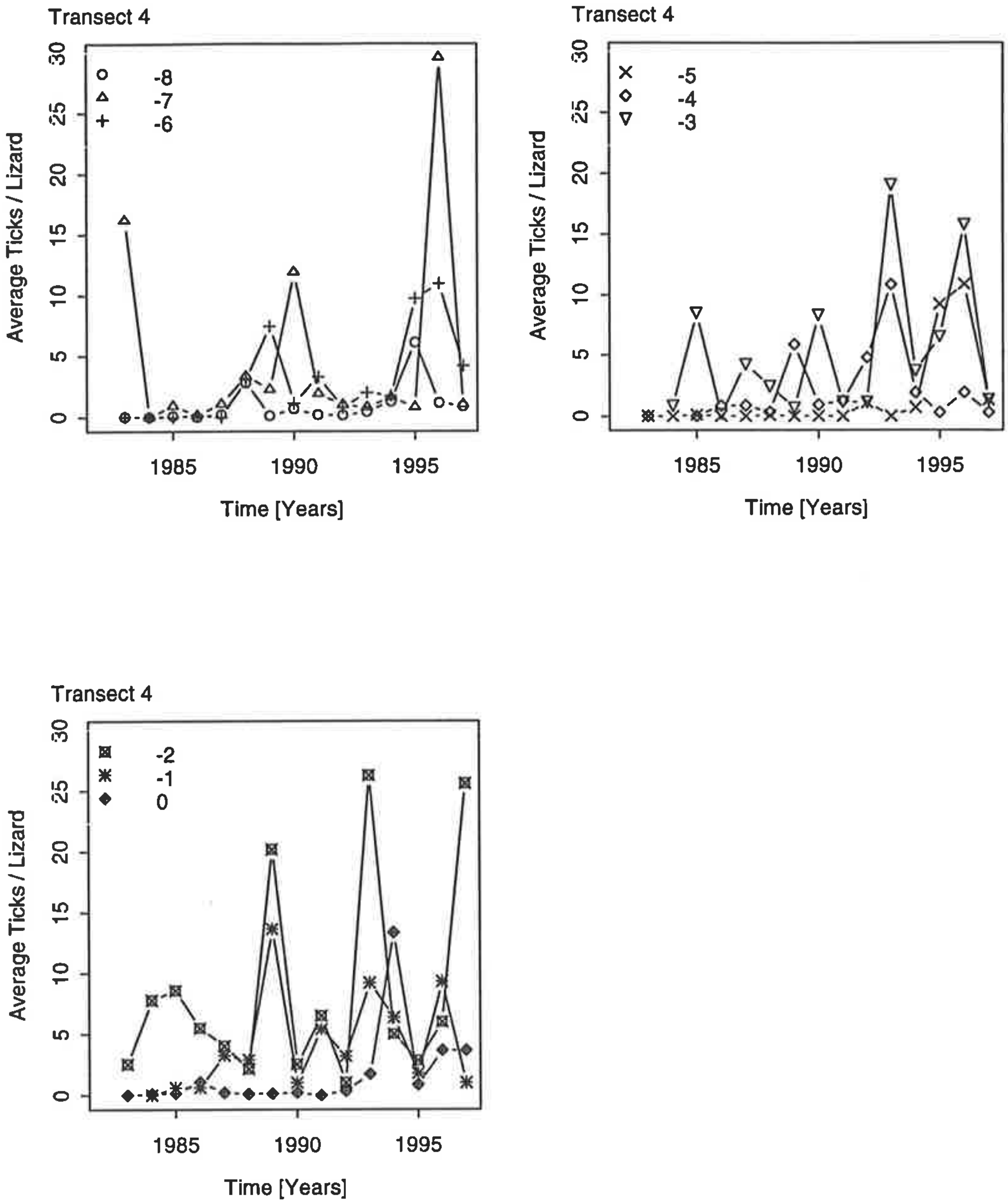


Figure 4.5 continued.



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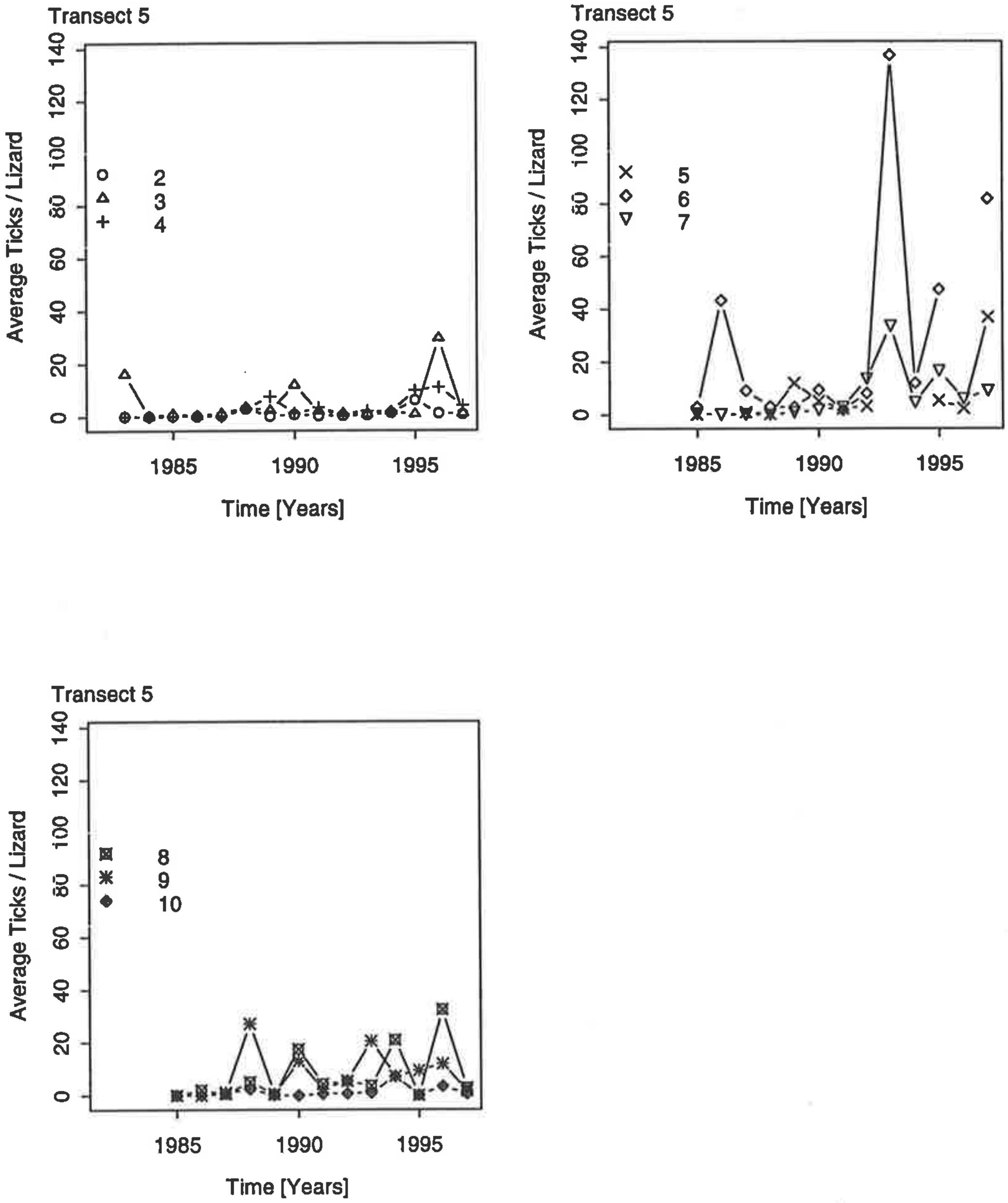

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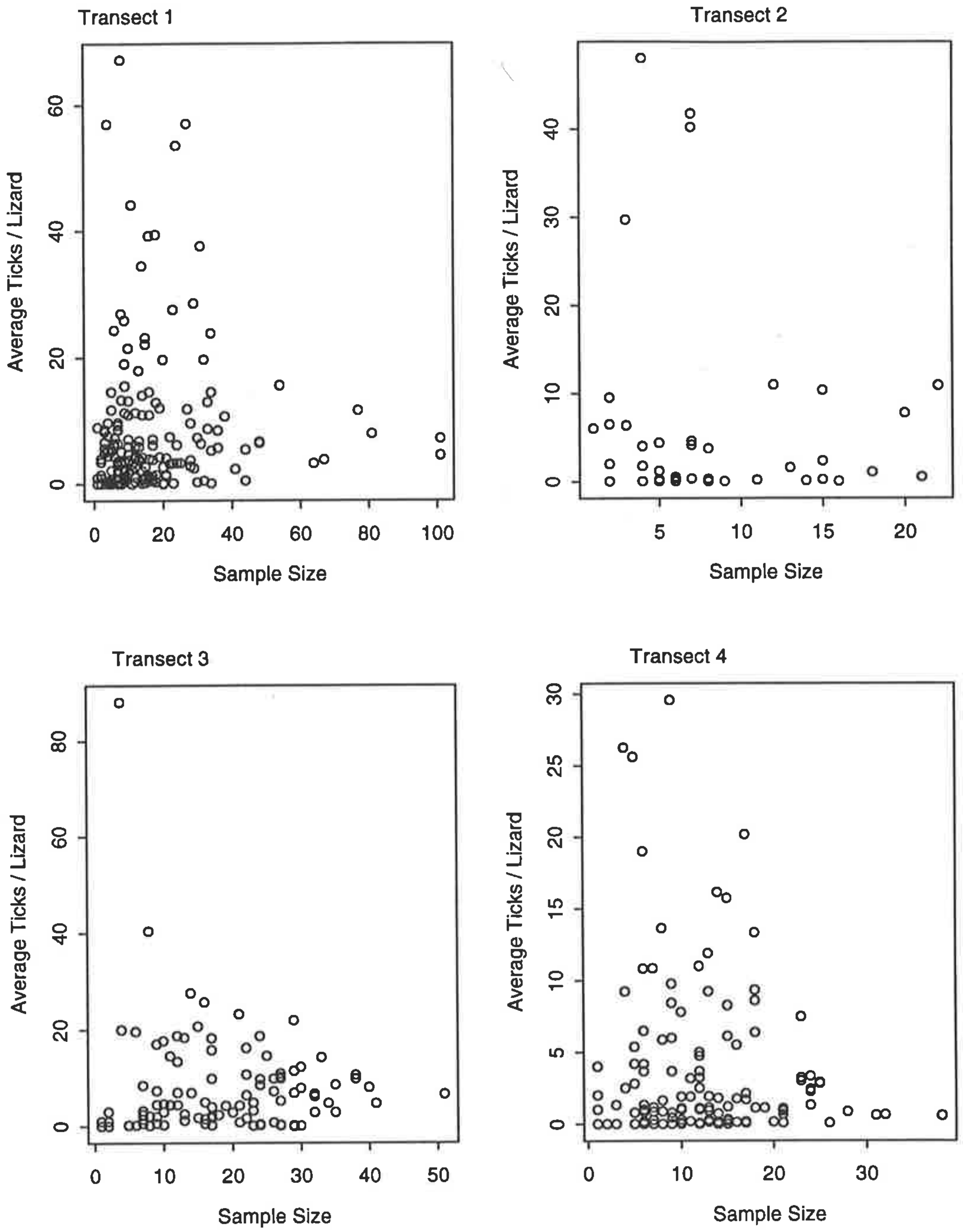

Figure 4.6 Tick abundance as a function of sample size. Each point is a location/year combination at the population scale. Transect 5 is not shown, but has a similar pattern.

Distribution of Ticks among Hosts

It might be possible to summarise the ecological processes that determine the distribution of ticks among lizards with a parametric distribution. If the parameters of the distribution have physical interpretations, then some insight into the variability of ecological processes across scales or through time can be gained. Counts of parasites among hosts are typically highly aggregated, with the variance being much larger than the mean, and these data are often summarised with the negative binomial distribution (Smith, 1994). The negative binomial can be derived from a physical model of a poisson (ie. random) process where the rate parameter has a gamma distribution (Hilborn & Mangel, 1997).

In this case, if ticks board lizards independently of each other, the number of ticks on a lizard would be a poisson distribution with a rate parameter *m*

$$\Pr\{N(t)=x\}=\frac{e^{-mt}(mt)^x}{x!} \qquad (4.1)$$

However, *m* is not a constant, because it will vary with the local tick abundance, the number of refuge sites, and the local host population abundance. If I assume that this variability in the rate parameter can be modelled with a gamma distribution with parameters *k* and *a*

$$\Pr\{m(t)=s\}=\frac{a^k}{\Gamma(k)}e^{-as}s^{k-1} \qquad (4.2)$$

then the negative binomial distribution will be a good description of the distribution of ticks among lizards (Hilborn & Mangel, 1997). The extra "clumping" parameter *k* describes the shape of the variability in the rate parameter *m*: if $k \leq 1$ the mode of the rate parameter is zero and the distribution tails off quickly, while if $k > 1$ *m* has a non-zero mode (Figure 4.7). *a* is a nuisance parameter when the poisson and gamma distributions are combined because $m = k/a$. If *a* is assumed to be constant, *k* will increase linearly with *m* and the slope will be *a*.

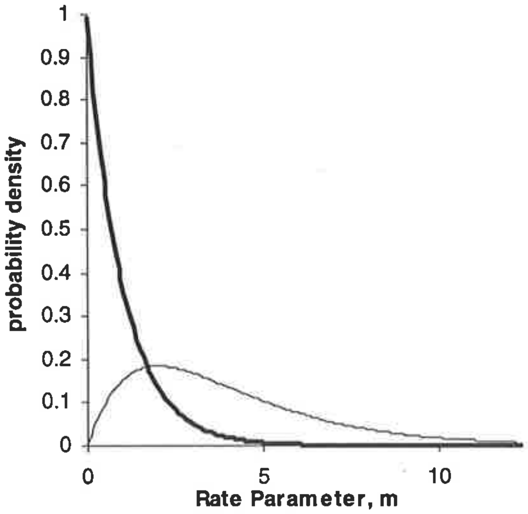

Figure 4.7 Two gamma distributions with the same mean. The mean rate parameter of the resulting negative binomial distribution, $m = k / a$. Thick line has $k = 1$, $a = 1$, and consequently $m = 1$. Thin line has $k = 2$, $a = 2$, and consequently $m = 1$.

I determined the best fit parameters for the negative binomial by minimising the negative log likelihood (Hilborn & Mangel, 1997) calculated as:

$$L(\mathbf{Y}|m,k)=-\sum_{i=1}^{n}\ln\left(\frac{\Gamma(k+Y_i)}{\Gamma(k)Y_i!}\left(\frac{k}{k+m}\right)^k\left(\frac{m}{m+k}\right)^{Y_i}\right) \qquad (4.3)$$

where **Y** is *n* observations of numbers of ticks on lizards, *m* is the mean, and *k* is the aggregation coefficient. I used the nlminb algorithm in S+ V4.0 to perform the calculations. I checked that the negative binomial model is a reasonable description of the data using *G*-tests (Sokal & Rohlf, 1981). High numbers of ticks were lumped together to ensure that all categories in the G-test were non-zero, with the same lumping used in all years for a given life history stage. I eliminated 1982 and 1983 from all these tests because the minimisation algorithm to encountered numerical difficulties with the smaller numbers of captures.

Results & Discussion

The frequency distribution of ticks among lizards at the landscape scale over all years is highly skewed with a mode of 0 and a median of 1 (Figure 4.8). The maximum number of ticks observed on a single lizard was 1060, but 95% of lizards captured have 30 or fewer ticks. Less than 1% of captured lizards had more than 100 ticks. The negative binomial distribution does not fit the data well, under-predicting the smallest and largest categories and over-predicting all others.

The lack of a satisfactory fit for the distribution of total tick numbers could arise from multiple causes. First, there could be variation in the parameters between years, over and above what can be incorporated by assuming a gamma distributed rate parameter for a poisson distribution. The second reason could be a failure of the assumption of independence between ticks. This is particularly likely to be false for larvae, because they will tend to be found in clumps wherever an adult female has laid eggs. I re-estimated the parameters of the total tick distribution within each year at the landscape scale. All but one year still do not fit a negative binomial distribution (Table 4.3). If the parameters are estimated for each of the three life history stages within each year, the negative binomial distribution does fit for most years (Table 4.3). The distribution of adults fits a negative binomial distribution most often, and the distribution of larvae fits least often. This intuitively matches the observation that larvae board lizards in the least independent fashion. The number of random processes that separate individual nymphs (engorgement, moulting, waiting for a host) and adults means that they are more likely to be boarding hosts independently of one another.

If the estimated parameters are in some way related to ecological processes underlying the observed distribution, it is of interest to see if they vary systematically with density or time. For all three life history stages *k*, the aggregation coefficient, increases with increasing density (Figure 4.9). In addition, the average density of all three life history stages show strong positive trends with time, matching the observation at the landscape scale for the total population.

The observation that *k*, the clumping parameter of the negative binomial, increases with density is interesting. This matches the intuitive expectation from the physical interpretation of the negative binomial given above: an increasing *k* means that the average rate at which ticks board lizards is increasing. This pattern has also been interpreted as evidence of a decrease in "aggregation" as a result of density dependent processes (Lampo & Bayliss, 1996). However, as highlighted above, the parameter *k* does not independently determine the degree of aggregation as measured by the variance to mean ratio (VMR). The variance also increases with the mean, as can be seen in the larger error bars at higher densities in Figure 4.4 and Figure 4.5. If the negative binomial distribution is a reasonable description of the distributions, then the increase in variance must be arising from the direct relationship between the mean and variance in this distribution (Hilborn & Mangel, 1997):

$$\sigma^2 = \mu + \frac{\mu^2}{k} \qquad (4.4)$$

If *k* is linearly related to μ, then the variance will still be linearly related to increases in the mean, because the net effect of a density dependent *k* reduces the square term to a linear term. Replacing *k* with $a \cdot \mu$ (ie. *k* is a linear function of μ with a slope of *a* and an intercept of 0), and rearranging (4.4) to find the variance to mean ratio:

$$\sigma^2 / \mu = 1 + \frac{1}{a} \qquad (4.5)$$

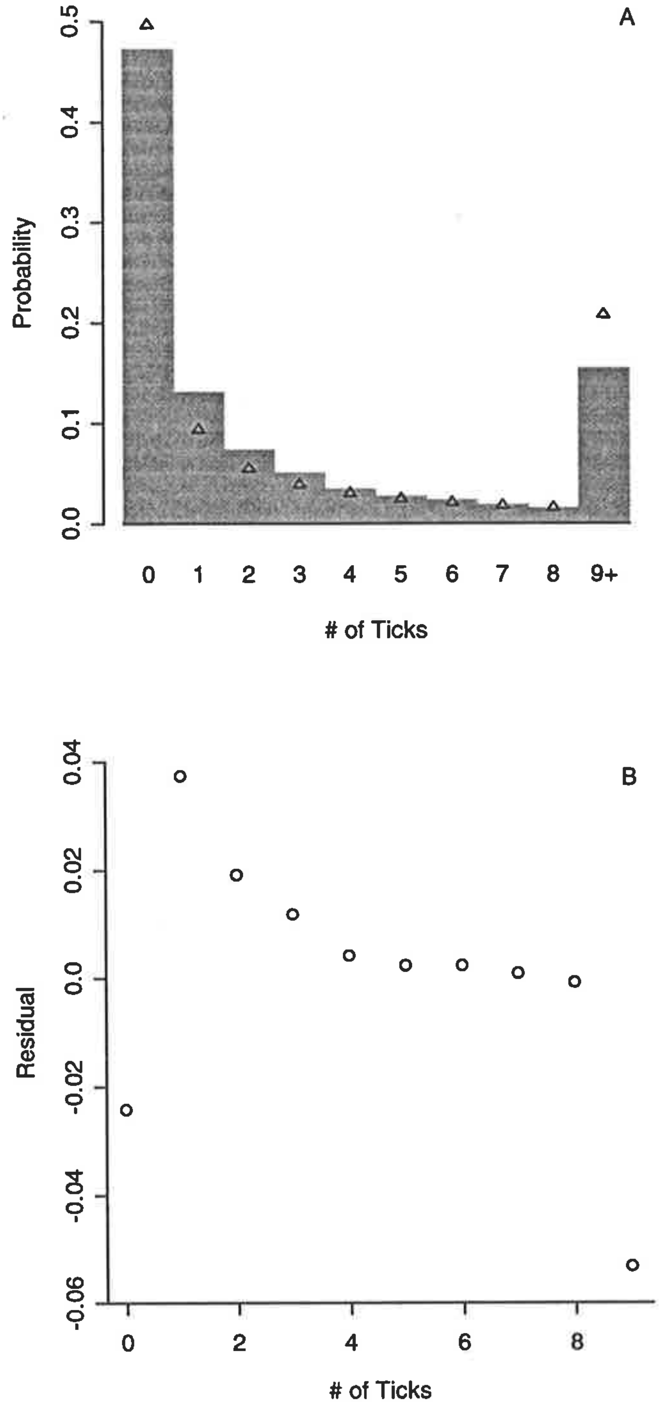

Figure 4.8 A) Frequency plot of the number of ticks per lizard in all years for the whole landscape. Triangles are the negative binomial distribution with parameters $m = 6.95$ and $k = 0.19$ fit by maximum likelihood. B) Residuals for the maximum likelihood fit. The data do not fit the expected distribution well ($G = 310$, df=7, $p << 0.0001$).

Table 4.3 Goodness of fit tests using the G statistic for each life history stage, and the total population in each year at the landscape scale. The degrees of freedom were calculated as n - m - 1, with n being the number of categories, m the number of parameters estimated from the data (m=2 in all cases). Counts higher than n were lumped into the nth category for the test. Tests significantly differing from a negative binomial distribution are highlighted by shading.

	Larvae		Nymphs		Adults		Total	
Year	G (8 df)	p	G (5 df)	p	G (1 df)	p	G (6 df)	p
1984	10.27	0.25	4.87	0.43	1.36	0.24	31.45	0.00
1985	12.83	0.12	6.45	0.27	8.80	0.00	51.31	0.00
1986	16.59	0.03	4.63	0.46	0.18	0.67	30.15	0.00
1987	25.02	0.00	5.11	0.40	1.68	0.20	30.35	0.00
1988	27.12	0.00	2.32	0.80	0.97	0.32	64.55	0.00
1989	27.67	0.00	14.80	0.01	3.07	0.08	55.03	0.00
1990	19.82	0.01	9.81	0.08	0.46	0.50	42.39	0.00
1991	14.84	0.06	7.41	0.19	0.18	0.67	43.40	0.00
1992	10.41	0.24	5.23	0.39	0.93	0.33	45.57	0.00
1993	9.96	0.27	3.52	0.62	2.45	0.12	8.51	0.20
1994	9.99	0.27	2.88	0.72	1.34	0.25	36.52	0.00
1995	10.52	0.23	33.26	0.00	1.51	0.22	32.78	0.00
1996	7.98	0.44	15.03	0.01	0.23	0.63	22.09	0.00
1997	13.03	0.11	9.94	0.08	1.63	0.20	22.09	0.00

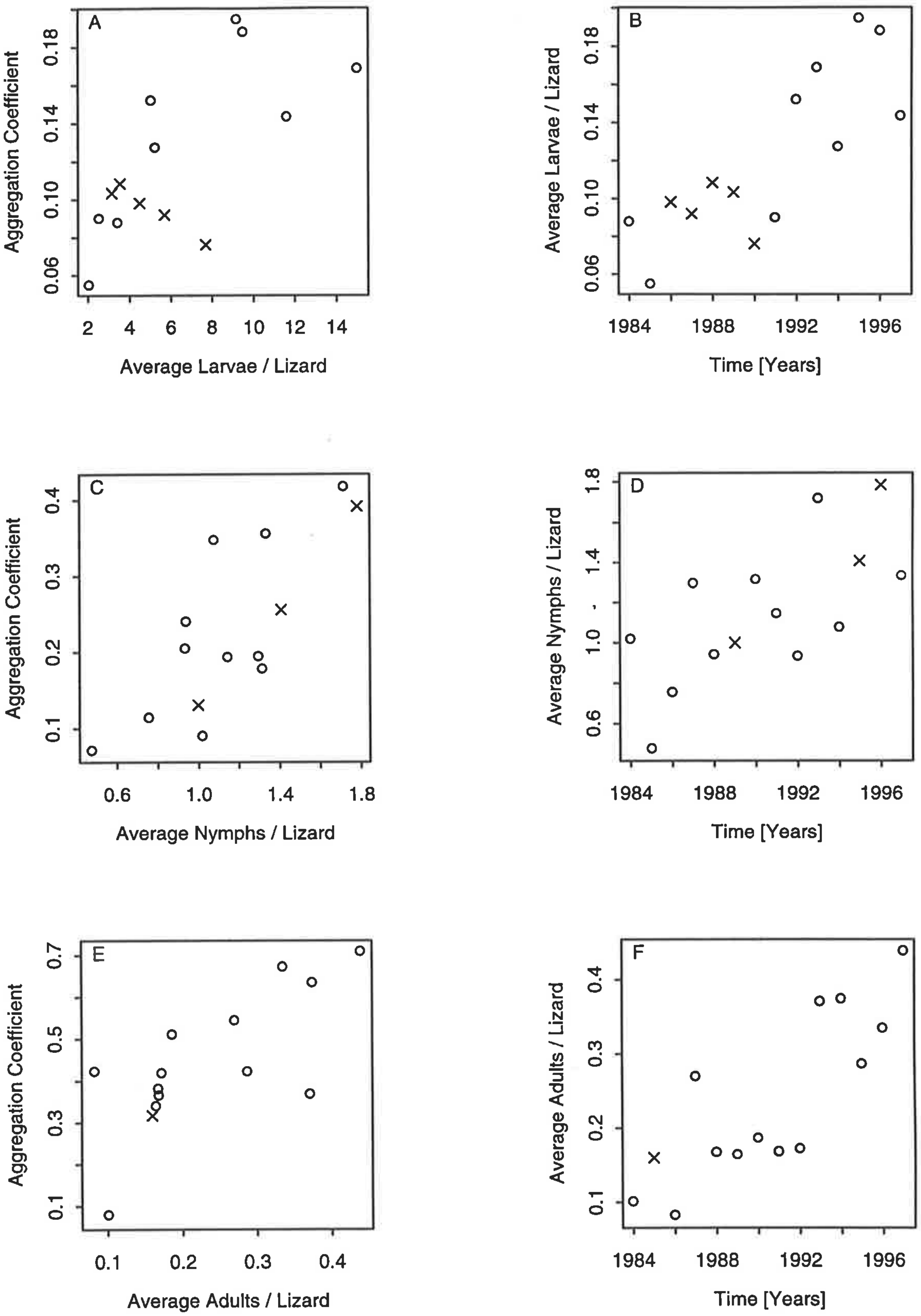

Figure 4.9 Plots of the average density vs. the aggregation coefficient (*k;* A, C, E) or time (B, D, F) for larvae (A, B), nymphs (C, D), and adults (E, F) at the landscape scale. Points marked with X do not fit a negative binomial distribution (Table 4.3). The correlations between the aggregation coefficient and average density are A) $r = 0.7$, B) $r = 0.78$, and C) $r = 0.72$. $p << 0.01$ for all three correlations.

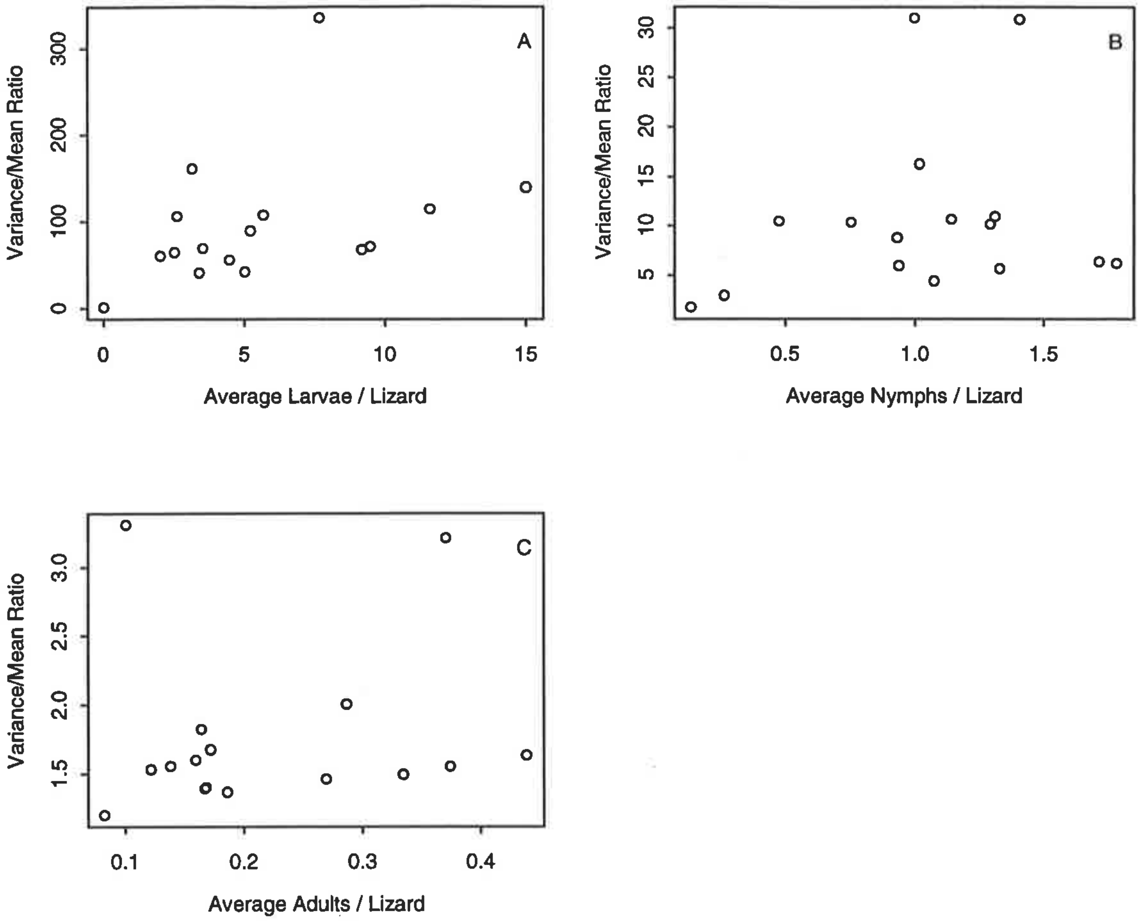

Figure 4.10 Variance/mean ratio as a function of tick density for each of the three life stages. Correlation coefficients, calculated with 1982 (lower left corner point in each plot) excluded: A) 0.28 ($p = 0.31$), B) 0.10 ($p = 0.74$), C) 0.11 ($p = 0.71$).

it is clear that a linearly density dependent k implies that the variance to mean ratio is not changing with density. Therefore the "dispersion" (sensu Anderson & Gordon, 1982) will not change with density if a is a constant, and in fact it does not (Figure 4.10). There is a hint of a positive trend for larvae, but it is not significant if the anomalous value for 1982 is excluded. The power of these correlations to detect weak effects ($r \approx 0.1$) is less than 30%. However, density dependent processes should lead to negative relationships (a decrease in VMR is a decrease in dispersion), and none of the calculated coefficients is negative. There does not appear to be any evidence that dispersion is changing in a manner suggestive of density dependent processes.

As noted in the introduction, a positive relationship between the mean and the aggregation parameter k can stabilise models of host-parasite dynamics (Kretzschmar & Adler, 1993), if increased parasite load increases host mortality. Unfortunately, there is no support in the *A. hydrosauri - T. rugosa* system for this assumption: Bull & Burzacott (1993) examined field data for evidence of impacts of tick load on host mortality and fecundity, and found no effect. Regardless of the underlying mechanism leading to density dependence in k, it will not lead to population regulation through host-parasite dynamics.

I conclude that the "density dependence" in the aggregation coefficient detected here has little or nothing to do with the main question of this chapter, population regulation. It arises as a simple consequence of a functional relationship between tick abundance and the probability of a tick boarding a lizard. This relationship might contribute to population regulation if it was non-linear, for example, if the probability of a tick boarding a lizard increased less at high densities than at low densities. Such a relationship might occur if lizard hosts tended to avoid areas with high tick abundance. Detecting such an effect in the current data seems unlikely, given the amount of variability. In the next section I will employ a range of methods for detecting signals of density dependence that is important for population regulation by looking for evidence of equilibrium population abundances in the time series.

Detecting density dependence in time series at multiple spatial scales

The detection of density dependence in time series data is a topic that has interested ecologists for nearly three decades. In this chapter I use three tests. The first two were proposed by Bulmer (1975), and correspond to testing the following random walk model:

$$x_{t+1} = x_t + e_t \qquad (4.6)$$

where x is the logarithm of the population size, and e is a normally distributed random variable with a mean of 0 and a variance σ^2, against the alternative

$$x_{t+1} = \beta x_t + e_t \qquad (4.7)$$

which is a density dependent model for $\beta \neq 1$. This model corresponds to the following equation in untransformed population densities:

$$X_{t+1} = E_t X_t^{\beta}\,. \qquad (4.8)$$

where β=1 gives the density independent model, and E_t is log-normally distributed with a mean of 1. The equilibrium value X^* that a population following this model will tend to is given by:

$$X^* = \overline{E}^{\,1/1-\beta} \qquad (4.9)$$

where E is the arithmetic expectation of the random growth rate. The unusual thing about this model is that in the absence of a trend (E = 1), the equilibrium population size is always 1, regardless of the strength of density dependence. Rewriting the equation in this way also makes clear the definition of density dependence these models are based on: a density dependent population is one with an equilibrium population size. A density independent population has no equilibrium; setting β=1 in (4.9) shows that the equilibrium is undefined.

The test statistic, R, is based on the correlation coefficient between x_{t+1} and x_t:

$$U = \sum_{t=1}^{N-1} \left(x_{t+1} - x_t\right)^2 \qquad (4.10)$$
$$V = \sum_{t=1}^{N} \left(x_t - \overline{x}\right)^2$$
$$R = V/U$$

Bulmer also developed a second test for use in the presence of measurement error, which tends to increase the likelihood of detecting density dependence. The statistic is R^* = W / V where:

$$W = \sum_{t=1}^{N-2} \left(x_{t+2} - x_{t+1}\right)\left(x_t - \overline{x}\right). \qquad (4.11)$$

The significance values for both tests are only available at the 5% and 1% levels, calculated by simulation in Bulmer (1975).

Bulmer's tests have been found to be ineffective in the presence of temporal trends (Pollard et al., 1987), and given the clear trends at larger scales in the data these tests will be suspect. Pollard et al. (1987) developed a randomisation test based on comparing model (4.6) with

$$x_{t+1} = r + \beta x_t + e_t \tag{4.12}$$

where r is a trend or drift parameter and all other symbols are the same. The untransformed version of this is the same as (4.8), except that now the log-normal random variable E_t has a mean different from 1. The test is carried out in several steps. First, I calculate the observed sequence of between year differences, $d_t = x_{t+1} - x_t$, and generate a large number (I used 1000) of random permutations of this sequence. Next, I use each sampled sequence of d_t's to calculate the x_t's that would result from that sequence of density changes, starting with the actual x_0. Finally, calculate the correlation coefficient r between the sampled sequence of d_t and new sequence of x_t. This generates a distribution of correlation coefficients against which the observed correlation coefficient can be compared. If fewer than 1% of the randomised correlation coefficients are less than the observed correlation coefficient, then I say that the test is significant at the 1% level. The power and Type I error rate of this randomisation test have not been considered in the presence of sampling error.

Results & Discussion

At the landscape scale, neither of Bulmer's tests detect density dependence ($R = 0.87, p >> 0.05$; $R^* = 0.062$, $p >> 0.05$). Neither of these tests is particularly conclusive, because the observed steady increase with time in tick abundance biases both tests against detecting density dependence (Pollard et al., 1987). Pollard et al.'s randomisation test was specifically designed with this scenario in mind. Nonetheless, the Pollard et al. test confirms that there is no observed density dependence at the landscape scale ($r_{observed} = -0.57, p = 0.131$).

At the transect scale, I eliminated 1982 for all transects. 1982 has the lowest number of captures, and also has a non-zero estimate only for transect 1. Transect 5 is also shorter than the other time series with $N = 13$. Bulmer's R ranged from 0.45 to 0.88, all of which are well above the 5% significance value of 0.0366. Bulmer's R^* ranged from -0.09 up to 0.32, which are well above the 5% significance value of -0.48 with $N = 15$. Pollard et al.'s test is significant at the 5% level for transects 1 and 2, and just outside the 5% level for transect 4 (Table 4.4). Thus there is density dependence at this scale, but the strength of the effect varies in space.

I did not attempt to analyse any of the population scale sequences for density dependence, because a single zero or missing value make the test impossible.

Concluding that density dependence is weak or absent at larger scales is a conservative conclusion, because time series analyses used are biased towards detecting density dependence in the presence of sampling error (ie. the probability of a Type I error increases with sampling error; Bulmer, 1975). Given the highly aggregated distribution of ticks among lizards, the sampling error is quite high, especially in those years with smaller numbers of captures. The finer the scale, the greater the sampling error (fewer captures per point), and this trend is directly correlated with the increased detection of density dependence at the smaller transect scale. The effect that sampling error has on the results of time series analyses has been generally ignored in recent studies using these methods (eg. Woiwod & Hanski, 1992).

Table 4.4 Pollard et al.'s tests of density dependence for each transect scale time series. N is the length of the time series used. The observed correlation is between the log density x_t and d_t, the difference in log densities (see methods). Significance levels are the lowest, 1% quantile, and 5% quantiles from 1000 random permutations.

			Significance level		
Transect	N	Observed correlation	0%	1%	5%
1	15	-0.69	-0.81	-0.76	-0.68
2	15	-0.75	-0.86	-0.80	-0.71
3	15	-0.49	-0.83	-0.77	-0.68
4	15	-0.68	-0.85	-0.77	-0.69
5	13	-0.63	-0.90	-0.84	-0.72

Before concluding that a non-significant result is an acceptance of the null hypothesis, it is important to consider the power of a test. The power of the Pollard et al. test may decrease with scale (Ray & Hastings, 1996), although this has not been explicitly calculated for the Pollard et al. test. However, for time series of 15 years the power of the Pollard test is quite low, less than 30%. In short, it is not possible to confidently conclude that density dependence does, or does not, exist at any spatial scale from the time series data presented.

The weaknesses of time series analysis for density dependence are not suffered to the same extent by regressions of mortality or development rates on density within single generations. These are the basic mechanisms that will lead to density dependence in time series, and I turn to this individual level analysis next.

Detecting density dependence at the individual lizard scale

Over the three year period from March 1983 to August 1985, Chilton (1989) kept records of the number of larval ticks of both species attached to lizards to obtain stocks of engorged larvae and unengorged nymphs for laboratory experiments. Fourteen *T. rugosa* were infested in this way with between 200 and 982 larvae. Ticks were attached by placing a known number of larvae in a calico bag together with the host, and then kept in the dark for 24-48 hours at 22°C. Lizards had their mouths taped so that ticks could not be consumed. The number of larvae successfully attaching was estimated by counting the ticks that remained in the bag after the host was removed. Hosts were then maintained on a 12:12 photoperiod in individual cages with wire floors. Ticks that engorged and detached from the host fell through the floor, where they were collected.

Originally, Chilton (1989) analysed the data with a Mann-Whitney U test to compare the proportion of successful engorgers with the proportion of successful engorgers in the second species, *Amblyomma limbatum*. Here I use generalised linear modelling (GLM; McCullagh & Nelder, 1983) to analyse how the probability of successful engorgement varies with the number of attached larvae within a single species. I use a binomial error distribution with a logit link. This is analogous to a single generation key factor analysis (Varley et al., 1973), and is similar to the regression methods commonly employed by both advocates (eg. Hassell et al., 1987) and critics (eg. Strong, 1989) of density dependence. The results must be interpreted with caution as the study is uncontrolled, and spread over many months.

Results & Discussion

Observations of the proportion of tick larvae successfully engorging in the lab suggest a density dependent response at high numbers (Figure 4.11). A binomial GLM for all the data is significant, however it explains only 14% of the deviance in the data, and the deviance residuals are strongly skewed (Table 4.5). For 4 of the 14 hosts the proportion engorging was less than 1%, substantially lower than that observed on other hosts. Presumably this indicates the presence of between host variation in quality for larva. When these hosts are eliminated from the analysis the linear model explains 61% of the deviance, and the skew in the residuals is greatly reduced (Table 4.6). For *A. hydrosauri* larvae the final model is

$$p\{successfulengorgement\} = \frac{e^{\beta}}{1+e^{\beta}} \qquad (4.13)$$
$$\beta = -0.243 - 0.002(\#of\ ticks)$$

This is circumstantial evidence of density dependence in the probability of engorgement success in larvae at the scale of individual lizards. However, the tick densities at which this would have a significant impact on the success rate are rare in the field; a larva on a lizard with 100 other ticks has a 39% chance of success compared with 44% for a larva alone. Densities of this magnitude or greater occur less than 1% of the time in the observation data set, suggesting that this level of density dependence is not contributing strongly to population regulation.

It is also unclear from these data what underlying mechanism is contributing to the observed effect. For example, if it arises from the presence of a limited number of attachment sites on a lizard, then the presence of ticks in any life stage at the time of attachment will influence the probability of success. Alternatively, the effect could take place after attachment, and be related to host physiology or immunological responses. The presence of obvious outliers (the hosts with less than one percent of larvae successfully engorging), and the fact that the proportion succeeding is based on the number actually attached suggests a post-attachment mechanism might also be operating. The outliers are also a clear indication that there is heterogeneity among hosts in the rate of successful engorgement, which as described in the section on among host distributions will tend to increase over-dispersion in the population. In contrast, the density dependence in engorgement success would lead to under-dispersion.

There are other possibilities for density dependence at scales smaller than the population including: density dependent predation by ants in refuges, density dependent engorgement success of nymphs or adults, and density dependent effects of mate availability on fertilisation of adult females. The frequency and magnitude of all of th0ese effects is unknown.

Overall Conclusions

This chapter has been concerned primarily with population regulation via intra-specific competition. This would seem unlikely to contribute to the maintenance of the parapatric boundary between *Aponomma hydrosauri* and *Amblyomma limbatum* (Bull & King, 1981). However, if the mechanisms involved in competition at the scale of individual lizards involve limited numbers of attachment sites, then this mechanism could lead to inter-specific competition as well. These two tick species do overlap in the distribution of attachment sites on hosts, indicating that the opportunity for competition exists, although there are some differences in the preferred sites of attachment (Bull et al., 1989; Chilton et al., 1992). Laboratory experiments designed to look for competition found no inter- or intra-specific competition in larvae or nymphs in the proportion attaching (Bull et al., 1989). However, the range of densities and the statistical tests (ANOVA of arc-sine transformed data; N < 10) used

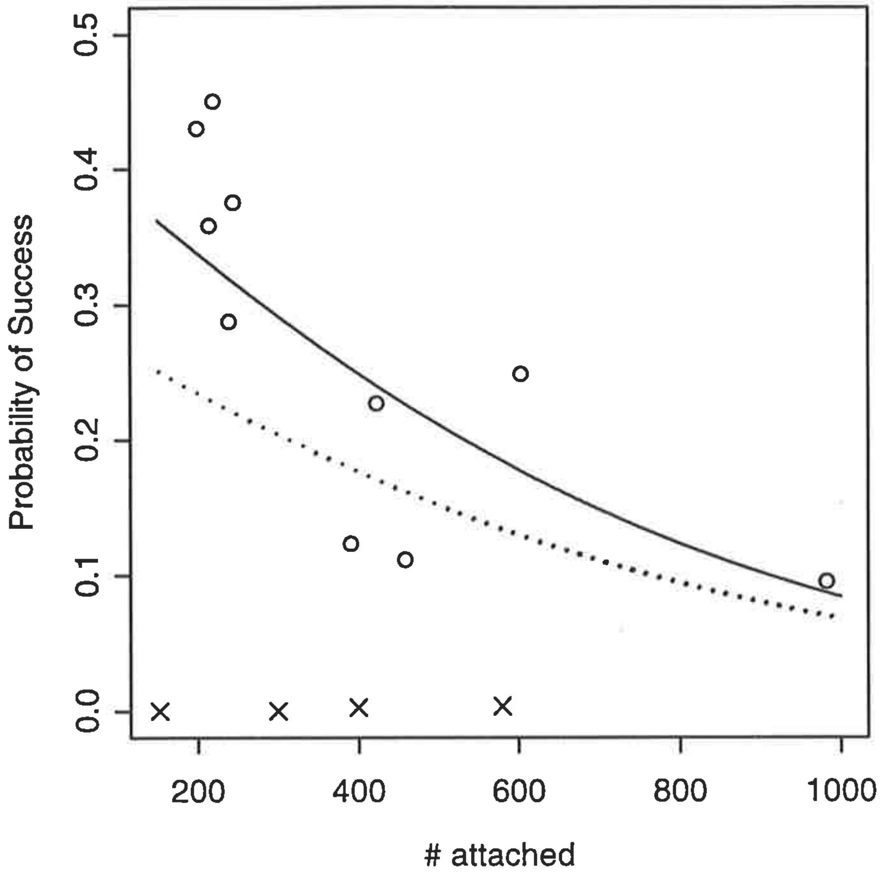

Figure 4.11 Proportion of successful engorging larvae as a function of the number of larvae attached to a single lizard. Each point is a different host. Points with less than 1% success are indicated with crosses. The dotted line is the predicted probability of success using all the data, and the solid line is the predicted probability using only the points indicated with circles.

Table 4.5 Analysis of deviance table for the binomial regression on all observations of larval engorgement success in Figure 4.11. The probability is for a Log-ratio test with 1 degree of freedom. The five-number summary of the deviance residuals is given in the bottom row.

	df	Deviance	Residual df	Residual Deviance	Pr(Chi)
NULL	13			886.18	
# attached	1	127.69	12	758.48	0
	Minimum	1Q	Median	3Q	Maximum
Residuals	-12.15	-7.80	2.63	5.18	7.91

Table 4.6 Analysis of deviance table for the binomial regression on the reduced number of observations of larval engorgement success in Figure 4.11. The probability is for a Log-ratio test with 1 degree of freedom. The five-number summary of the deviance residuals is given in the bottom row.

	df	Deviance	Residual df	Residual Deviance	Pr(Chi)
NULL	9			330.6486	
n.attach	1	201.389	8	129.2595	0
	Minimum	1Q	Median	3Q	Maximum
Residuals	-6.38	-0.95	0.86	2.52	4.43

in that study imply that the power to detect small differences in the proportion engorging was low. The statistics I have used here are designed to analyse proportions, and the range of densities is much greater. Very weak competition is able to generate and maintain a parapatric boundary (Bull & Possingham, 1995).

The detection of density dependence in field data is fraught with problems (Reddingius, 1990; Solow, 1990). Data sets as extensive in time and space as the one analysed in this chapter are rare. Even here, the variability in the system is extreme, and I cannot draw firm conclusions about the existence of density dependence at any scale. Solow and Steele (1990) demonstrated that even moderate density dependence was unlikely to be detected by time series methods in series of less than 30 years. The only other attempt on this temporal scale is by Woiwod and Hanski (1992), using data on thousands of species of moth and aphid from the Rothamstead Insect Survey. They concluded that density dependence was widespread, but did not examine how or if the prevalence changed with the spatial scale of the analysis.

In conclusion, I believe that the population of *Aponomma hydrosauri* near Mt. Mary, SA appears to be increasing with time over the duration of the study, at least in some areas. There is weak evidence of density dependence, and it appears to decrease with increasing spatial scale. At the level of individuals, there is correlative evidence of density dependence in at least one important life history process, engorgement by larvae. However, the densities over which this process would have a substantial effect are uncommon in the field. Whether or not this process alone can lead to regulation of tick densities to observed levels must be evaluated with a population model. The results of this chapter will be useful as benchmarks against which to compare the output of a model that incorporates the basic processes thought to be important to tick biology.

Chapter 5 Measuring the contribution of spatial and temporal variation in process rates to population regulation

Introduction

The results of Chapter 4 have raised a problem. There is some evidence of density dependence at the level of individual hosts. However, at the level of whole populations there is only sketchy evidence for density dependent regulation, confounded by problems of low power and biased tests. The question is how to reconcile the observations: a persistent, widespread population on the one hand, and uneven evidence (a generous assessment) for density dependence on the other. Can the individual level mechanisms of density dependent engorgement success on lizard hosts prevent outbreaks at the landscape scale? What mechanisms might generate the kind of dynamics observed? The primary question in this chapter is whether long term persistence in the tick population is possible when density dependent mechanisms are weak or absent. I address this problem by constructing a spatially explicit, individual based simulation model of the ticks and their lizard hosts.

Hanski et al. (1996) examined this question for spatially distributed populations with an analytical model of a metapopulation of random walking sub-populations. They argued that unlinked local dynamics could generate the appearance of a stable, persistent population with density dependence occurring only rarely. The form of density dependence in their model was a "ceiling" (K), above which sub-population abundance could not go. If a sub-population did fluctuate to a level above the ceiling, it was reflected down by the amount it exceeded the ceiling. They analysed the relationship between the variation in growth rates of sub-populations and the size of sub-populations on the persistence time and the frequency of density dependence. The latter was measured as the probability of reaching or exceeding the ceiling. They found that metapopulations could persist (defined as average time to extinction >22,000 generations) with very low frequencies of density dependence (<0.001 "hits to the ceiling"/generation), if the average growth rate was just slightly negative, the variance in growth rate was "small", and sub-populations were large (K = 1000). Their "small" variance leads to a coefficient of variation (CV) of growth rate greater than 790% for the persisting populations. Increasing the average or the variance of growth rate rapidly increased the frequency of density dependence, while decreasing either parameter quickly shortened the average time to extinction. The parameter values where populations persist without density dependence for a long time are therefore extremely limited. The mechanism for density dependence is also awkward, and unlikely to apply to arthropod populations, although it may be reasonable for territorial species. A similar metapopulation model based on host-parasitoid dynamics has been analysed by Taylor (1998), with similar conclusions.

If density dependence is not detected or absent in a population, there may be other factors leading to regulation. The notion that temporal variation in abiotic factors could regulate population abundance was first argued by Andrewartha and Birch (1954). This seminal work forced a rethink of the topic of population regulation by ecologists. However, it has been suggested that one of the classic examples of density independent population dynamics discussed by Andrewartha and Birch, rose thrip (Davidson & Andrewartha, 1948), does in fact show evidence of density dependence (Varley et al., 1973). Previous work has clearly demonstrated that nearly all developmental and mortality rates of the tick *Aponomma hydrosauri* vary significantly with temperature and/or relative humidity (RH; Chilton, 1989). The South Australian environment has variable temperatures, both within and between seasons. It is at least possible that variation in temperature through time leads to population regulation, by occasionally resetting populations back to very low levels and/or slowing growth at crucial times of year. Ultimately, density dependence must operate at some level. Recent contributions to the debate have begun to take the position that it is the *relative* contribution of density dependent and density independent processes to population regulation that matter (Leirs et al., 1997; Bonsall et al., 1998), and this relative contribution can vary in both time and space.

Process rates can also vary along another set of dimensions, space. Kareiva (1990) elegantly summarised the theoretical work on spatial variation, and posed the question, "when does space matter?". Classical metapopulation models show that assemblages of patches will not be completely full when there is some probability of local extinction (Levin, 1974). However, these models often make implicit assumptions about strong density dependence operating within patches (Diekmann et al., 1988). A plethora of spatially explicit models have arisen in recent years, but few have addressed the issue of spatial variation in process rates. The primary focus of these papers has been on the intrinsic generation of spatial variation as a result of self-organisation. In all cases, space is limiting, providing a hard upper bound on population size. This effect is obvious in the model used in Chapters 2 and 3, where increased mortality during dispersal from local crowding regulated populations to less than the maximum possible size.

A more interesting question is whether or not development or mortality rates that vary in space can lead to regulation without hard limits. In the case of the tick, *A. hydrosauri*, variation in space can arise intrinsically because of the interaction between it's main host, the lizard *Tiliqua rugosa*, and the host's overnight refuges, primarily bluebushes *Maireana sedifolia* at the Mt. Mary study site. If the refuges are randomly dispersed across the landscape, there will be some host home ranges where the number of refuges is above average, and some where it is below. When there are fewer refuges, lizards will visit individual refuges more frequently, and this will benefit ticks. Superimposed on this variation is random variation in the lizard population, both in space and time. The average refuge or lizard density may respond also to extrinsic spatial variation, such as soil type, rainfall, or competition from other plants. The variation in lizard population density is also quite dynamic in nature, and it seems reasonable to suggest that these density independent fluctuations could regulate tick populations. The basic question of this chapter is whether or not population regulation that is primarily density independent appears as an "emergent property" of the system when spatial and temporal variation at the individual level is incorporated.

Before the question of the existence of population regulation can be addressed, it is important to define, quantitatively, what conditions constitute a regulated population. This is particularly difficult for populations that fluctuate dramatically, and has generated some heated debates in the literature (eg. Wolda, 1989; Berryman, 1991; Krebs, 1995). Much of this debate centers around whether or not there is some kind of attractor, or equilibrium, influencing the dynamics of populations. For my purposes here I will use a simplified version of stochastic boundedness defined by Chesson (1978). "If $Z(t)$ is the population size at time t, then the population is stochastically bounded if for every positive probability ε there are numbers $U_\varepsilon < \infty$ and $L_\varepsilon > 0$, such that for any t, $Z(t)$ is greater than L_ε with probability at least $1-\varepsilon$ and less than U_ε with probability at least $1-\varepsilon$" (Chesson, 1978). Note that this definition excludes the possibility of extinction. Chesson (1978) noted that it is possible to admit extinction by weakening the lower bound to the condition that there is some probability less than one that the population is greater than zero. This definition is important, for it emphasises equally the upper and lower boundaries of population size. Models that include some kind of density dependence (eg. Hanski et al., 1996; Taylor, 1998) have implicitly focused on persistence as avoidance of the lower boundary. It should be possible to apply this definition directly to both models and empirical data (Chesson, 1978); in this chapter I have taken the simpler course of defining a fixed upper boundary, and associating the failure of population regulation with exceeding this boundary.

In this chapter, I address the question of population persistence in the absence of density dependence in several stages. I construct a spatially explicit, individual based model (IBM) of tick population dynamics, and consider how spatial and temporal variability influences regulation of the population within limits. At each stage I add different sorts of variation, and consider their effect on the average and variance of population growth rates. Finally, I generate output from a "virtual ecologist", allowing comparisons between the model and the empirical time series described in Chapter 4.

I begin by describing the empirical data used to parameterise the model. Then I describe the basic model without temporal or spatial variation in refuge quality, and examine the results. For each stage of model development I describe the changes to the model structure and then consider the impact on the results.

Empirical Data

Here I describe the empirical data that I use to parameterise the model. The population observations of *A. hydrosauri* were described in Chapter 4. This data set will be used to make qualitative comparisons with the model output. In Chapter 7 I calculate Jolly-Seber estimates of lizard density near Mt. Mary, South Australia (SA) from the same random capture data. Assuming that the random capture transect is sampling lizards from a 400 m wide strip (based on 200 m diameter home ranges on either side of the transect), lizard density ranges from 15 to 420 lizards / km^2. This range of densities is comparable with that estimated from the same data by other means (30 - 550 lizards / km2 Bull, 1995). The median lizard density was 100 lizards / km^2. Below I describe the other datasets involved: 31 years of temperature data from a site in the Riverland of SA, one season of temperature records from refuges in the field, laboratory experiments on life history parameters, and field measurements of refuge density.

Temperature variation within and between years

Average daily temperature in the field is highly variable over the length of a season (Figure 5.1). In addition, the temperature is autocorrelated (Figure 5.2). To simplify the use of these data in the model, I defined five temperature categories. The five categories ($T < 15^0\mathrm{C}$; $15^0\mathrm{C} \leq T < 20^0\mathrm{C}$; $20^0\mathrm{C} \leq T < 25^0\mathrm{C}$; $25^0\mathrm{C} \leq T < 30^0\mathrm{C}$; $30^0\mathrm{C} \leq T$) were chosen based on the availability of information about the response of survival and development to temperature (see below).

Thirty-one years (1967-1998) of daily minimum and maximum temperatures measured at Eudunda, SA approximately 30 km SW of the study area are available. The maximum temperatures in Eudunda in 1997 is highly correlated with the average daily temperature measured in bluebush refuges at the study site ($T_{avg} = 3.4057 + 0.6641T_{max}$, $R^2 = 0.87$, $F_{1,194} = 1345$, $p << 0.001$). I used this regression equation to predict average daily temperatures at the study site for 31 seasons. I use these temperatures to generate sequences of random seasons drawn with replacement from this set. The sequence of days within each season is used unmodified in order to include the effect of small scale correlations that are present in the weather.

Laboratory measurements of life history parameters

Chilton (1989) conducted extensive measurements of the response of life history parameters of *A. hydrosauri,* such as development time and survival, to temperature and humidity. In general, these experiments involved placing ticks on lizards or in vials, and then holding them under the appropriate conditions until the appropriate developmental process was complete. The times to engorge, develop, or die were recorded to the nearest day. Where possible, I calculate the baseline parameters from the observations for ticks held at 21^{0}C and 50-55% relative humidity (RH). The basic averages and standard deviations are given in Table 5.1. Chilton (1989) only reports standard errors in his results, so I estimate standard deviations for development times etc. by multiplying the standard errors by the square root of the sample size.

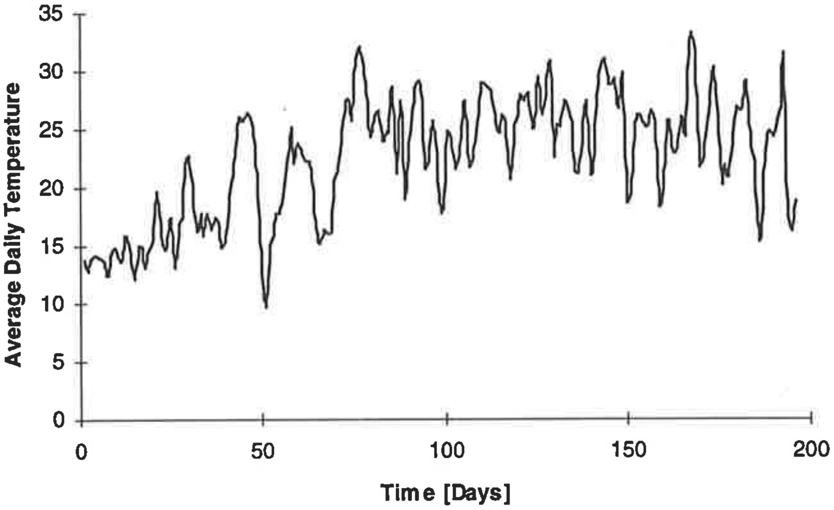

Figure 5.1 Average daily temperature in a bluebush shrub at Mt. Mary's, SA, 1997 - 1998 recorded from data loggers in the litter layer of six bushes. Temperature was recorded at 10 minute intervals, and the average over 24 hours is shown. Day 0 is September 9.

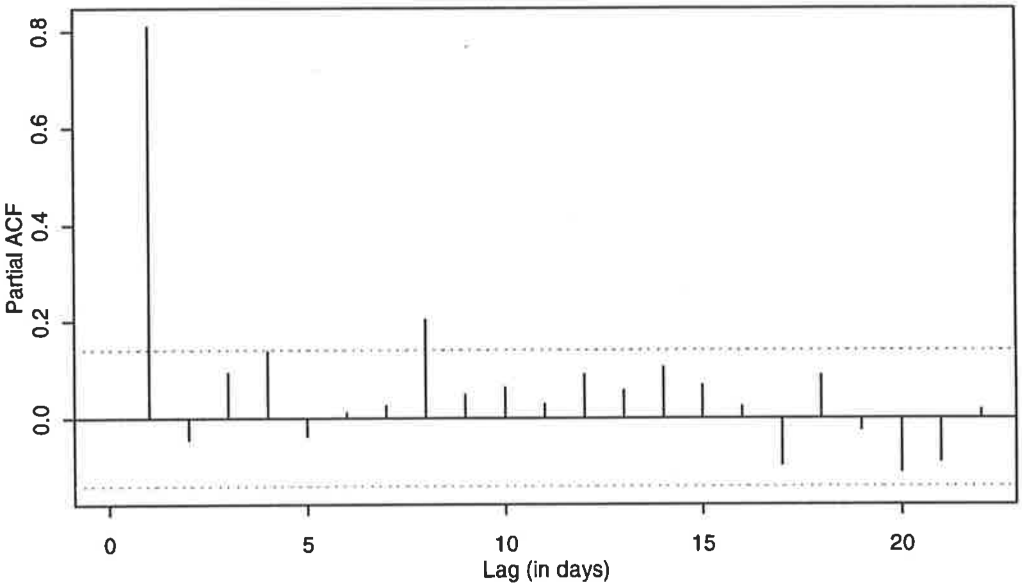

Figure 5.2 Partial autocorrelation between temperature in a bluebush refuge Lag days apart (data from Figure 5.1). Dotted lines indicate the magnitude of significant correlations. Correlations at lag 1 and lag 8 are significant.

Table 5.1 Developmental, feeding, and mortality parameters used in the baseline model. All values are estimated from data in (Chilton, 1989), assuming temperatures of 21^0C and 50-55% RH. All means have units of days. Feeding times for adult females includes the time required to be mated. Values in italics were extrapolated from estimates for larvae; see text for details.

			Stage durations	
Stage	Location	Process	Mean [days]	SD
Egg	Refuge	Hatching	53	1.32
Unfed Larvae	Refuge	Waiting	13.8	4.9
Unfed Larvae	Lizard	Feeding	30.6	11.7
Engorged Larvae	Refuge	Moulting	21.9	4.07
Unfed Nymphs	Refuge	Waiting	*37.3*	*5.5*
Unfed Nymphs	Lizard	Feeding	22.7	16.7
Engorged Nymphs	Refuge	Moulting	28	7.34
Unfed Adults	Refuge	Waiting	*100*	*7.3*
Unfed Females	Lizard	Feeding	39	17.6
Engorged Females	Refuge	Pre-oviposition	55.2	8.44
Mature Females	Refuge	egg-laying	40	--

Chilton (1989) did not estimate the survival parameters for nymphs and adults at as wide a range of temperatures and RH as for was done for larvae. In the absence of sufficient data for rigorous statistical analysis Caswell (1989) recommends "no-holds barred" parameter estimation, on the basis that estimates derived in some objective fashion from observation are better than guesses. The average survival time of unfed adults is still a completely free parameter (ie. a guess). There are two estimates of nymph average survival time at 30^0C and 34^0C, both measured at 0% RH. I converted these into estimates for all temperature classes and 50-55% RH with the following process. First, average survival time for larvae as a function of temperature roughly fits a power law (Figure 5.3 A). Moreover, the exponent does not vary (much) with humidity, although the coefficient does. The change in the coefficient with increasing humidity is well described with a straight line (Figure 5.3 B). Assuming that the survival time/temperature relationship for nymphs has the same exponent as the average exponent for larvae, I can rearrange the power law equation to get two estimates of the coefficient for nymphs at 0% RH:

$$
\begin{aligned}
&\textit{average survival} = a \cdot e^{\textit{temperature}\cdot b} \\
&\therefore \quad a = \frac{\textit{average survival}}{e^{\textit{temperature}\cdot b}}
\end{aligned} \qquad (5.1)
$$

I set b=-0.091, and the observed average survival time was either 12.6 (30^0C) or 9.4 (34^0C) days. The average estimate of a is therefore 203.3 days/degree. This is the estimated coefficient of the temperature/survival time relationship at 0% RH for nymphs. I then used the slope of the coefficient/RH line calculated from larvae to calculate how the nymph coefficient would increase with increasing RH. For 50-55% RH the estimated coefficient is 254 days / degree. A higher coefficient means an increased survival time, commensurate with the intuition that ticks desiccate slower when the environment is moister. Finally, I calculated the average survival times for nymphs at RH=50-55% and all temperature classes using (5.1) with a = 254 and b = -0.091.

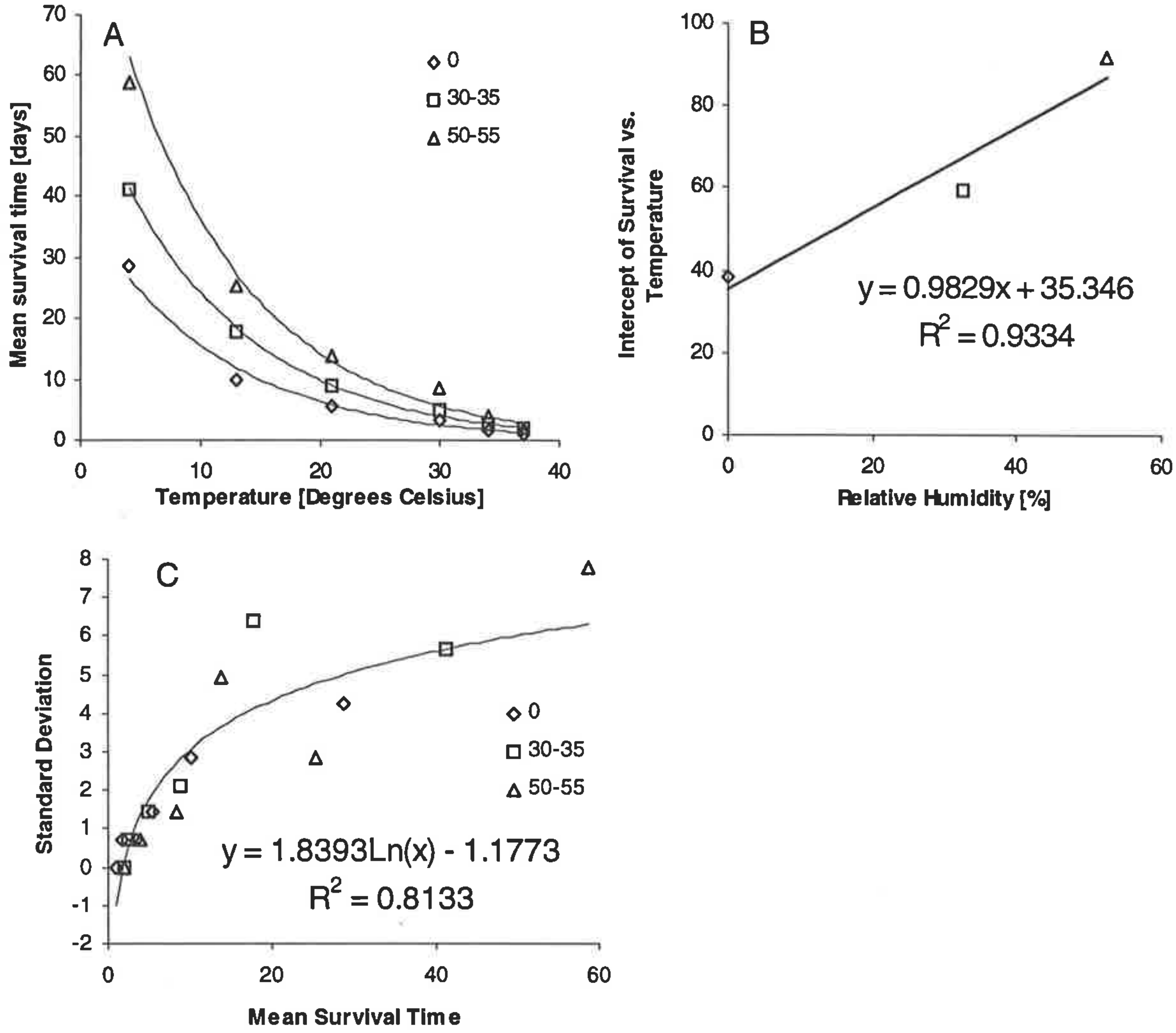

Figure 5.3 A) Exponential relationship between survival time for larvae and temperature for three different relative humidities. The equations are 0% RH: $y=38.4e^{-0.091x}$ (R^2=0.98), 30-35% RH: $y= 59.3e^{-0.090x}$ (R^2=0.99), $y=91.9e^{-0.094x}$. **B)** The intercepts for the three exponential curves in A as a function of RH. **C)** Relationship between the mean and standard deviation of survival time for nymphs at three different relative humidities. The R^2 values for all these curves must be treated with scepticism because of the small sample sizes.

The variance in survival times of both nymphs and adults was estimated from the relationship between the mean and standard deviation for larvae (Figure 5.3 C) across all temperature/humidity combinations. I applied this equation to the estimated mean survival times for nymphs and adults to calculate the standard deviations.

Temperature has a strong effect on average development and survival times of ticks. There are nearly as many ways of incorporating such variability in models of arthropod dynamics as there are models. For example, Logan et al. (1976) discussed an analytic model that allows non-linear changes in rate with temperature and is therefore superior to the degree-day concept which is inherently linear. Unfortunately the Logan et al. (1976) method relies on data across a wider range of temperatures than have been measured for ticks. I choose to discretise temperature into the five classes introduced above. This allows me to incorporate the observed non-linear temperature response with limited data. I assumed that temperature acts by increasing or decreasing the relative development or mortality rate. I calculated this relative effect for each of the five temperature classes by dividing the average time needed at the midpoint of the temperature class by that needed at the baseline temperature (Table 5.2). There was no development data for nymphs in the two lowest temperature classes, so I assumed that these relative rates were the same as for larvae. I discussed the estimation of survival times at different temperatures for nymphs above. I applied the relative rates for nymphs to adult survival, because there is no data of any kind for adult survival.

Table 5.2 Relative rates for development and survival for ticks in each temperature class. Bigger values indicate that development or mortality indices are moving faster. A value of zero means no development occurs. Values in italics were extrapolated from available data as described in the text. Development rates for adults females are for duration of the pre-oviposition stage.

	Relative Developmental Rate			
Temperature Class	Eggs	Larvae	Nymphs	Adult Females
$T < 15^0C$	0	0.24	*0.24*	0.20
$15^0C < T < 20^0C$	0	0.41	*0.41*	0.50
$20^0C < T < 25^0C$	1	1	1	1
$25^0C < T < 30^0C$	1.95	1.56	1.52	1.74
$30^0C < T$	0	1.71	2.04	2.75

	Relative Survival Rate		
Temperature Class	Larvae	Nymphs	Adults
$T < 15^0C$	0.24	*0.21*	*0.21*
$15^0C < T < 20^0C$	0.54	*0.48*	*0.48*
$20^0C < T < 25^0C$	1	*1*	*1*
$25^0C < T < 30^0C$	1.64	*2.28*	*2.28*
$30^0C < T$	3.54	*3.28*	*3.28*

Spatial distribution of refuges

Burzacott (unpublished data, 1998) tested the assumption that lizard refuges were distributed randomly on the landscape, and obtained preliminary estimates of refuge density. Every bluebush in a 30 m x 30 m plot at the Mt. Mary, SA study site was mapped to 0.5 m accuracy.

Each bush was also categorised as 1) not suitable as a refuge, 2) possible "day only" refuge, and 3) possible overnight refuge, based on the observer's long experience with finding lizards in bushes. This classification is clearly highly subjective. However, I will be using these estimates primarily to provide a context for interpreting the results of the model, rather than as accurate parameter estimates. In the model I am primarily concerned with refuges that are used overnight by lizards (these may also be used by lizards during the day).

There are no obvious patterns in the spatial distribution of bushes, although unsuitable refuges appear slightly clumped in the middle of the plot (Figure 5.4). I tested the hypothesis that bluebushes are randomly distributed in the landscape with a k-function analysis (Venables & Ripley, 1994). A k-function tests both the first and second moments of the spatial distribution (mean and variance), unlike a test of quadrat counts which only tests the first moment. The standardised k-function, L(t), is a straight line if the underlying point process is random, and is estimated with the equation:

$$K(t) = \frac{a}{n^2} \sum_{x \in D, d(y,x) \le t} \frac{1}{p(x,y)} \qquad (5.2)$$

$$L(t) = \sqrt{K/\pi}$$

where *D* is the region being sampled, *a* is the area of that region, *n* is the total number of observed points in *D*, *d(x,y)* is the distance between two points *x* and *y*, and *p(x,y)* is the proportion of a circle, centered on *x* and passing through *y*, that is inside *D*. Essentially the summation in (5.2) counts all points that are a distance *t* or closer to each point *x*, weighted by an edge correction factor. Points that are close to the edge of *D* will tend to have smaller proportions of the circle around them inside *D*. In the extreme, a point right in a corner of *D* would have *p(x,y)* = 0.25 for all *t*, and therefore an edge correction of 1 / 0.25 = 4. Tests of significant departures from randomness are performed by simulating a random spatial point process in a 30 m x 30 m square 100 times, and calculating an envelope for the k-function, a null model approach.

The estimated k-function for the 29 overnight refuges is well within a simulated envelope for a poisson process with 29 points in a 30 x 30 m square out to scales of 20 m (Figure 5.5). I conclude that using a random process to generate refuge locations in the model will be adequate.

If I only consider bluebushes classified as overnight refuges (n = 29), then I can calculate 95% "confidence limits" on the average number of refuges by finding the average that makes 29 the 97.5% quantile or 2.5% quantile of a poisson distribution. This observation is consistent with an average of 20 - 41 overnight quality refuges per 30 m x 30 m plot. This translates to an average of 22,000 - 45,000 refuges / km^2. The corresponding 99% limits are 18,900 - 50,000 refuges / km^2. Again, these values will not be used directly in the model, but provide a context for interpreting the results obtained at the parameter values I do use.

Individual Based, Spatially Explicit Model

In this section I use the data synthesised from the previous section to construct an individual based, spatially explicit model of tick population dynamics. From a tick's point of view, the landscape consists of the lizard hosts and their nocturnal refuge sites. There are *R* randomly distributed refuges in a 1 km x 1 km square, used by *L* lizards whose home ranges are centred on a randomly chosen refuge. All refuges within some distance *h* of the center refuge are included in the home range.

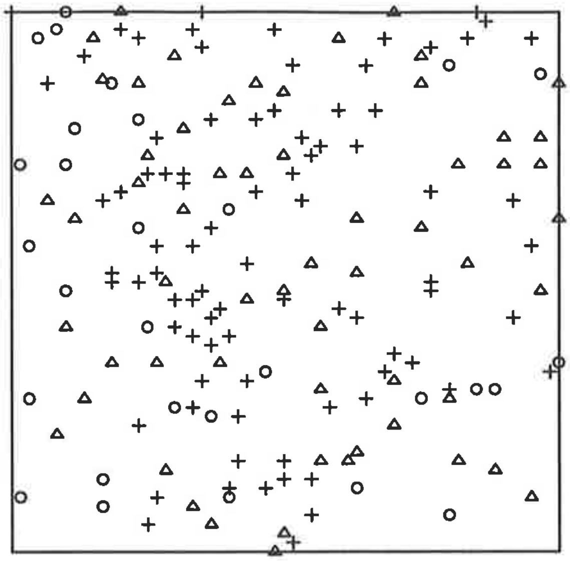

Figure 5.4 Spatial distribution of 172 bluebush refuges in the study plot. Daytime refuges (triangles, n = 59), overnight refuges (circles, n = 29), unsuitable refuges (pluses, n = 84). North is the top of the figure.

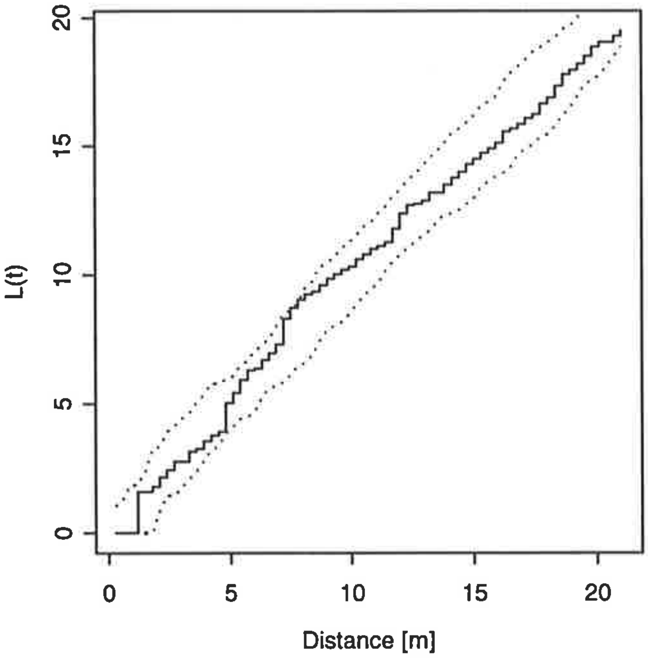

Figure 5.5 K-function analysis of the spatial distribution of overnight refuges in the study plot (n=29). The solid "staircase" is the observed K-function. The dotted lines are an envelope for the k-function from simulating a poisson process 100 times.

There are two time scales in the model. On the short time scale, movement of lizards, birth, development, and death of ticks is modelled each day. A series of days is then aggregated into a season, which I assume to be 210 days (1st September to 31st March) long. Development is frozen between seasons, under the assumption that autumn/winter temperatures are too low for tick activity. Ticks experience overwintering mortality, and a simplified form of population dynamics among lizard hosts also takes place between seasons. Later I introduce temporal variation in temperature both within and between seasons.

The choice of a single day as the basic time step is logical given the assumption that all significant movement of ticks on and off lizards occurs only in refuges entered at night. Ticks are adapted to detach in the nocturnal refuges of their hosts, where desiccation risks are lower, and the chances of finding another host are higher (Bull & Smyth, 1973). Boarding a lizard requires that a tick in the right life history state detects and moves toward a lizard that has entered a refuge. This movement ability is not great; in the engorgement success experiments described in Chapter 4 some ticks were unsuccessful in boarding lizards even when confined together with a host in a calico bag for 48 hours.

Within a single day, the model goes through several steps in the following order: ticks board lizards, lizards move between refuges, engorged ticks disembark from lizards, and ticks develop (Figure 5.6). I will now consider each step in more detail.

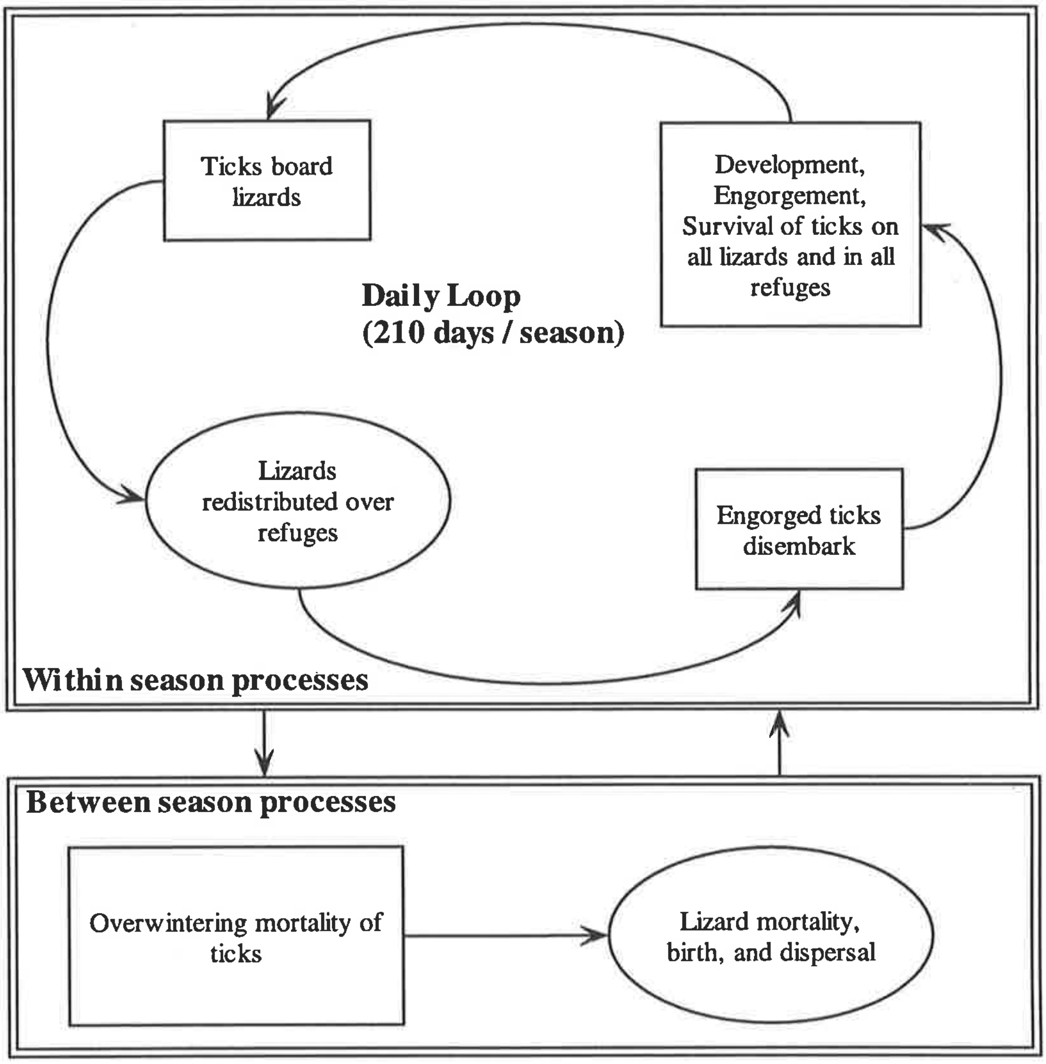

Figure 5.6 Flowchart of main model processes. Processes that are attributes of lizard population dynamics and behaviour which indirectly affect the ticks are placed in ovals, while processes directly affecting ticks are in rectangles.

Tick embarkation, Lizard movement, Tick disembarkation

At the beginning of a model day, all lizards are in the overnight refuges in which they spent the previous night. The model checks all ticks in lizard occupied refuges, and any ticks that are found to be in a suitable state (ie. unfed larvae, nymphs, or adults) are moved onto the lizard. As noted above, assuming that all suitable ticks board lizards is almost certainly an overestimate. If there is more than one lizard in a particular refuge, the number of ticks boarding a lizard will be binomially distributed with n trials (the number of ticks in the refuge in the correct life history stage) and probability of boarding b. For all lizards except the last lizard in the refuge, *b* is the reciprocal of the number of lizards using the refuge that night. All remaining ticks in the refuge board the last lizard listed as being present in that refuge on that night. The position within the refuge list is random with respect to landscape location, and age class of lizard. As adult ticks board a lizard, the sex of each is determined randomly assuming a 1:1 sex ratio. The final process that occurs in this part of the model is to assign the number of days each tick will require to engorge. This is a normally distributed variable with a stage specific mean and standard deviation. This engorgement "index" is used during subsequent model days to determine when a tick has successfully engorged in the tick development step.

In the next step of the daily cycle, lizards move to new refuges. Each day, lizards move from one overnight refuge to another overnight refuge chosen randomly with equal probability from among those in their home range. Note that this means they can spend consecutive nights in a refuge, and more than one lizard can occupy a refuge overnight. This is the simplest scenario that can be implemented in the absence of information about the distribution of different types of refuges, the way in which neighbouring refuges are utilised by individual lizards, and the way in which lizards may interact on contact with other lizards. I assume that individual lizards are capable of moving over their entire home range during the day, and that there is no systematic bias either toward or away from particular kinds of refuges, or from their previously occupied refuge.

One fact of lizard behaviour that contradicts the random uncorrelated movement behaviour of the lizards in the model involves mated pairs of lizards. A mated male and female have broadly overlapping home ranges. From September to early November, mated lizards closely track each other, often sharing the same refuge from night to night (Bull, 1988; Bull, 1990; Bull et al., 1991). Following mating, the partners separate and move independently within their home ranges. This tracking of mates would tend to slightly increase the average waiting time for ticks in refuges, increasing mortality rates when compared with the assumption of totally independent movement. For the purposes of this chapter, I ignore this complication, and all lizards move independently and randomly throughout the entire season.

The next step within the daily cycle is to drop off successfully engorged ticks into their new refuges. Essentially, ticks that are on lizards, which completed engorgement on the previous development step (ie. the previous night), are dropped off in the new refuge chosen by their host lizard.

The final step of the daily cycle handles development and mortality of all ticks, regardless of their current location. During this step, each tick is checked to see whether it ages, survives, or lays eggs, depending on its current stage and whether it is on a lizard or not.

Growth and Feeding

Stages that are engaged in growth or feeding (eggs, engorged stages in refuges, and unfed stages on lizards) follow a threshold process, where each stage lasts for a fixed number of days for each individual. Each individual is assigned a normally distributed random number as a development or engorgement time on entry to a new life history stage (Figure5.7). Both the mean and the variance can be stage specific (Table 5.1). For example, newly oviposited eggs are given a hatching threshold with a mean of 53 days (SD 1.32). During the daily development step, each individual tick has its development or engorgement index decreased by one day. On the day the index reaches 0, the individual moves to the next stage (eg. an egg hatches to an unfed larvae, or a feeding nymph detaches). This means that the duration of all growing and feeding stages are normally distributed. This method is similar to those used for physiologically structured population models (Gurney et al., 1986), but includes variability between individuals.

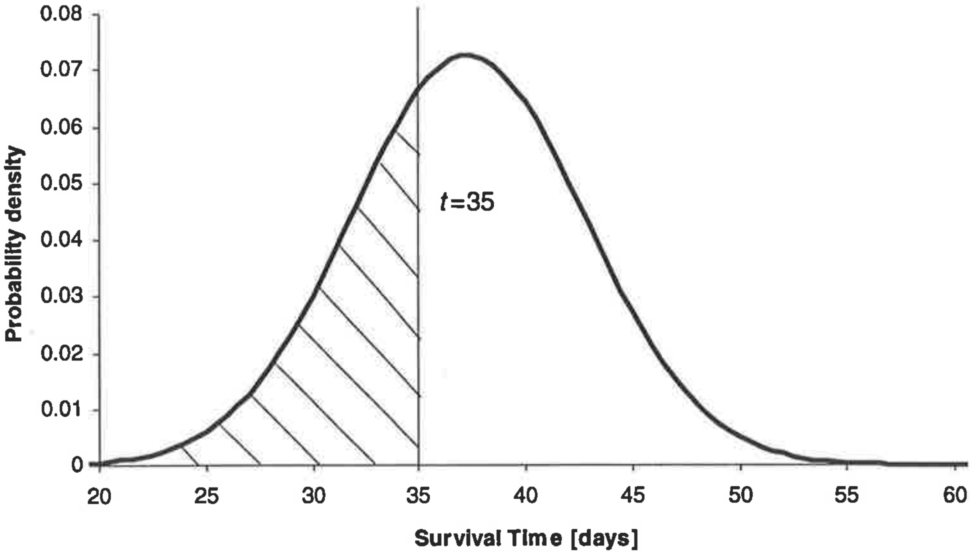

Figure 5.7 Distribution of survival time thresholds for nymphs. The hatched area is the probability of dying before 35 days. Development and engorgement thresholds are calculated similarly.

Feeding has one additional complication. As noted in Chapter 4, not all individuals succeed in attaching, engorging and detaching, and this is one of the few places where density dependence appears in the system. I use (4.13) to calculate the probability of successfully engorging, assuming that this probability depends on the total number of ticks of all stages at the time engorgement is complete. The mechanism underlying the relationship between tick density and engorgement success is presently unknown, and this arrangement is the simplest to implement in the model. I currently have no evidence of density dependence in engorgement success for nymphs or adults. I assume nymphs have a 50% chance of success, and adults 100%, regardless of the number of ticks present on the lizard.

Survival

Predation on ticks within refuges by other invertebrates does occur (Bull et al., 1988), but is both spatially and temporally unpredictable, and I do not include it in the current model. When a host lizard dies from predation (primarily automobiles near Mt. Mary) or old age all ticks on the lizard also die. I include this mortality in a single, between season event (see below). I assume that the primary source of daily mortality is desiccation. The habitat has low rainfall (150-250 mm annually), and most development occurs during the hot, dry summer. The only moisture source available to ticks is a blood meal, and newly moulted, unfed ticks must wait until another host arrives before they can replenish their moisture supply. Eggs, engorged ticks in refuges, and ticks feeding on lizards are assumed to be unaffected by desiccation. I model mortality similarly to development, by providing each individual with a normally distributed time to death. This is the number of days that each individual is expected to survive without feeding. The time is decreased by one day in each developmental step, and individuals that reach zero are killed. Death is presumed to have occurred as a result of higher temperatures during the day, and so mortality in a refuge precedes ticks boarding lizards that enter that refuge on the next day.

Random variation in the number of lizards using a refuge, and the number of refuges in a home range will influence average survival of ticks only if the relationship between the number of lizards and refuges and the probability of mortality is non-linear. I develop an analytical approximation of the probability of survival to visualise the effect of the tick and refuge density on the survival process in the model. This approximation is not used in the model; its purpose is purely heuristic. The probability that one or more lizards arrives in a refuge occupied by an unfed tick depends on the assumed structure of the landscape, and how lizards move around on it. The average number of refuges, $\bar{r}$, in a home range is the density of refuges on the landscape multiplied by the area of a home range:

$$\bar{r} = R\pi h^2 \qquad (5.3)$$

where R is the density of refuges on the landscape (units of km^{-2}), and h is the radius of a lizards home range (units of km). The number of refuges in a home range has a poisson distribution, and so the variance is equal to the mean, and the probability of there being x refuges in one home range is:

$$P\{r = x\} = \frac{e^{-\bar{r}}\bar{r}^x}{x!}. \qquad (5.4)$$

P{r=x} is the probability that a particular home range has x refuges. This works because I assume that refuges are distributed at random, and lizards choose their home range centres independently from the list of possible refuges. Similarly, the number of lizards that use a particular refuge is just the number of lizards whose home range centres are h or less kilometers away from that refuge. Therefore, the number of lizards using a refuge has a poisson distribution with average

$$\bar{l} = L\pi h^2 \qquad (5.5)$$

where L is the density of lizards (units of km^{-2}). If lizards have an equal chance of visiting every refuge in their home range on a given day, then there is a $1/\bar{r}$ chance of visiting any particular refuge. Furthermore, the distribution of waiting times for ticks until one or more lizards shows up is geometric, and the average waiting time is the same as the number of refuges in an average home range, $\bar{r}$ days. The number of lizards visiting a refuge is binomially distributed, with $\bar{l}$ trials and $1/\bar{r}$ chance of success. The average probability that one or more lizards visits a particular refuge on a particular night is then

$$P\{one\,or\,more\,lizards\} = 1 - \left(1 - \frac{1}{\bar{r}}\right)^{\bar{l}} = \lambda \qquad (5.6)$$

and this is the probability that an unfed tick transits to the next stage, feeding on a host. This is not strictly correct, because the number of trials in a binomial distribution can only be an integer, and $\bar{l}$ is unlikely to be an integer. However, (5.6) appears to work as a reasonable approximation in simulation tests.

I can use the probability of one or more lizards arriving in a refuge on a single day to calculate the probability of an individual tick surviving until one or more lizards arrive. In order to survive, one or more lizards must arrive before the tick dies, so the probability of surviving from one stage to the next is:

$$p\{survival\} = \sum_{t=1}^{\infty} p\{dying\ t\,or\,later\}\lambda(1-\lambda)^{t-1} \qquad (5.7)$$

where λ is the probability one or more lizards visits a refuge on a given night (5.6), and the second term is the probability that the first visit by a lizard occurs t days after the start of waiting. The probability of dying at time *t* or later is simply one minus the cumulative normal probability of having

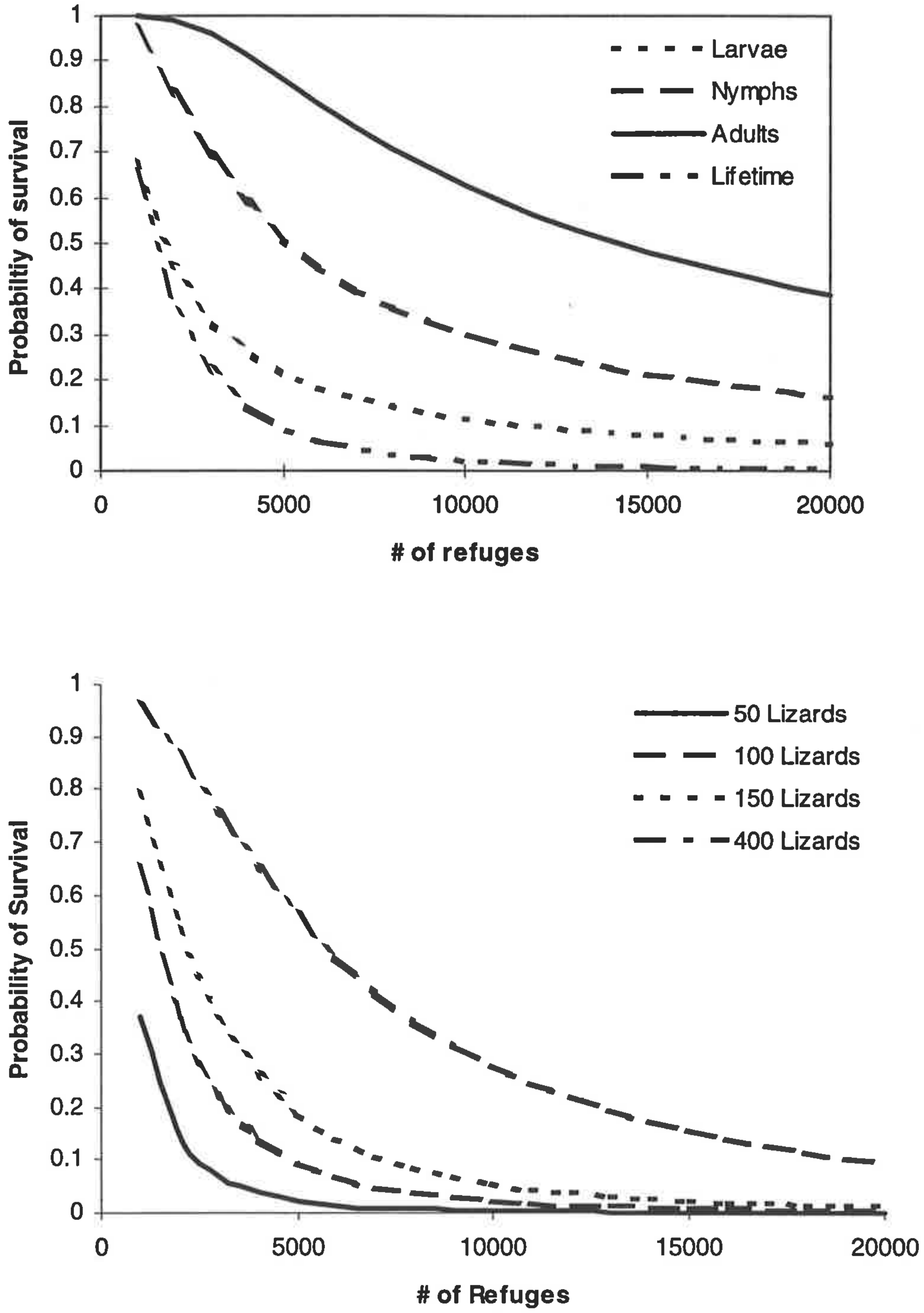

Figure 5.8 A) Probability of surviving a particular life stage given a certain number of lizards and refuges until one or more lizards visit the refuge. The "lifetime" curve is the product of the other three curves, and is therefore the probability of surviving from egg to adult, ignoring host and overwintering mortality. B) Lifetime survival probability as a function of refuge density at different lizard densities.

a development threshold at *t* or earlier (Figure 5.7). The probability of survival decays with increasing numbers of refuges (Figure 5.8), reflecting the fact that when lizards have more refuges that they can visit, the probability of visiting any single refuge decreases. Note that (5.4) - (5.7) are not used directly in the model, which calculates survival as individual mechanistic processes. The marked non-linearity in survival with the number of refuges will means that random spatial variation can influence population dynamics of ticks.

Mating and Oviposition

When an unfed adult tick boards a lizard, it is randomly assigned to be a male or female with a sex ratio of 1:1. Adult male ticks remain on lizards for the remainder of their life, assumed to be a fixed 180 days. The only contribution they have beyond this point is to mate with unfed female ticks. After boarding a lizard there is a fixed five day period before an adult male is mature and capable of mating. When an unfed female boards a lizard, if there is one or more mature males aboard she is mated immediately. Otherwise, she waits on that lizard until a mature male appears, or 180 days passes. There is no negative impact of waiting to mate on a females subsequent reproductive output, although a negative impact has been observed in laboratory experiments (Chilton, 1989). Once a female is mated, then she begins to engorge as described above for all other stages. This does introduce a slight Allee effect through delaying reproduction by females that board lizards without males.

Adult female ticks that have mated, successfully engorged, and dropped off in a refuge enter a pre-oviposition stage, the duration of which is normally distributed and handled identically to aging, feeding, and moulting. Once the pre-oviposition period is complete, each day for 40 days they add a number of new eggs to that refuge. The number to be added is time dependent, and taken from a two period moving average of laboratory observations (Figure 5.9). I round individual values down to the nearest integer. I have not introduced any stochasticity in oviposition.

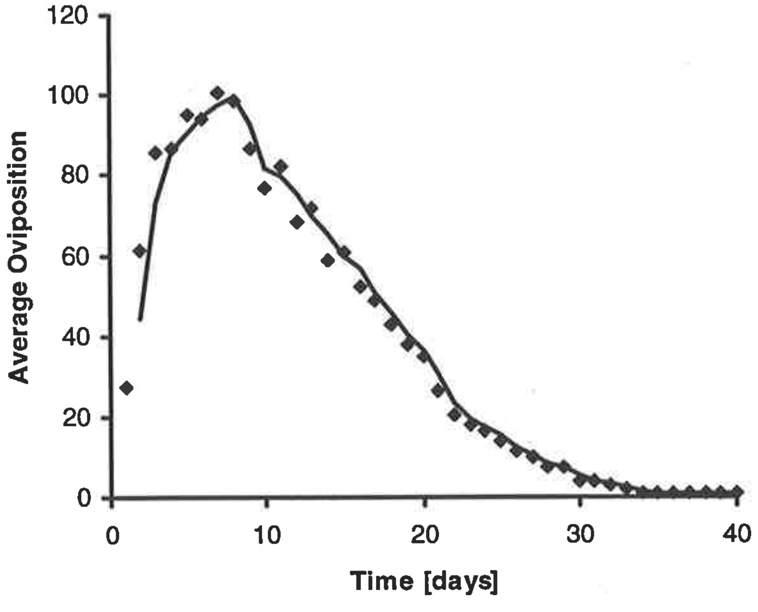

Figure 5.9 Oviposition [eggs / day] as a function of time for *A. hydrosauri*. Solid line is a two point moving average to smooth the bumps out.

Between season processes

There are two processes that occur between the end of one season and the beginning of the next: overwintering tick mortality and lizard population dynamics. All ticks, regardless of location, have a stage specific chance of mortality over winter. This reflects exposure, desiccation, disease, predation, and fungal infection. I have set this to 10% for all stages other than eggs. It is set low relative to mortality during the active season because the risk of desiccation is reduced in the cooler, wetter climate of winter, and invertebrate predators are less active. However, laboratory observations indicate that no eggs hatch when held at temperatures of less than 15°C. Therefore, egg mortality is 95% over the winter in the model, which allows for a small margin of error in the laboratory estimate of 100%.

Lizard population dynamics is also simplified. A flat 10% of all lizards are chosen at random and killed at the end of each season. Empirical observations place annual adult survival at around 90% (Bull, 1995). Any ticks on the killed lizards are likewise killed. The killed lizards are replaced from newborns whose mothers are chosen at random from the surviving lizards. These newborn lizards spend one season in their mother's home range, before randomly choosing a home range of their own (natal dispersal). This results in no net change in the number of lizards available, but tends to redistribute 10% of the population to new locations each season after the first two.

Table 5.3 shows all survival and landscape parameters not described in Table 5.1 or Table 5.2.

Table 5.3 All parameters of the model other than developmental/mortality times and temperature effects.

Parameter description	Value
h, home range diameter	200 m
R, refuge density	10,000 - 20,000 km^{-2}
L, lizard density	50 - 150 km^{-2}
sex ratio	1:1
Maximum time on host as adult	180 days
lizard mortality	10% $year^{-1}$
between season tick mortality	10% $year^{-1}$, 95% $year^{-1}$ (eggs only)

Population growth rates and estimation of extinction or outbreak risk

I associate regulation with "boundedness". In the model, I will identify population regulation failure with either extinction or exceeding an upper threshold. The upper threshold is chosen based on field observations of average tick density on lizards (Chapter 4), and computational constraints. Clearly the larger I allow populations to get in an individual based model, the longer the model takes to run, and the more memory is required. Preliminary runs indicated that if the model exceeded 200,000 ticks / km^2, then the average number of ticks per lizard often exceeded 50. Tick densities per lizard larger than 50 Ticks/Lizard were never observed at the transect or landscape scale in the real tick population, and in only 6 out of more than 500 density estimates at the population scale (Figure 4.4 to Figure 4.6). Whenever a density estimate did exceed 50 ticks / lizard at the population scale, the density in the following year is much lower. When the number of ticks in the model exceed this threshold, the model population rarely drops back below 200,000 / km^2, and has not been observed to go extinct. I refer to the event of exceeding this upper threshold of 200,000 / km^2 as an "outbreak".

The cumulative probability that the population hits either the upper or lower boundary can be calculated as a function of time using the Kaplan-Meier estimator (K-M; Venables & Ripley, 1994). The presence of an upper boundary that terminates a model run means that some observations are "right-censored". Right censoring arises in this case because runs that outbreak may go extinct eventually. For example, if a run breaks out in year 11, I only know the run didn't go extinct over the previous 11 years. The K-M estimator takes this right censoring into account by calculating the probability based on the "risk set", r_t, which is the number of runs currently at risk of going extinct (ie. have not yet gone extinct or broken out). The estimator is then calculated as

$$S(t) = \prod_i \frac{r_i - d_i}{r_i} \tag{5.8}$$

where d_i is the number of extinctions occurring in interval i, and the product is taken over all intervals $i<t$. I calculate the cumulative probability of not having an outbreak by redefining d as the number of outbreaks occurring in interval i. I usually show the median time to extinction or outbreak as the first season in which the cumulative survival curve drops below 0.5.

I calculate the growth rate between years based on the total number of ticks in all stages on lizards or in refuges at the end of each season prior to overwintering mortality (n_t). The growth rate from year t to $t + 1$ is

$$\Delta_t = \ln \frac{n_{t+1}}{n_t} . \tag{5.9}$$

I exclude values from the first year, and from years that precede the model hitting either the upper or lower boundary.

Results

In the basic scenario I explore the response of the model to variation in some of the unknown or uncertain parameters. In particular, the density of lizards and the number of refuges. I consider both the effect on the average growth rate of the population, and the median time (in years) to either go extinct or outbreak. Unless otherwise noted, all results are calculated from 100 replicate runs at each combination of parameter values, and the model is seeded with 1000 ticks (85% larvae, 10% nymphs, and 5% adults), each attached to a randomly chosen lizard. Note that this probably does not correspond to a population of 10 ticks / lizard in the empirical data (eg. Figure 4.4), because in the empirical data the population of ticks on lizards is supported by a (presumably) much larger and unobserved population in refuges.

The average population growth rate decreases with increasing refuge density, and with decreasing lizard density (Figure 5.10). On a natural log scale, 1 represents an increase of a factor of e, or more than a doubling of tick numbers in a single season. With 100 or more lizards, most populations are exponentially increasing, on average. The points for 10 - 11, 000 refuges with 150 lizards are missing because all runs went over the upper boundary within 2 seasons, and therefore I am unable to calculate growth rates. The standard errors of runs with 150 lizards are also large because at low refuge numbers most runs broke out within two seasons, leaving small sample sizes for estimating the average population growth. There does not appear to be an interaction between the number of lizards and the number of refuges on the average growth rate. A decrease of 50 lizards appears to have approximately the same effect as adding 7-8,000 refuges.

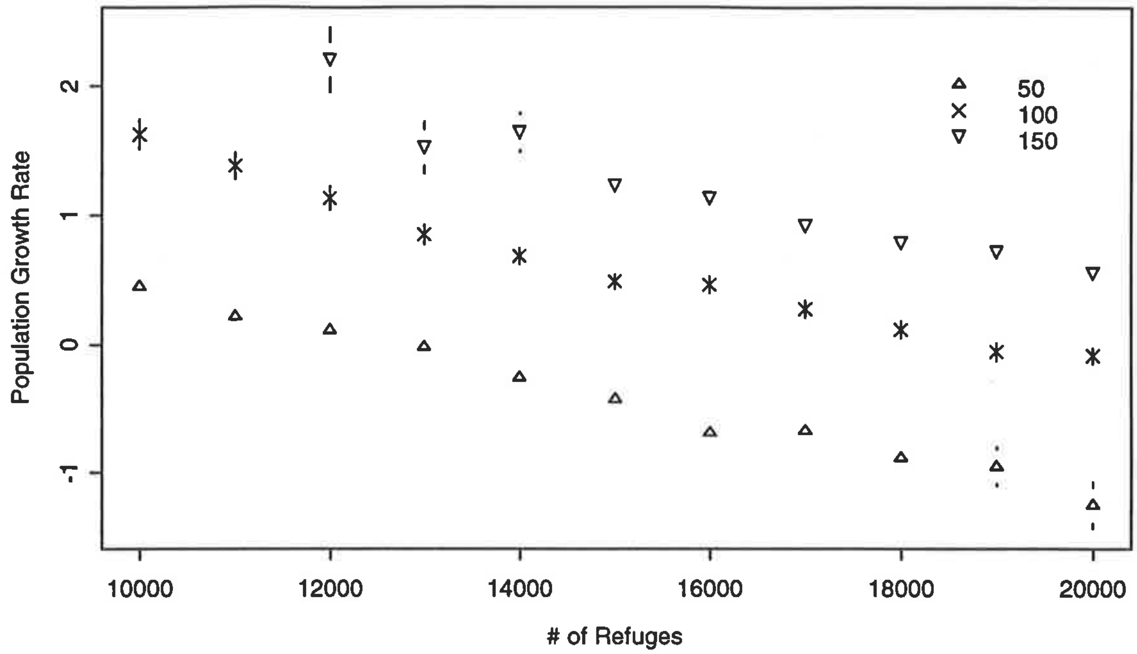

Figure 5.10 Average population growth rate as a function of refuge density for three different lizard densities. Error bars are standard errors, and where not shown are smaller than the displayed points.

More than 93% of the runs for all parameter combinations either went extinct or broke out before the simulations were terminated at 50 years. The median time to outbreak increases with increasing refuge density, and decreases with increasing lizard number (Figure 5.11). There appears to be an interaction between lizard number and refuge density, because increasing the number of lizards at low refuge densities has a much smaller impact on median outbreak time than an increase in lizard numbers at high refuge densities. This arises because the population is growing exponentially, and a given decrease in average growth rate has a non-linear effect on the time to reach the upper boundary. The average growth rate (Figure 5.10) is on a logarithmic scale, so the exponential changes are not noticeable. The median time to extinction decreases with increasing refuge density, and increases with lizard density. Generally, extinction is only common when the average growth rate is around or less than 0 (ie. fewer lizards and/or many refuges).

Temporal Variation in Mortality/Development

The basic model assumes that temperature does not vary with time, and therefore mortality and developmental rates are temporal averages. However, mortality in the smaller stages is particularly sensitive to high temperatures. I used the observed average developmental or survival time at different temperatures, relative to the average at 21^0C, to work out the relative rate at different temperatures for different processes (Table 5.2). Each value is the ratio of developmental time at 21^0C to developmental time at the midpoint of the temperature class. This value is then used in the model to decrement the development or survival index. Therefore, nymphs die 3.28 times quicker at temperatures above 30^0C than at temperatures of 20-25^0C. This mechanism of incorporating temperature variability has the desired property of reducing variance in development time at higher temperatures, as observed in laboratory trials (Chilton, 1989). Engorgement is relatively independent of temperature, because lizards behaviourally thermoregulate their body temperature close to 30^0C. However, this is difficult in the field when temperatures are low (C.M. Bull, personal communication). Therefore, I set relative engorgement rates to 0 when $T \leq 15°C$, and to 0.5 when $T \leq 20°C$.

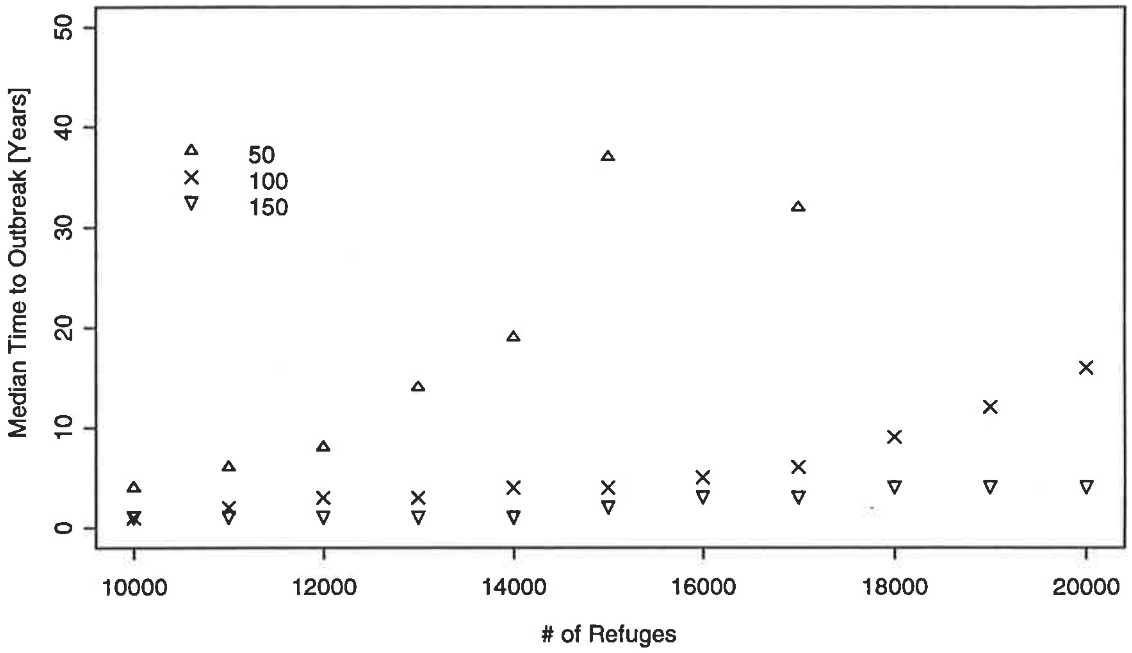

Figure 5.11 Median time to outbreak as a function of refuge density for three different lizard densities. Points where the cumulative probability of outbreak was less than 50% over 50 years are not shown.

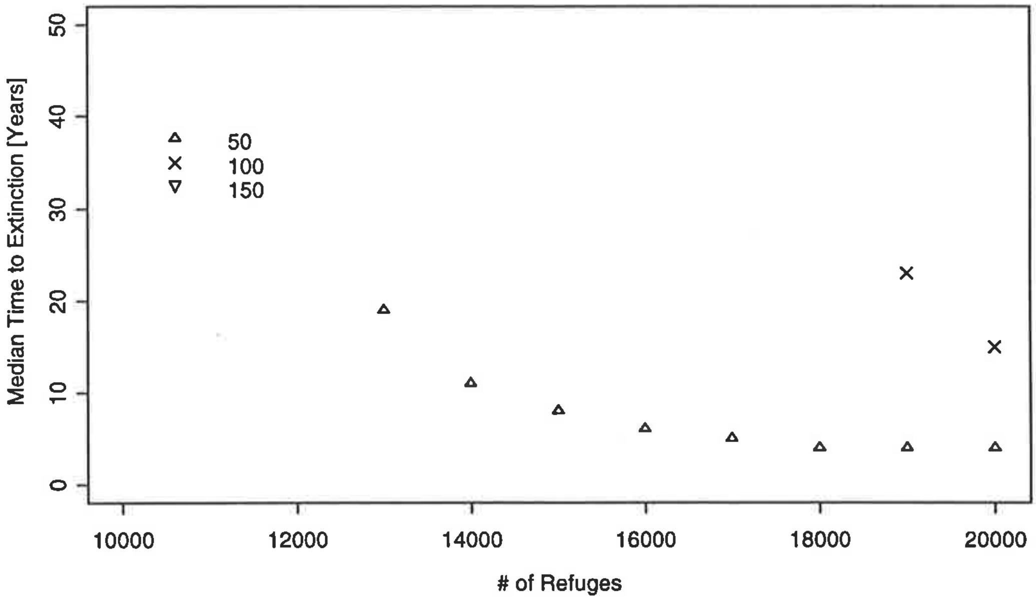

Figure 5.12 Median time to extinction as a function of refuge density for three lizard densities. None of the runs with 150 lizards / km^2 went extinct within 50 years.

I have ignored variation in mortality rates due to changes in relative humidity, because I have no data with which to estimate the time course of changes in humidity in refuges in the field.

Results

The average growth rate decreases with increasing refuge density and decreasing lizard density, the same as when there is no fine grained variation in developmental rates (Figure 5.13). The rate of decrease is similar to that in the absence of temporal variation. However, it is clear that introducing temporal variation in development and mortality has drastically reduced the population growth rate. In addition, the variability in growth rates is higher at all parameter combinations. These results are probably driven by the fact that the population growth rate varies non-linearly with temperature — a form of Jensen's inequality. All parameter combinations now produce negative average growth rates. At high lizard density and 19,000 refuges the average growth rate falls outside the monotonic decrease.

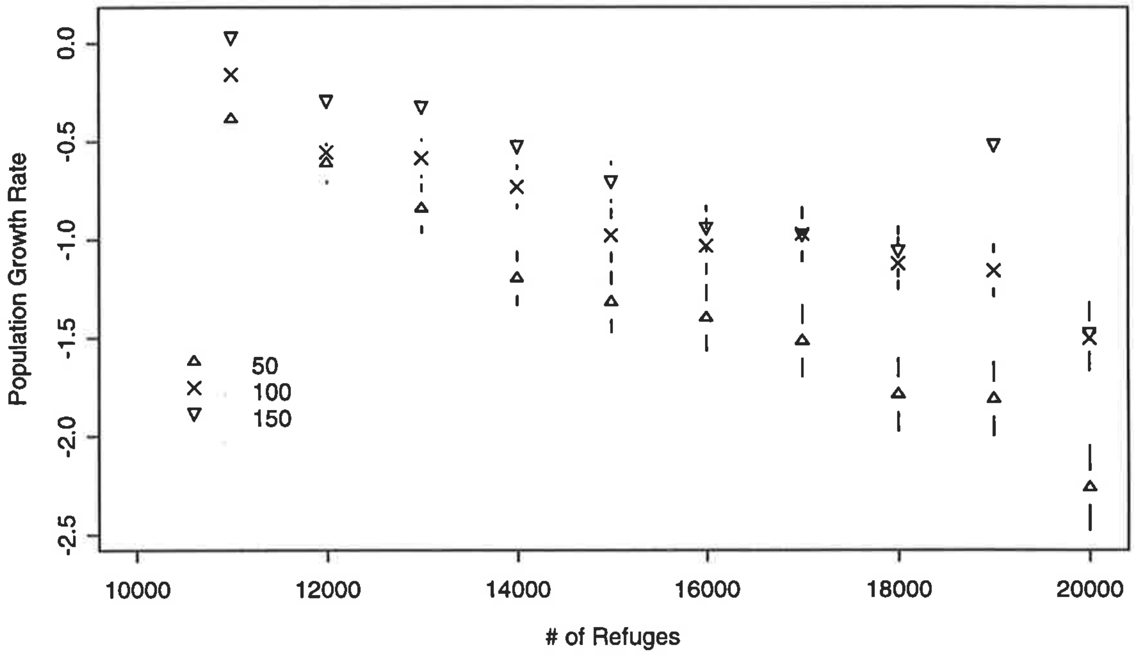

Figure 5.13 Average population growth rate as a function of refuge number and lizard density in the presence of temporal variation. Error bars are standard errors.

The median time to extinction (Figure 5.14) and the median time (Figure 5.15) to outbreak follow similar patterns to the average growth rate, and also reflect the anomalous result at a refuge density of 19,000. The lizard density appears to have less of an impact on persistence than refuge density, especially when compared to the effect of lizard density on persistence when there is no temporal variation. A median outbreak time of 50 years simply means that less than 50% of the runs "at risk" failed to hit the upper boundary before the simulation finished. The is because most runs went extinct, right-censoring the observation of median outbreak time.

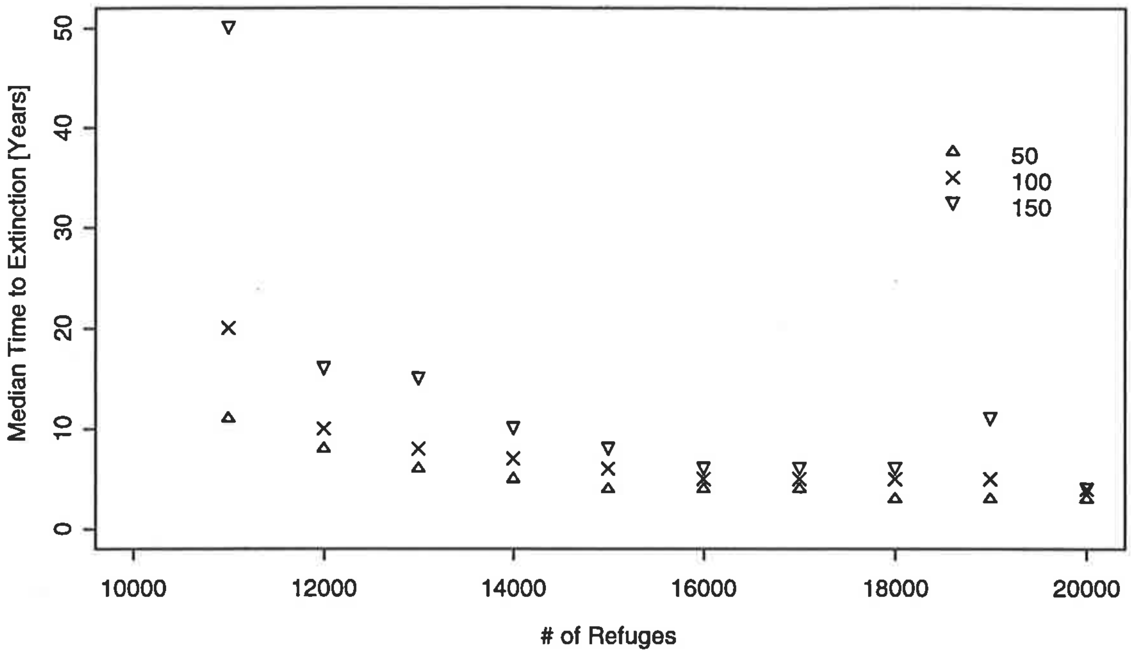

Figure 5.14 Median time to extinction as a function of refuge density with temporal variation.

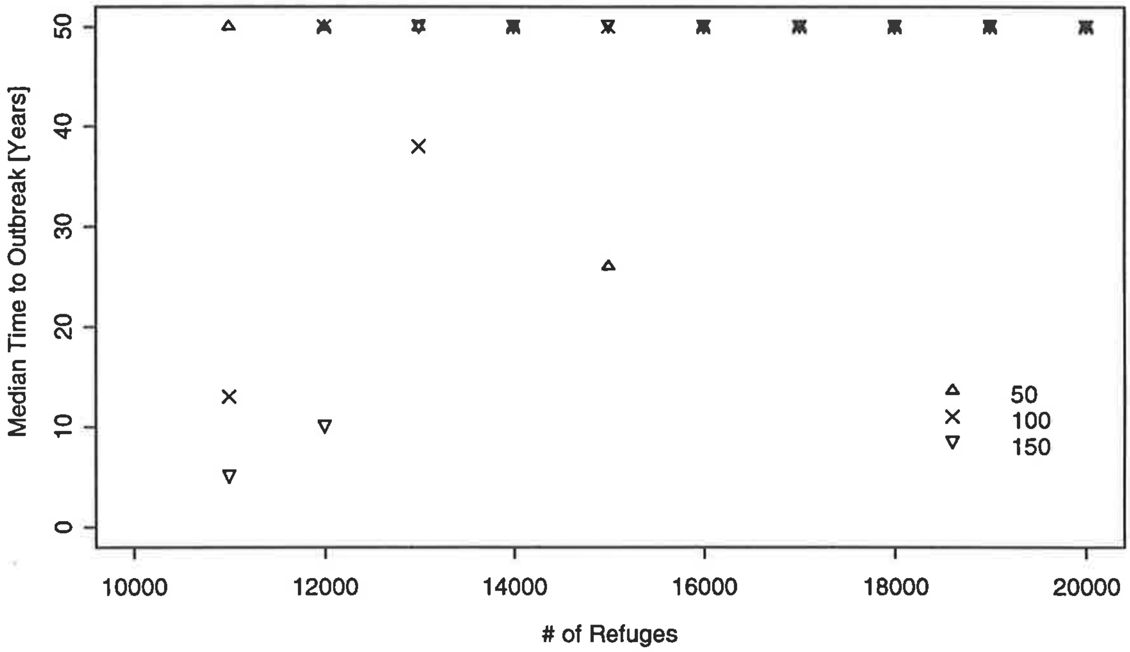

Figure 5.15 Median time to outbreak as a function of refuge density when there is temporal variation in developmental rates.

The model used a total of 31 different seasons in random order. There is less than 2°C variation in the average temperature over the entire season, making the seasonal average an unsuitable estimate of the "quality" of a year for ticks. There is considerable variation between seasons in the number of days for which the average temperature exceeded 25°C (Figure 5.16). This is the number of days in the season where the model used the upper two temperature classes, for which developmental and mortality rates are higher than those used in the no variability scenario. I assume that more hot days in season *t* will increase mortality rates, leading to lower average population growth from season *t* to *t*+1. However, there is no discernible effect of "season quality" on population growth rate (Figure 5.17).

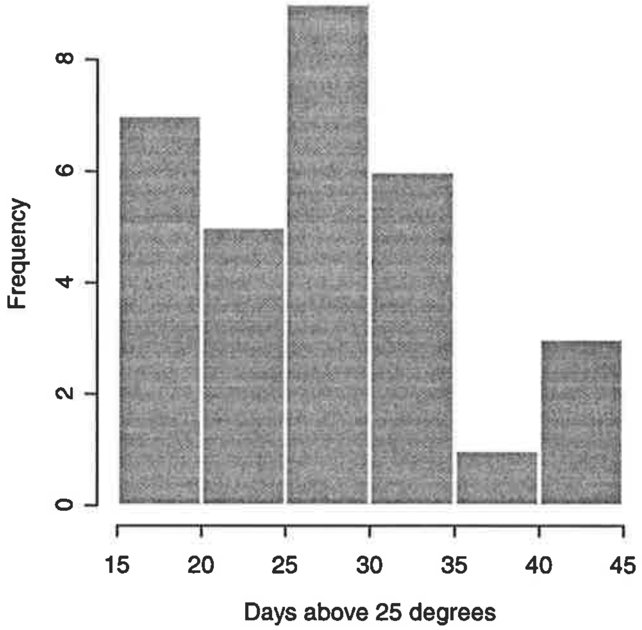

Figure 5.16 Frequency histogram of season quality, measured by the number of days (out of 210) on which the average temperature exceeded 25°C.

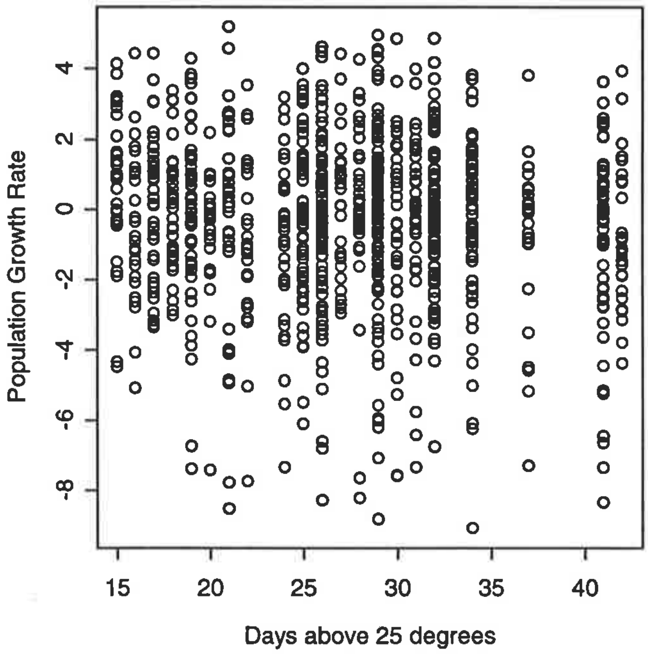

Figure 5.17 Population growth rate as a function of "season quality" for 100 replicate runs with 15,000 refuges and 100 lizards.

Variability in Space and Time

Introducing temporal variability in development and mortality rates drastically decreased the average population growth rate and increased the variability. Consequently, the persistence of populations was also decreased. In this next section, I consider the additional impact, if any, of variation between refuges on top of variation in time. Variability in space is added through different classes of refuge. In the simplest scenario possible, each refuge class is given a property that describes the temperature class relative to that in the environment. For example, rabbit burrows are cooler than the outside world, and so are always one temperature class lower than the environment. Grass clumps are more exposed, so are one temperature class higher. I introduce three basic classes, cool, normal, and warm, in equal proportions randomly distributed on the landscape.

Results

Combining both types of variation (Figure 5.18) has little impact on the average growth rates when compared with temporal variation alone (Figure 5.13). The average growth rates are slightly lower, and increasing refuge densities may have a slightly lower effect on growth rates (smaller slope). Compared with the absence of variation (Figure 5.10) the effect of increased numbers of lizards is reduced. In addition, the amount of variability in growth rates has increased, and the general trend is more difficult to discern. Most runs have zero outbreaks, with a few having less than 10%. The exception is runs with 11,000 refuges and 100 and 150 lizards had 11% and 34% outbreaks respectively. Median extinction time decreases with increasing refuge numbers, while increasing with increasing lizard density (Figure 5.19). Time to extinction is generally much less than with temporal variation alone, especially at 11,000 refuges.

Virtual Mike

In order to better understand the observation process that was used in collecting the data analysed in Chapter 4, I sampled the model data with a "virtual ecologist" modelled after Prof. Mike Bull of Flinders University. Virtual Mike sampled lizards along a linear transect placed through the middle of the landscape. All lizards whose home ranges overlapped the transect could be captured. The probability of capture varied between lizards according to the extent to which their home range overlapped the transect, how many refuges there are in the home range, and on which side of the transect the lizard spent the previous night. For each lizard, I counted how many refuges were on either side of the transect. On a sample day, each lizard had a probability of capture given by dividing the number of refuges on the other side of the transect from the lizards previous position, divided by the total number of refuges in the home range. This raw capture probability was then multiplied by an "efficiency modifier", which varied between 0 and 1. This modifier reflects the fact that even if a lizard crosses the road on a day when Mike is sampling, he may not be there to capture it. Captured lizards have their ticks accurately enumerated.

Results

The effect of capture efficiency is clearly demonstrated with three runs of the model with different levels of capture efficiency. In one run with capture efficiency equal 1 and 120 lizards/km^2, Virtual Mike caught an average of 167 (range 129 - 231) lizards each year along a one kilometre transect. Consequently the sampling error, measured as the standard error of the mean, varied between 0.03 and 2.1. This average is comparable to the annual number of lizards captured along the entire length of Transect 1 (12 km; Table 4.1). Reducing capture efficiency to 0.5 the average number of captures per year drops to 116, and the sampling error varies between 0.07 and 7.4. With a capture efficiency of 0.1, the average number of captures per year is 27, and sampling error varied between 1.0 and 23.4. This compares more closely with the average number of captures per kilometre analysed in Chapter 4.

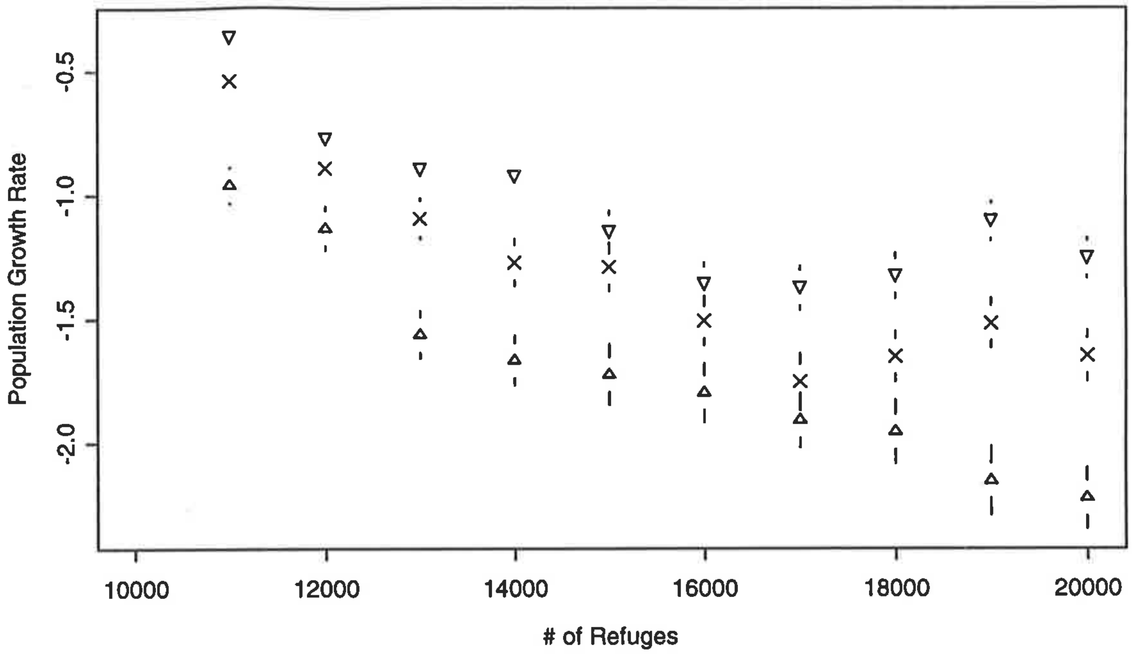

Figure 5.18 Average population growth rate as a function of refuge density in the presence of both spatial and temporal variation. Error bars are standard errors.

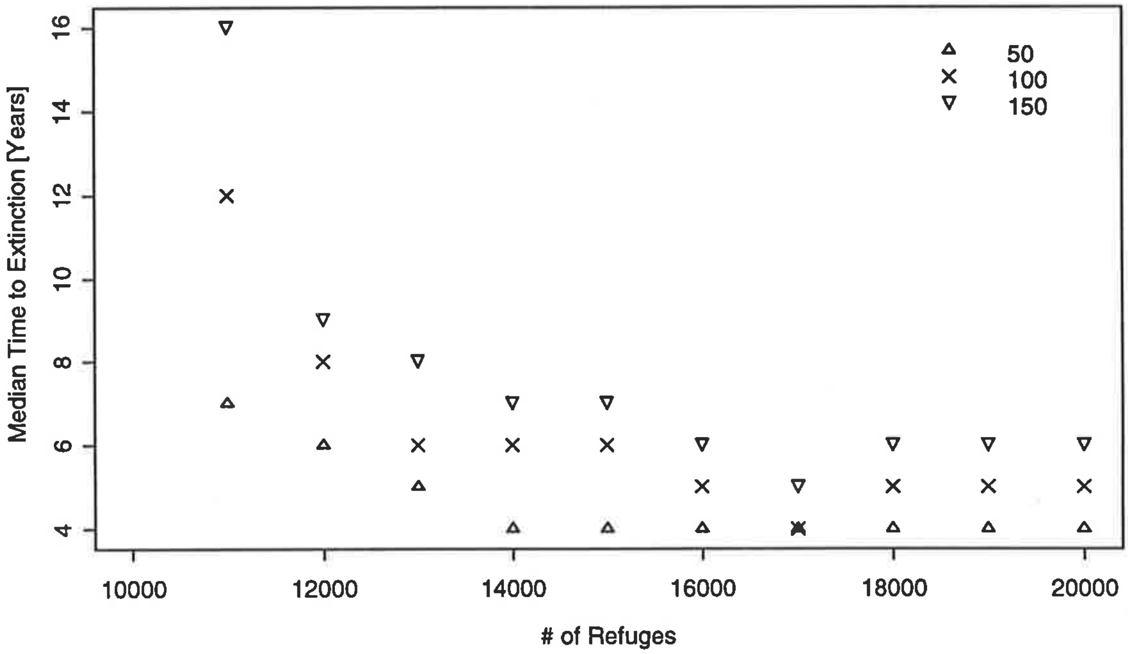

Figure 5.19 Median time to extinction with both temporal and spatial variation.

The number of ticks counted on lizards is not a good estimator of the total number of ticks on the landscape, even when there is no sampling error associated with the random capture process (ie. all ticks on every lizard on the landscape are counted; Figure 5.20). An average of 10 ticks / lizard can correspond to any population density between ≈4000 and 100 000 ticks / km^2. There is a rough positive relationship apparent when total tick density exceeds 10 000 ticks / km^2. When data collected by Virtual Mike for the same series of runs is used to calculate the average ticks / lizard, as was done in Chapter 4, there are two features worth noting. First, when total density is less than 10,000 ticks / km^2, there are many years in which the sampled density is 0, even though there are ticks present on the landscape (Figure 5.21).

Second, the average densities tend to be higher, and any trend with total tick density is virtually non-existent.

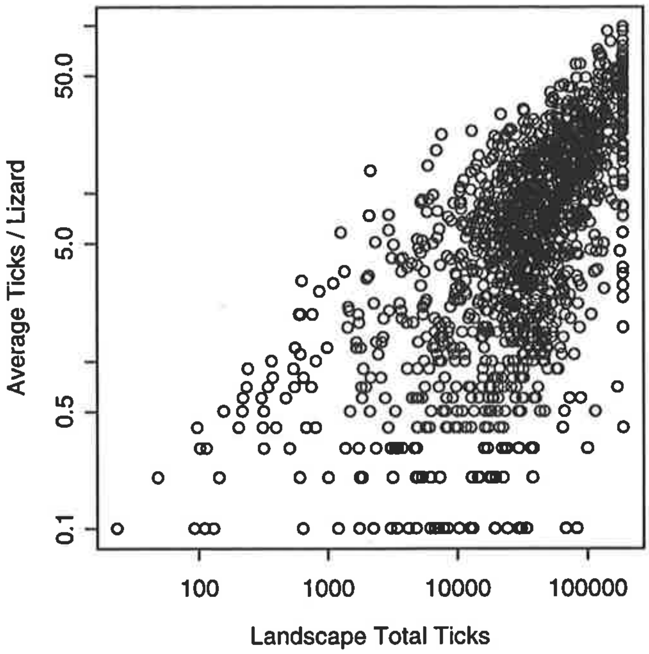

Figure 5.20 Correlation between the average number of ticks on lizards, and the total number of ticks on lizards and in refuges for 100 replicate runs with 15,000 refuges and 100 lizards. Note the logarithmic scale on both axes. Average tick density was calculated from all lizards at the same time as total tick numbers were enumerated; this is not Virtual Mike data.

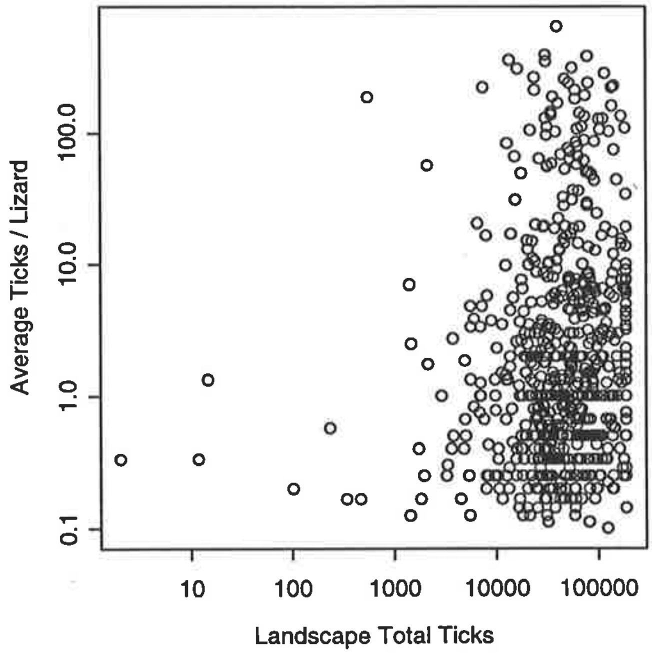

Figure 5.21 Correlation between the average number of ticks on lizards captured by Virtual Mike, and the total number of ticks on lizards and in refuges for the same runs as Figure 5.20. Note the logarithmic scale on both axes. Average tick density was calculated from all lizards captured every 28 days throughout the season.

Discussion

It is clear that the density dependent larval engorgement success observed in Chapter 4 is insufficient to lead to population regulation. Once the total number of ticks exceeds 200,000 / km^2, the population is acting in a close to deterministic fashion, with greatly decreased variability in average numbers of births and deaths. If the average growth rate is greater than zero, these populations explode. The average number of ticks per lizard at this threshold density is between 5 and 50 (Figure 5.20), which is quite comparable with the peak population densities observed in the field at the population scale (1 km segments; Figure 4.5). However, the engorgement success at a density of 50 is 0.415 compared to 0.439 for a single larva (4.12). This small change is unlikely to have an effect on the average population growth rate. Clearly some lizards will have enough ticks for the density dependent reduction in engorgement success to occur, but this will be a rare event at densities typically observed in the field.

The second point from this model is that the "tick sampling process" that is being employed in the field to understand tick population dynamics (Chapter 4) is unlikely to lead to firm conclusions about the dynamics of the ticks. It is not well related to the actual dynamics of the tick population. This effect arises from two main reasons. First, most ticks in the population are unobservable because they are in refuges where they are impossible to count. Second, the random capture process often leads to low sample sizes. As a result, low density tick populations are often missed, while high density tick populations are often overestimated. This effect was clear for the empirical data in Figure 4.6, and the same effect occurs in the model for the data sampled by Virtual Mike (Figure 5.22). This effect is not unique to ticks; any effort to sample an organism with a highly variable population distribution will face these problems. Clearly, the random capture data of chapter 4 can provide little more than a broad outline of the population dynamics, especially at smaller scales. Detailed time series of tick numbers on individual lizards would provide more information.

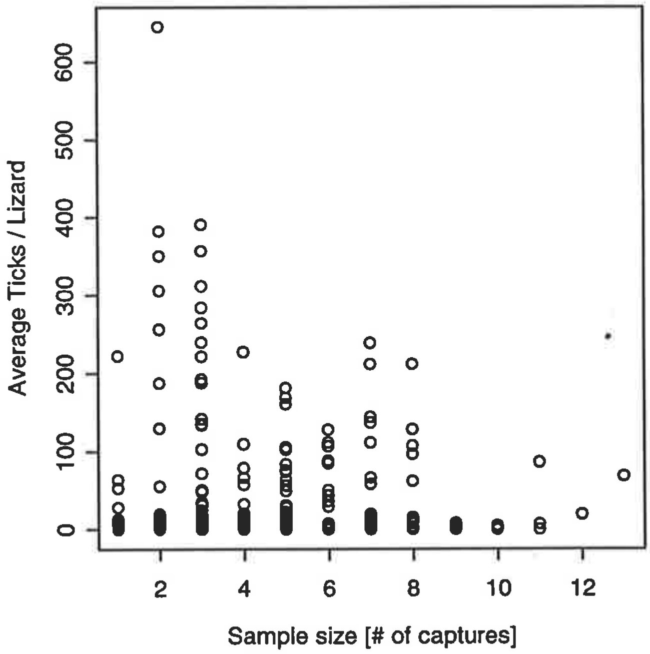

Figure 5.22 Average Ticks / Lizard in each year as a function of sample size (number of lizards captured in that year) for the same data as Figure 5.21.

Modellers often comment that models can be used to identify parameters or processes that are inadequately quantified. There are at least two examples of this in the present model. First, I found that the density dependent engorgement process identified in Chapter 4 is insufficiently understood. It has only been measured over a range of densities that are extremely uncommon in the field. It is not known whether the same mechanism applies during other engorging stages. Proper characterisation of this response could demonstrate that there is some scope for population regulation through this mechanism. For example, if engorgement success is very high (≈ 1) with fewer than 10 ticks per lizard, but drops off sharply to the levels observed in the experiment, then this mechanism could lead to population regulation. Improved engorgement success at low densities would tend to raise the average population growth rates, while forcing these to drop off to the levels observed in the current model when densities increased (ie. to strongly negative values).

The second problematic assumption identified by the model is that all bluebushes are created equal in the eyes of a lizard. The estimated density of bluebushes in the field is much larger than the refuge densities used in the simulation results shown here. In every scenario, the maximum refuge density (usually 20,000 / km^2) leads to rapid extinction of the tick population. Therefore, either the model has left out some crucial process that improves tick survival, or the assumption that all bluebushes are equally useable by lizards as refuges is false. Many things have been left out of the model: predation in refuges, crushing mortality during engorgement, high temperature mortality, less than 100% boarding rates. All of these would increase the mortality of ticks, and therefore increase the rate at which populations go extinct. Thus, I am left with the conclusion that lizards must not use all refuges equally. The estimates of Burzacott (unpublished data) already distinguished between possible overnight and other types of refuge. The only process that could increase the survival of ticks waiting in refuges for lizards is non-random use of the available refuges, ie. if there are some refuges they are more likely to visit than others. If neighbouring lizards tend to use the same criteria to pick refuges, this will then also increase the rate of transmission. Otherwise, non-random use within a home range, but not between home ranges (ie. lizards don't know each other's choice criteria), will increase survival but not transmission. Correlated movement of mates will not increase transmission across the landscape by much, because the home ranges of mates overlap to a large degree even outside the mating season.

That there is little or no correlation between the number of hot days in the season and tick population growth rates can be interpreted in a number of ways. First, it could be that an annual, between season increment is an inappropriate time scale over which to integrate the effects of climate on ticks. For example, in Davidson and Andrewartha's (1948) classic paper on density independent population regulation, the fluctuations of the thrips population were considered on a daily basis. The tick model is unlikely to show strong effects at the level of individual days, because mortality is a cumulative process, taking several days to occur even at the highest temperatures. Considering the frequency of runs of high temperature days may be a better method. The second possible interpretation is that my modelling of the effects of temperature on development and mortality is incorrect. Particularly at very high temperatures, it is possible that the maximum temperature reached during the day, rather than the average, is what determines mortality. Such mortality may also be more "catastrophic" in nature, ie. act immediately, rather than cumulatively. Finally, I have not included any effect of humidity on tick mortality in the model, although it does have an effect in lab experiments. It could be that soil moisture content is a better predictor of mortality than temperature.

Spatial variability enters this model in three ways. First, there is the obvious inclusion of variation between refuge types in the full variability scenario. This appears to have little effect, other than lowering the average, between season, population growth rate. Second, even the "no variation" scenario incorporates some spatial variability through random variation in the number of refuges in each lizards home range, and the number of lizards using a particular refuge. This will create regions on the landscape which have poor population growth, and regions with better population growth. As we will see in Chapter 7, there is substantial spatial and temporal variability in lizard population dynamics, which has been included here in only the simplest of outlines. Some of the spatial variability in lizard dynamics could be a response to variation in habitat, which would further enhance the extrinsic variation experienced by the tick population. Third, there could be intrinsic variability arising as a result of self-organisation in the tick population. This is unlikely to occur outside of patterns imposed on the system by the pattern of refuges and lizards, because there is little or no interaction between individual ticks. In the glider model of Chapters 2, 3 and 7, intrinsic patterning arises because of competition for space. In the tick model, there is only weak intra-specific competition at the larval engorgement phase. Given that this competition does not appear to contribute to population regulation, it seems unlikely to lead to pattern formation. The possibility that competition of this nature could maintain a parapatric boundary as described in Chapter 4 remains to be tested.

This chapter has employed a spatially explicit, individual based model to look for population regulation as an emergent property from spatial and temporal variation in survival and developmental rates. It does not seem as though population regulation is likely in this system without the addition of explicit density dependence.

Chapter 6 Predicting the outcome of pulse additions of ticks to a landscape

Introduction

One of the values of ecological modelling is that it is possible to extrapolate to temporal and spatial scales beyond the reach of experimental manipulation. Nonetheless, it is important to subject models to experimental validation if at all possible. In this chapter I use the tick model developed in Chapter 5 to make predictions that can be tested in an experiment proposed for the 1998-99 season. I also develop a simple matrix model of the tick population to provide an alternative prediction.

This chapter demonstrates the use of the "virtual ecologist" approach in a pro-active way, to design empirical experiments that can answer questions of interest. It is useful to have predictions from alternate models (Hilborn & Mangel, 1997), because if an experiment rejects one model, it may not reject another, and this speeds the development of insights into the ecological processes. This multiple model approach is particularly important in a management context, where management decisions must be made, whether there is an extant (ie. not rejected) model or not.

The experiment will consist of releasing a large number (500-1000) larval ticks onto a lizard, and making detailed observations of the tick population in the immediate vicinity on a daily or sub-weekly basis. A pilot experiment with one lizard was conducted during September 1998 - January 1999, but the results of this experiment are not available.

Methods

I generated predictions for this scenario from the individual based model (IBM) of Chapter 5 by choosing a lizard whose home range was centred between 367 and 666 m of both axes (ie. the centre 1/9th of the landscape). On day 0 this lizard is infested with 1000 larval ticks. No other ticks are introduced. All lizards that share one or more refuges with the release lizard are identified. These are generally the lizards whose home range centres are less than $2h$ distant from the home range centre of the release lizard, although lizards at the outer margin of this criterion may not share a refuge by chance. The ticks on these lizards are checked daily. I run the model for an entire season, 210 days.

I record two criteria, the total number of nymphs observed, and a K-S comparison of the distribution of nymph arrivals with a cumulative curve. All records are for the first time a nymph was observed; it is possible to distinguish previously recorded nymphs on lizards without marking them, by keeping records of the locations of each nymph on its host (C.M. Bull, personal communication). The number of new nymphs recorded on each sampling date is independent of nymphs recorded on earlier dates. An easier measure, the total number of nymphs observed on each sampling date, is not independent across time, because nymphs observed on one day may, or may not, have been present the previous time. In the initial test, I generate predicted distributions from 1000 replicate runs with 125 lizards and 7000 refuges. All predicted runs used weather sequences from the 1997 season (Sept 1 - March 30).

Matix model

I constructed a simple stage-structured matrix model (Caswell, 1989) to generate predictions without any stochastic influence. The disadvantage of this approach is that it does not predict a variance, but only a mean value. I used a projection interval of one day, and based the growth and survival probabilities on the parameters used in the IBM. I ignore development beyond the engorged nymph stage to eliminate oviposition flow from experimental ticks. I projected 1000 larvae on lizards forward 210 days, and recorded the cumulative number of nymphs feeding on lizards.

The daily growth and survival probabilities were calculated from the average duration of each stage (or average survival time) by assuming that the within stage age distribution is stable, and that individuals have a constant probability of moving up to the next stage (or of dying). This assumption means that the within stage age distributions are geometric, and therefore the per day probability of completing development (or of dying) is simply the reciprocal of the average duration. These probabilities are then assembled into a projection matrix by recognising that the probability of staying in the same stage is the product of the probability of not growing and surviving, while the probability of moving to the next stage is the product of the probability of growing and surviving (Table 6.1). For larvae and nymphs, the probability of "growth" represents the probability that one or more lizards visit their current refuge (see equation (5.6)). For feeding and moulting stages, the survival probability is assumed to be 1.

Table 6.1 Projection matrix for the stage structured model. ρ_i is the probability of surviving each day in stage i, τ_i is the probability of growing to stage i+1, and λ is the probability one or more lizards visits a refuge. Blank cells are 0. The matrix is initialised with 1000 individuals in stage 2 (feeding larvae).

	Larvae	Feeding Larvae	Moulting Larvae	Nymphs	Feeding Nymphs
Larvae	$\rho_1(1-\lambda)$				
Feeding Larvae	$\rho_1\lambda$	$\rho_2(1-\tau_2)$			
Moulting Larvae		$\rho_2\tau_2$	$\rho_3(1-\tau_3)$		
Nymphs			$\rho_3\tau_3$	$\rho_4(1-\lambda)$	
Feeding Nymphs				$\rho_4\lambda$	$\rho_5(1-\tau_5)$
Moulting Nymphs					$\rho_5\tau_5$

Predictions

The total number of nymphs recorded on the designated lizards tests the mortality and engorgement success rates in the model. It provides little information about development rates, because errors in the development process would slow down or speed up the arrival rates of ticks, but have little or no impact on how many are ultimately observed. A two-tailed test with $\alpha = 0.05$ is performed by comparing the observed value with the predicted distribution (Figure 6.1). The total number of nymphs is 95% likely to lie between 96 and 294. The minimum observed was 59, and the maximum 351.

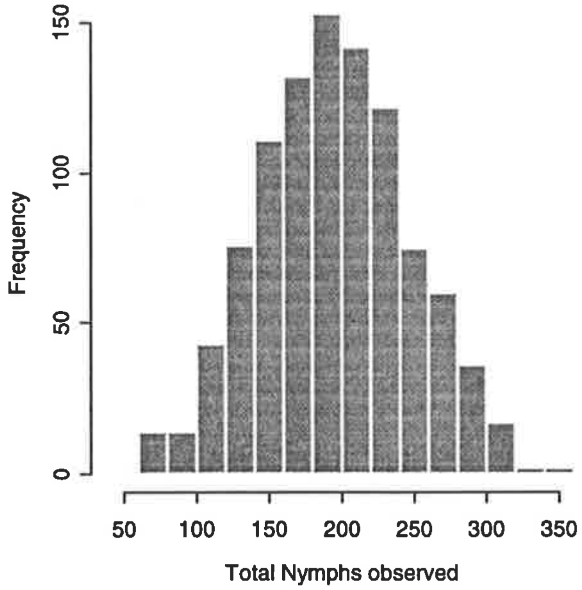

Figure 6.1 Predicted distribution of total nymphs observed over 210 days in 1000 replicates of the experiment. An average of 15.5 (SD=3.7, range 5-27) lizards were observed.

Testing the developmental processes in the model requires information about the arrival time of nymphs on lizards. This information is mixed up together with the movement rules used by lizards, and the assumption that refuges are used independently. I initially generated a "predicted" cumulative distribution of nymph arrivals with a preliminary run of 40 replicates, yielding 9218 observations (Figure 6.2). This predicted curve was then compared with the actual curve from each of the 1000 replicates using a two-sample Kolmogorov-Smirnov D statistic (Press et al., 1992). This is the absolute greatest distance between the two cumulative curves, which is a well known and sensitive test of the position of two distributions. It is most sensitive to differences in the median position, although it will respond to differences in the tails as well. Although the predicted curve appears to be normally distributed, it is significantly different from a normal curve, primarily in the tails (KS $D = 0.076$, $p < 0.001$, df=9216). This is an excellent reason for not using a parametric test of the center of the distribution relative to a prediction (eg. t test). This non-normality probably arises from the geometric distribution of waiting times for nymphs in refuges.

The observed D statistics ranged from 0.077 to 0.5028, with 95% of values less than 0.295 (Figure 6.3) The sampling distribution of D is well known, and there are algorithms for calculating *p* values. However, these distributions rely on the assumption that the underlying distribution is continuous. Both the predicted and observed distributions in this case are discrete, with many tied values especially in the vicinity of the median. Therefore, 95% of the p-values for the runs in Figure 6.3 are less than 0.02. Clearly, given that these runs are generated from an identical model, too many values are being rejected. Therefore, I will predict only that the D between the experimental and the predicted distributions of arrival times is 95% likely to be less than 0.295. Values larger than this will constitute a rejection of the model.

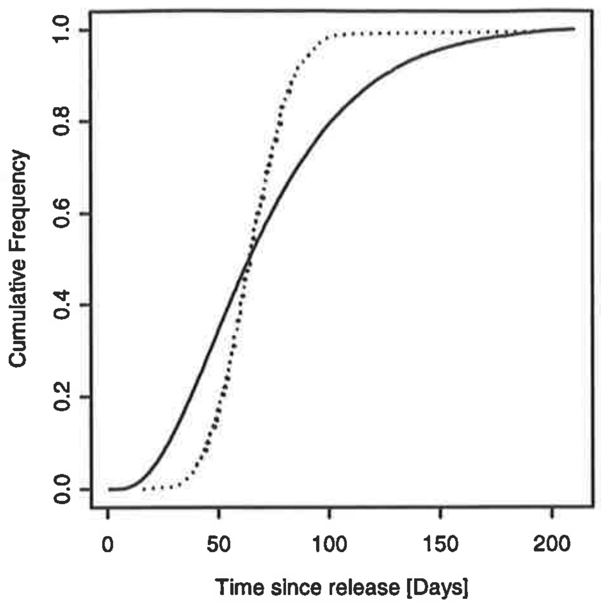

Figure 6.2 Predicted cumulative distribution of nymph arrivals in experiment. Solid line = matrix model, dotted line = IBM.

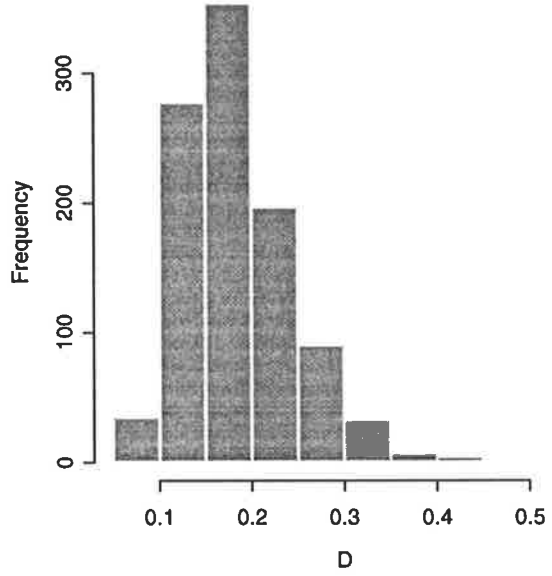

Figure 6.3 Frequency distribution of Kolmogorov Smirnov comparisons for 1000 replicate runs against the predicted distribution from the IBM in Figure 6.2.

The matrix model suggests that 207 nymphs will be observed over the 210 days of the experiment. This is only slightly larger than the median prediction of the IBM (194 nymphs over 210 days). The arrival time distribution from the matrix model has a sharper rise and a longer tail (Figure 6.2). This is because of the geometric distributions of developmental times, which have considerably more weight in the tails than the normal distributions used in the IBM.

Discussion

The two biggest sources of variation in the predictions are the random variation in both the number of refuges, and the number of lizards using those refuges within $2h$ of the release lizard. Both of these quantities will vary between replicates as a result of the random locations of refuges and lizards. It is conceivable that these things could be measured in the field, and the exact values and locations used to generate the predicted results. However, given the large number of refuges in the region, and the uncertainty associated with identifying those refuges that are actually used by lizards, it seems unlikely to be a useful exercise.

The large amount of variability in the number of lizards that share refuges with the release lizard is also responsible for my inability to make predictions at the level of individual lizards.

I chose to ignore the presence of background ticks when generating predictions for the landscape experiment. One source of error in the experimental test therefore is that more nymphs will be observed than came from the original release. Initially, I attempted to include variation in the number of background ticks in the predictions. However, given the propensity of model tick populations to either grow exponentially or go extinct (Chapter 5), it was very difficult to reliably generate average background tick densities on the order of one to five ticks per lizard.

The extent to which this omission biases the prediction can be determined post-hoc by looking at the number of nymphs that appear on lizards whose home range centres are more than one home range diameter from the release lizard's home range centre. These lizards could not receive nymphs from the release, and the number of nymphs appearing on them is an indication of the background tick density. As long as these densities are reasonably low (< 10% of the total number observed on experimental lizards), the bias in the experiment is minimal. The site for the pilot release was chosen for its low background tick density. The second consequence of omitting background ticks is that the lower predicted boundary is conservative. If the number of observed ticks is less than that, then the model is quite seriously over-predicting the survival of ticks through 2 stages of development.

A second source of error in the experiment is that not all lizards in the release zone are necessarily captured and radio collared. In particular, there may be transient lizards passing through the region that are not captured at any point. These lizards, if they pick up ticks in the release zone, will reduce the observed total number of nymphs. It is difficult or impossible to estimate the impact such lizards will have. Itinerant lizards will be captured, marked, and counted when observed, so some estimate of their impact in the field will be available post-hoc.

It seems unlikely at first glance that this experiment is a strong test of the model. However, it will identify gross inconsistencies in the model (eg. no nymphs observed, or 500 nymphs observed). If the model is consistent with the data collected in this experiment, it would suggest that more effort invested in greater replication and better background assessment would pay dividends.

Chapter 7 Characteristic Scales in Ecology: Fact, Fiction or Futility

Introduction

Complex dynamics in both space and time are a striking feature of ecological systems. Ecosystems that appear simple from an anthropocentric scale are often composed of dozens of species performing many different functions. Heterogeneity is created by variation in soil type, moisture, light availability and other landscape features. The result is a mosaic of habitat types in space that varies with time. Overlaid on this mosaic is a further layer of complexity that arises when individual organisms consume resources, interact, reproduce and die in this heterogenous landscape. Moreover, this heterogeneity is scale dependent; different organisms exploit the landscape at different scales (Allen & Starr, 1982). The net result is spatial heterogeneity in population dynamics.

It is possible that many processes contribute to variation in population size in space. Whether or not the neighbourhoods, or scales, of multiple processes can be detected individually, or if they combine to show a single dominant scale for a population, is an open question. For the remainder of this chapter I will take "characteristic scale" to mean the distance an ecologist would have to travel to find a significant change in the quantity or process being measured. A quantity could be population density; the process could be mortality. The characteristic scale could also be an area measure; the area within which similar processes are responsible for the dynamics of a quantity. If a process is contributing to variation in space, then I assume that it generates a signature detectable by the methods that I are exploring.

If calculations are not done at many different possible scales the correct one cannot be identified. Therefore, I can ignore traditional ecological pattern analyses such as fitting frequency distributions or calculating nearest neighbour distributions (Krebs, 1989). These analyses are performed at a single scale of observation, and so presume that the correct scale is already known. What I need is a way to identify the scale at which an ecosystem should be sampled to understand the processes that drive it. A quantitative analysis of scale is only possible using the operations of zooming or lagging (Schneider, 1994). Zooming is the process of lumping together sampling units to form larger units. The analyses I will examine in this paper use this technique. Lagging, common in geostatistical applications such as semivariograms or autocorrelation functions (Cressie, 1993), is the process of looking at points at successively greater separations. I did not consider these methods here because of time limitations. In addition, they generally require much longer time and space series to be useful.

There has been a growing recognition of the need for explicit analyses of the scale of ecological systems (eg. Schneider, 1994; Mac Nally & Watson, 1997), but as yet few attempts to perform such analyses with empirical data. Even those analyses that have been performed are virtually incomparable because of variability in method, data, and a lack of mechanistic interpretations to the observed patterns. I will outline the historical background of characteristic scales in ecology, compare the performance of two scale analyses with a computer population model in the spirit of the virtual ecologist, and examine some empirical data.

Historical and Conceptual Background

Multiscale analyses have a longer history in plant ecology than animal ecology. Grieg-Smith (1979) reviewed nearly 30 years of pattern analysis work in plant ecology using block variance methods. They have spawned a plethora of methods including fractals, spectral analysis, and variance decay spectra. Fractals were first used in ecology by Bradbury et al. (1984) to look at variation in coral reef structure as a function of scale. Their use has since expanded to measures of home range structure (Loehle, 1990), habitat distribution (Milne et al., 1992), and animal movement (Wiens et al., 1995; Nams, 1996). Spectral analysis (Platt & Denman, 1975) has found more limited application in ecology, primarily in the analysis of oceanic plankton distributions (eg. Steele & Henderson, 1979). The biggest drawback to spectral analyses is the amount of data required. Variance decay spectra are the focus of this paper. For a comprehensive review of spatial analysis methods, at least for vegetation patterns, Turner et al. (1991) is excellent.

The null premise of variance decay spectra is that neighbouring samples are independent; that is, the value of the ecological quantity being measured is unaffected by the value of that quantity at a neighbouring location. This premise is obviously false at small scales; what is needed is a method of quantifying the degree to which it is false, and the distance one must move before it is true. A further premise is that the value of the quantity at all spatial locations is drawn from the same distribution; in other words the mean and variance of that quantity are identical everywhere in the area of interest. A sample at a particular location can be thought of as an estimate of this mean. Combining two neighbouring samples will be a more precise estimate of this mean; in fact, the standard error of the estimated mean will decrease as

$$s_n = \frac{\sigma}{\sqrt{n}} \qquad (7.1)$$

where σ is the standard deviation of the population of samples, n is the number of neighbouring samples being combined, and s_n is the standard error of n combined samples. Taking the logarithms of both sides shows us that the standard error of combined samples should decrease with the number of samples with a slope of -1/2. If these samples are neighbours, then the number n is the spatial scale, and the above formula describes how the standard deviation of the ecological quantity should decrease with increasing sampling scale. Smith (1938) was the first to point this statistical fact out, and used it to develop a method for determining the optimal plot size in crop yield experiments.

A decrease in variance can also be interpreted as an increase in predictability with scale. This process of increasing predictability has been explored with a self-organising model for coral reef communities (Green et al., 1987). Models formed from samples at a scale of 20 - 25 m were better able to predict the abundance of single species of coral, both within and between reefs, than models formed from data sampled at scales of 5 - 10 m. den Boer (1981) showed a similar result for two species of ground dwelling carabid beetles. The decrease in variance with scale for one of the species was later attributed to the importance of a small scale abiotic factor influencing mortality (van Dijk & den Boer, 1992).

Levin and Buttel (1986) suggested that a shallower slope than -1/2 on a variance decay plot is evidence of spatial correlation between the sample points. Levin and Buttel (1986) generated this sort of plot for the output of a single species, spatially explicit population model, and observed that at small scales the slope was significantly less than -1/2, up to a threshold, beyond which the slope was not distinguishable from -1/2. They suggested that this threshold point marked the characteristic scale of the system. In their model the characteristic scale depended on the size of disturbances applied to their model population. O'Neill *et al.* (1991) have utilised this method, which they dubbed the "Variance Staircase", to look for multiple scales of variation in remotely sensed land use data. They found that there could be several plateaus in a variance plot, interspersed with regions where the variance decreased linearly with a slope of -1/2.

In what appears to be an entirely separate line of inquiry, Crowley (1977) proposed a similar relationship between the temporal coefficient of variation (CV) and scale for animal populations. The temporal CV is the coefficient of variation of samples taken at one point many times. This is different from the variance in the variance staircase method, which is the variance of samples taken at many points at one time. The notion in the temporal CV analysis is that within small regions, populations will fluctuate synchronously. Small regions far apart relative to the characteristic scale will be subject to different random influences, and so will fluctuate asynchronously. When the variance of small regions over time is measured, it will be found to be large compared with the variance of regions large enough to enclose subregions that are out of synchrony with each other. This is because the population fluctuations within large regions tend to cancel out, leading to decreased variance. As with the Variance Staircase, the expected result of plotting the temporal CV against scale is a linear decrease with low slope at small scales, followed by a steeper, but still linear decrease at scales larger than the characteristic scale. Over scales where fluctuations in population density are asynchronous the slope is -1/2 (Crowley, 1977). De Roos *et al.* (1991) used this method to analyse a spatially explicit predator prey model, and found that the drop off to a slope of -1/2 was determined by the distance predators could move in search of prey.

Both the Variance Staircase and Temporal CV analyses have been used to find characteristic scales in spatially explicit population models. Given the underlying differences, one measuring variance in space, another in time, it can be legitimately asked if the characteristic scales detected by these two methods are in fact the same thing. The only way to do this is to perform both analyses on the same data set and compare the results. To my knowledge, this is the first time these two methods have been compared.

Spatially explicit population models and dispersal

I use the greater glider (*Petauroides volans*) model described in Chapter 2 to compare the performance of the above scale analysis methods on a single set of data. The model is individual based, and the position and life history state of all females in the population are tracked at one year intervals. The basic spatial unit is a female home range (assumed to be 1 ha in size), and all runs are performed on a 100 x 100 grid of home ranges. I use a uniform landscape in this chapter, with no introduced heterogeneity. I altered the adult age-related mortality, and fecundity slightly to ensure that populations reached an approximate equilibrium after 150 years to facilitate the spatial data analysis (Table 7.1). All runs in this chapter were 200 years in length, and data for the analyses were collected from either the last 25 years, or only the final year.

I use only two of the dispersal strategies outlined in Chapter 2: random walkers and global jumpers. The global jumping dispersal rule permits dispersing juveniles to access any territory on the landscape, while the random walkers can only move to their neighbouring territories.

Some typical examples of population sizes over time are shown in Figure 7.1 for the two different dispersal scenarios. By 150 years, regardless of the starting population, the total number of occupied territories in the system has reached a rough equilibrium, determined by the balance between births and deaths, especially deaths during dispersal (see Chapter 2). Obviously, the greater the proportion of territories that are occupied, the greater the mortality during dispersal, because newborns will have to move more often, on average, to find unoccupied home ranges. This introduces a form of density dependence in the model, stabilising the long term dynamics. The only apparent difference between the two dispersal scenarios at this level is the stronger density dependence shown when dispersal is localised.

Table 7.1 Life history parameters for the Greater Glider (*Petauroides volans*). All values are per capita rates. Where two values are given for a parameter, the first is for global dispersal, and the second is for localised dispersal. Where values have been altered from Chapter 2 the original values are in brackets.

Parameter	Newborn	Juvenile	Adult
Aging related mortality (per year)	0.5	0.15	0.137, 0.13 (0.15)
Dispersal mortality (per movement)	0.05	--	--
Fecundity (per year)	0	0	0.35 (0.5)

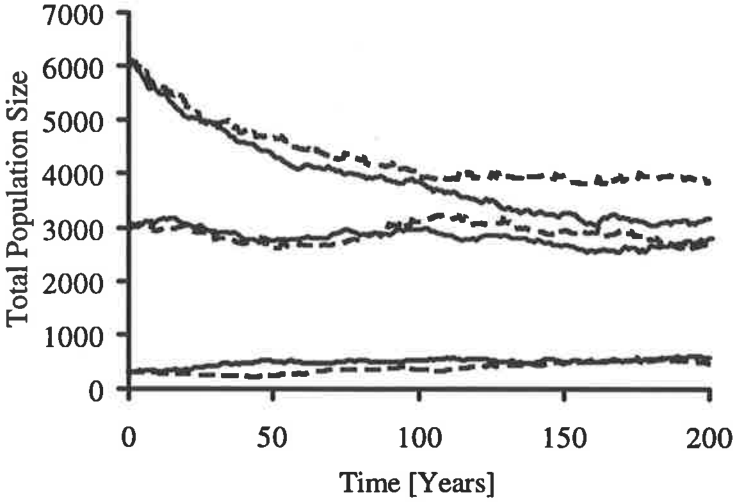

Figure 7.1 Typical population dynamics generated by the Greater Glider model. The three different starting population sizes are 6000, 3000, and 100. All runs used the same seed value for the random number generator. Solid lines are for localised dispersal. Dashed lines are for global dispersal.

If the population dynamics of this model appear uncomplicated, the same cannot be said of the spatial pattern of occupancy (Figure 7.2). Now a strong qualitative difference between the two dispersal scenarios is apparent; localised dispersal leads to "clumpier" patterns of occupation. This difference between global and local dispersal is not new; Green (1989) found similar effects of changes in dispersal ability for a model of vegetation subject to fire. The difficulty is to quantify this difference in a way that will allow us to determine the process that is responsible for the clumping. In the analyses that follow I use the methodology of the original authors as far as possible.

I applied the Variance Staircase method to these maps by running 20 transects horizontally across the landscape on every 5th row of territories. For a given scale, I calculated the proportion of territories occupied by all age classes along a segment of the transect of that length, and then computed the standard deviation among the 20 transects. For example, at the 1 km scale (10 territories) for each of the 20 transects, the proportion of the 10 territories occupied on the leftmost side of the landscape was calculated. The standard deviation at 2 km was calculated using the 20 leftmost territories of each transect, and so on. I expect that this quantity, the spatial standard deviation in proportion of territories occupied, will decrease with a slope of -1/2 at scales above the characteristic scale. In fact, this is exactly what occurs for both dispersal scenarios (Figure 7.3). The difference is that localised dispersal introduces a plateau at small scales where the spatial variance does not decrease as quickly as scale increases. This plateau is presumably related to the average size of the clumps that can be seen in Figure 7.2A.

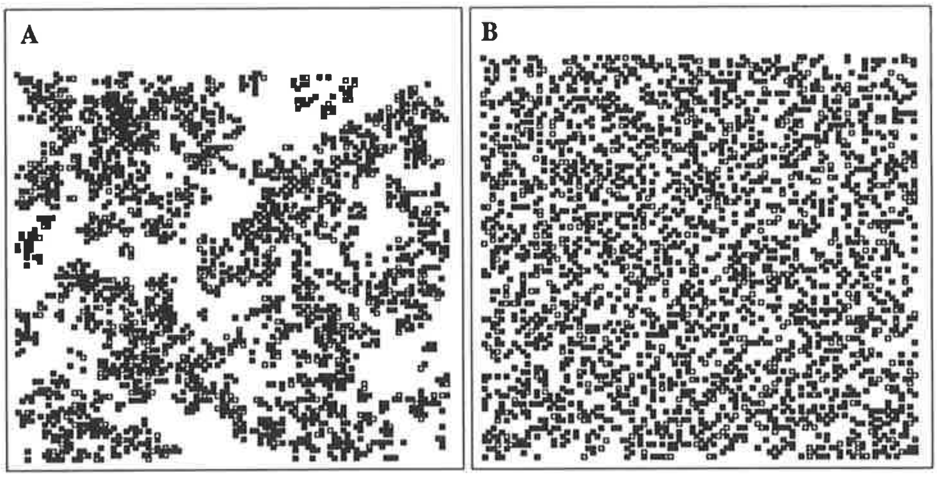

Figure 7.2 Maps of the landscape after 200 years, from starting populations of 3000 individuals. Closed squares represent adult gliders, open squares juvenile gliders. A) localised dispersal. B) global dispersal.

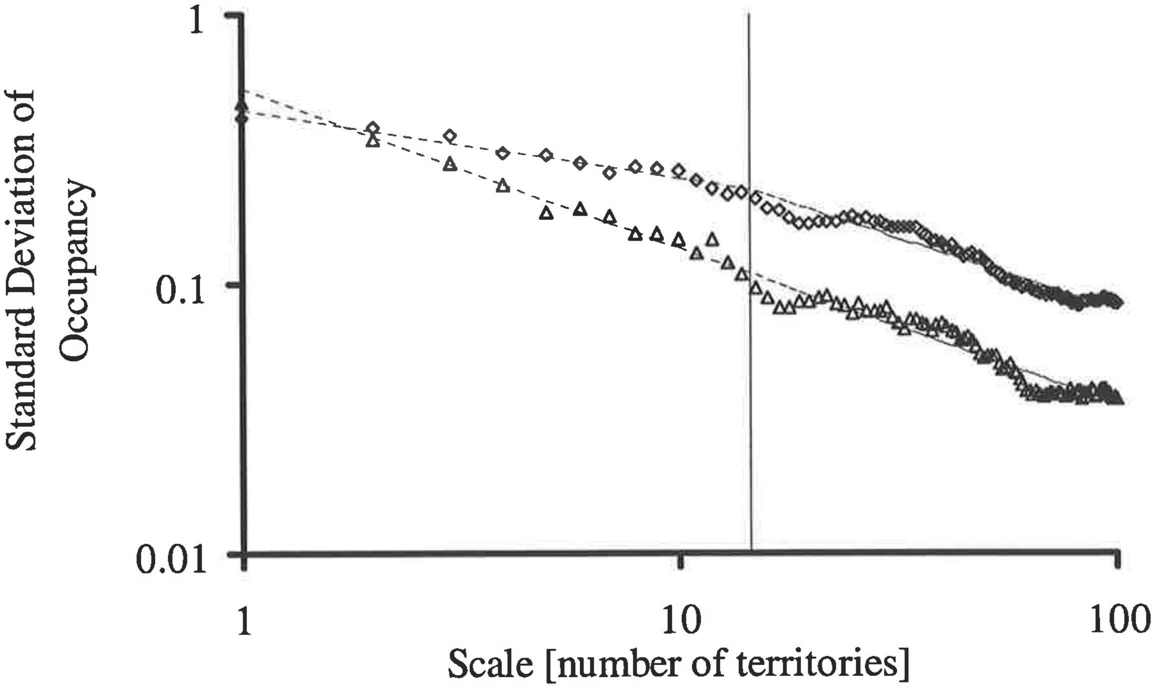

Figure 7.3 The standard deviation of the proportion of territories occupied among transects as a function of scale. Scale is the number of territories included in the transect, which is between 1 and 100. Open triangles are for global dispersal. Open diamonds are for localised dispersal. Fine vertical line is the characteristic scale identified by the split-line analysis. The split line for the local dispersal data has parameters β_1= -0.25, β_2 = -0.54, c = 1.16, d = -0.65, SSQ_m = 0.000898, n = 100. SSQ_m for the corresponding straight line was 0.00187. The line for the global dispersal data has parameters β = -0.59, a = -0.27, SSQ_m = 0.00151. SSQ_m for the corresponding split line was 0.00154

At this point I introduce an objective method of defining the point at which the variance begins to decrease, or the characteristic scale. It is a modification of the "split lines" method discussed by Perry (1982), and operates by minimising the sum of the squared differences (SSQ; Hilborn & Mangel, 1997) between the predicted and the observed log transformed variances. I use SSQ rather than a likelihood function because I have not worked out the proper sampling distribution of log-transformed variances and coefficients of variance, and the SSQ method does not require knowledge of the sampling distribution. Assuming that there is only a single point at which the variance begins to decrease more sharply, a "split line" can be defined as follows:

$$y = \begin{cases} if \;\; x \le c, d + \beta_1 (x - c) \\ if \;\; x > c, d + \beta_2 (x - c) \end{cases} \tag{7.2}$$

where β_i is the slope of either the first or second line, c is the point on the x axis where the break occurs, and d is the value of y at $x = c$. Note that this model requires four parameters, versus two for a normal straight line. The SSQ is defined as:

$$SSQ = \sum_i \left(y_{observed,i} - y_{predicted,i} \right)^2 \tag{7.3}$$

The parameters are chosen by minimising (7.3) with a Newton-Raphson minimisation algorithm from arbitrary starting points using the solver in Microsoft Excel (Version 7.0a) that obtains gradient information from a numerical approximation.

This method is not perfect, and different starting points for the parameters often leading to different local minima. The main difficulty was that the solver tended to push c out beyond the range of the data, at which point it would then quickly fit a straight line using d (ie. an intercept) and one of the slope parameters. This problem was readily detectable by a visual comparison of the model with the data and an ordinary least-squares fitted line, and could be corrected by choosing a different set of starting values for the parameters.

I compared the SSQ from the split line model with that from an ordinary straight line (the solver generated parameters identical to an ordinary least squares method) by using a modified SSQ that penalises a model for extra parameters (Hilborn & Mangel, 1997):

$$SSQ_m = \frac{SSQ}{n - 2m}$$

where n is the number of data points and m is the number of parameters. For each data set I picked the model with the lowest SSQ_m.

For the global dispersal data, the two parameter straight line was a better fit by SSQ_m. The local dispersal data was better fit with a split line, the parameter c indicating that characteristic scale occurred at about 14 territories (Figure 7.3). The slopes of the terminal segments for both dispersal methods are in the neighbourhood of -1/2. It is not possible to test if the difference is significant for the split line, but standard t-tests of the slope parameter for the global data indicate that it is significantly different from -1/2.

To perform the Temporal CV analysis, I calculated the coefficient of variation in the proportion of cells occupied in a square sample area centred on the landscape. The smallest scale examined was 4 territories; the largest was the entire landscape. I used only the last 25 years of data, during which there is little directional change in the total population size for both dispersal scenarios. Note that "scale" in this analysis refers to an area, whereas for the Variance Staircase (Figure 7.3) "scale" was referring to a linear distance. The expected slope on a log-log scale for this plot is -1/2. At scales less than the characteristic scale, the slope should be closer to zero. For both dispersal scenarios the split line model is a better fit than a straight line, and the temporal coefficient of variation is decreasing with approximately the same slope and less than -1/2 (β_1; Figure 7.4). For both split lines β_1 is also less than β_2, indicating a stabilisation of temporal variance at scales above 1180 - 1380 territories. This analysis detects no differences between the dispersal scenarios, unlike the previous analysis.

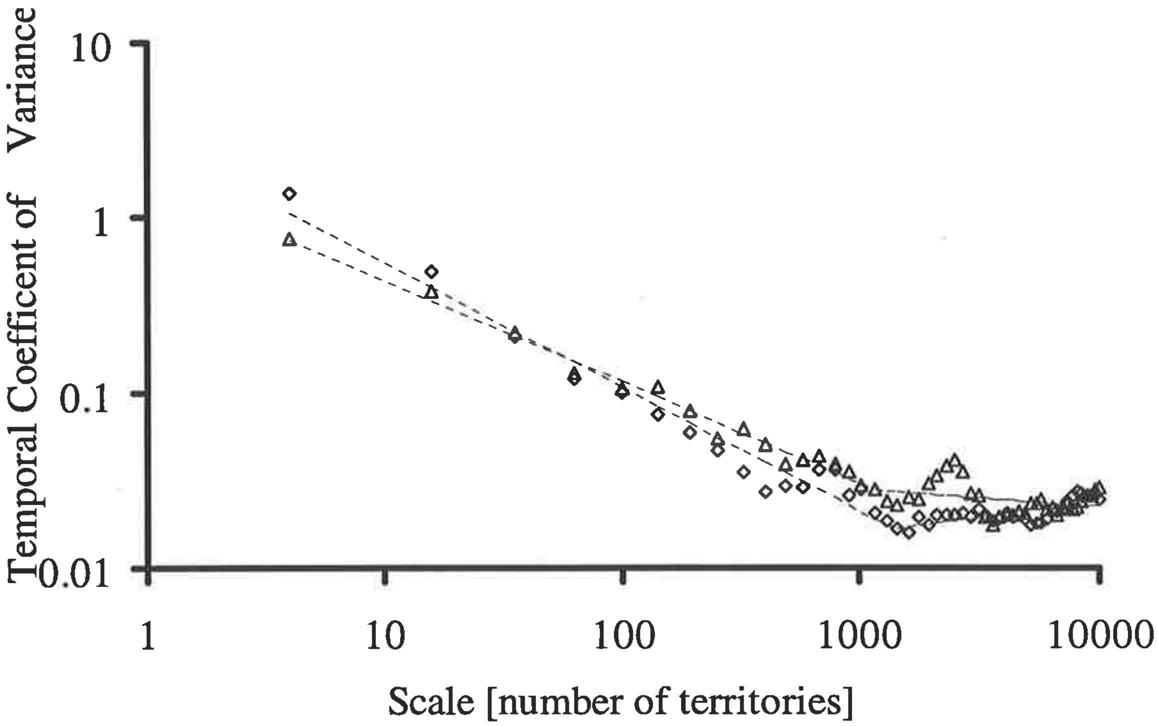

Figure 7.4 Temporal coefficient of variation in proportion of territories occupied as a function of the number of territories under observation (scale). Measurements were taken from a square centred on the landscape over the last 25 years of the runs started with population sizes of 3000. Open triangles are for global dispersal. Open diamonds are for localised dispersal. The parameters for the split lines are: local dispersal $\beta_1 = -0.71$, $\beta_2 = 0.19$, $c = 7.23$, $d = -4.1$, $SSQ_m = 0.026$ (versus 0.19 for a straight line); global dispersal $\beta_1 = -0.58$, $\beta_2 = -0.09$, $c = 7.08$, $d = -3.6$, $SSQ_m = 0.031$ (versus 0.08 for a straight line). $n = 50$ for both series.

Discussion

In this section I tested both the variance staircase and the temporal CV analysis against a simulated data set, and introduced an objective method for identifying characteristic scale breaks. Like the other models these methods have been applied to in the literature, I used a simulated landscape with no heterogeneity. Therefore the variance of the ecological processes on the landscape is homogenous. Even though both methods were proposed to measure characteristic scale, they yield different results when applied to the same data set. While the notion of a characteristic scale has intuitive appeal, it is clear that it is poorly defined quantitatively.

The Temporal CV method measures how temporal variability is reduced at larger scales of observation. Thus, the characteristic scale in this sense is truly related to a population dynamics process. The scale measured in this way should be related to the strength of processes like dispersal and disturbance that could couple the dynamics of neighbouring regions. Nonetheless, the Temporal CV method did not detect any differences between the global and local dispersal scenarios in the simulation model. This could be because the temporal variation in the model is homogenous. Even though it appears from a snapshot that there are clumps of high density (Figure 7.2) when dispersal is localised, these clumps are not static. A sequence of snapshots (not shown) indicates that these clumps tend to drift randomly about the landscape through time. Observing any small portion of the landscape will yield the same temporal variation, regardless of where that point is located. The actual abundance at any one point in time may well be asynchronous between different regions in space, but this pattern is not what the temporal CV method is analysing.

It is interesting to note that the Temporal CV method detects a break to non-decreasing or even increasing variance at large scales. In his original paper, Crowley (1977) suggested that the variance - scale relationship would be initially flat, then decreasing with slope -1/2, and then tend to flatten out again. It appears as though the first break is undetected in my analysis, although the second break is. The method of fitting split lines appears to be a useful and objective method of finding the breakpoints.

The Variance Staircase did detect differences between dispersal scenarios, which is reassuring given the qualitative differences in the locations of individuals in the population. This suggests that the Variance Staircase might be good at distinguishing random from localised processes. This analysis clearly is picking up differences present in snapshot data. Further testing would be required to determine if the Variance Staircase can provide additional information. For example, it may be that it would detect changes in the occupancy pattern when gliders in the localised dispersal scenario can take bigger steps.

At least one prominent ecological theorist has asserted that variation in space and time are 'ergodic' or replaceable (Levin & Buttel, 1986). Clearly in the model analysed here that is not true, or else the two analyses would have identified similar patterns. Assumptions that might be valid for analytical models do not necessarily hold in individual based simulations, even when the background variation is homogenous.

Characteristic scales using real data

Applying a series of statistical analyses to the output of a simulation model can be enlightening, and highlights the differences between concepts to which the same name has been applied. However, none of these analyses can be truly shown to have any utility before they have been applied to empirical ecological data. Unfortunately, population dynamics data on temporal and spatial extents large enough, and spatial resolutions fine enough, to test these methods are rare. In Chapter 4 15 years of mark-recapture data of Sleepy Lizards (*Tiliqua rugosa*) along over 70 km of transects in South Australia, at a spatial resolution of 50 m (see Bull 1995 for details) are described. I calculated Jolly-Seber estimates of population size for contiguous regions 500 m in length along three of the transects (1, 3, and 4, details in Chapter 4). After discarding estimates for years with too few recaptures, and for sparsely sampled regions of the transects, I have estimates over 5 consecutive years (1988 - 1992) along 11 km of all three transects. The estimates for Transect 1 are shown in Figure 7.5.

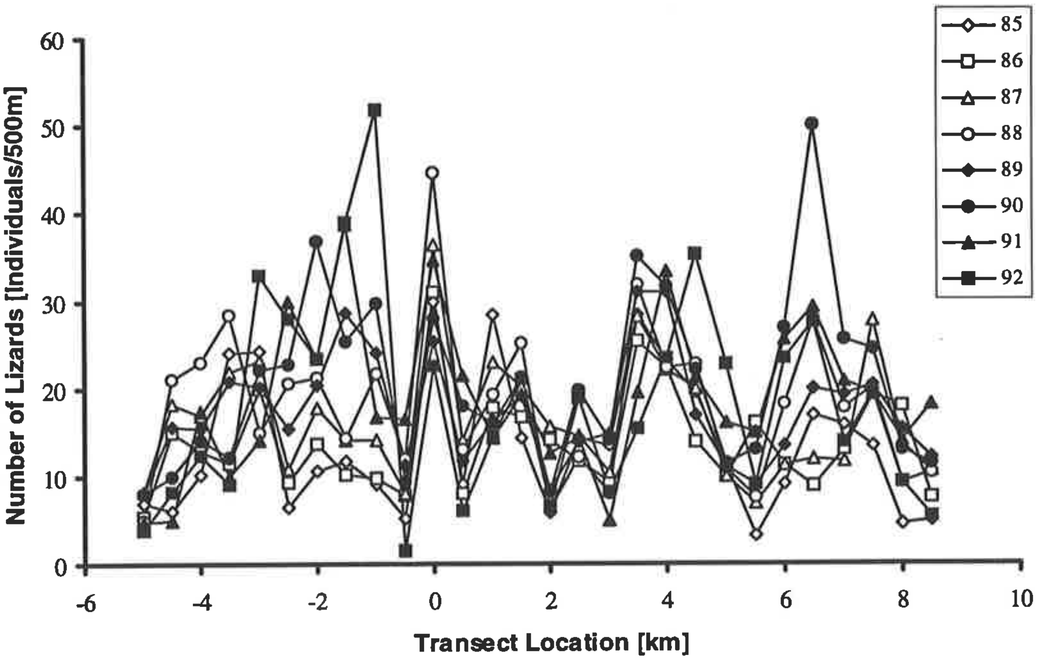

Figure 7.5 Spatial and temporal variation in lizard abundance along Transect 1 between 1985 and 1992. Confidence intervals not shown for clarity. Temporal trends vary with space; to see this, note that open symbols are early in the sequence, filled symbols late. At some locations filled symbols are above empty ones, indicating a positive trend, in other the reverse is true.

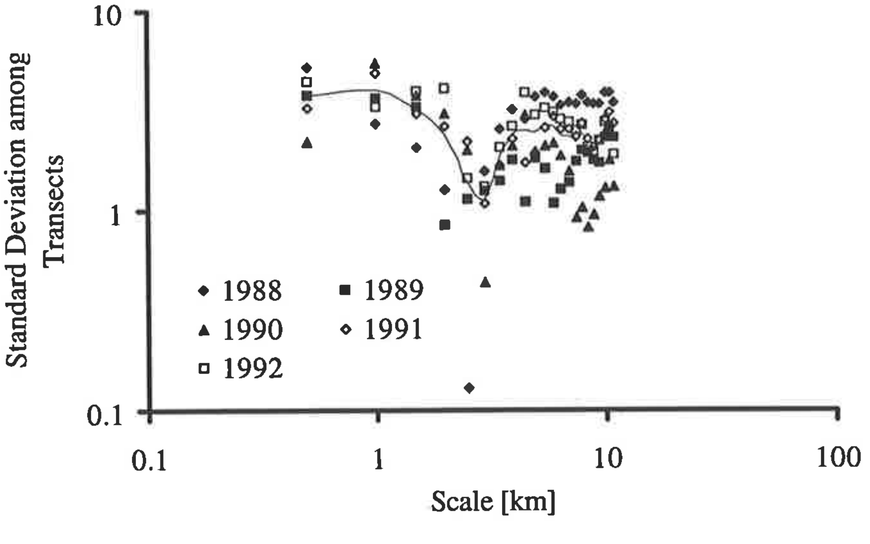

Figure 7.6 Variance staircase analysis of Sleepy Lizard mark-recapture data. Each point is the variance among the three transects for that year and scale. The solid line is a cubic spline fitted through the average SD among all five years.

The Temporal CV analysis was conducted by calculating the coefficient of variation for a lumped series of segments among all 5 years. As before, neighbouring segments were lumped by averaging, and the zooming process started with the most northerly or westerly segments of the transect. Each of the transects yields a separate plot, so there are 3 replicates.

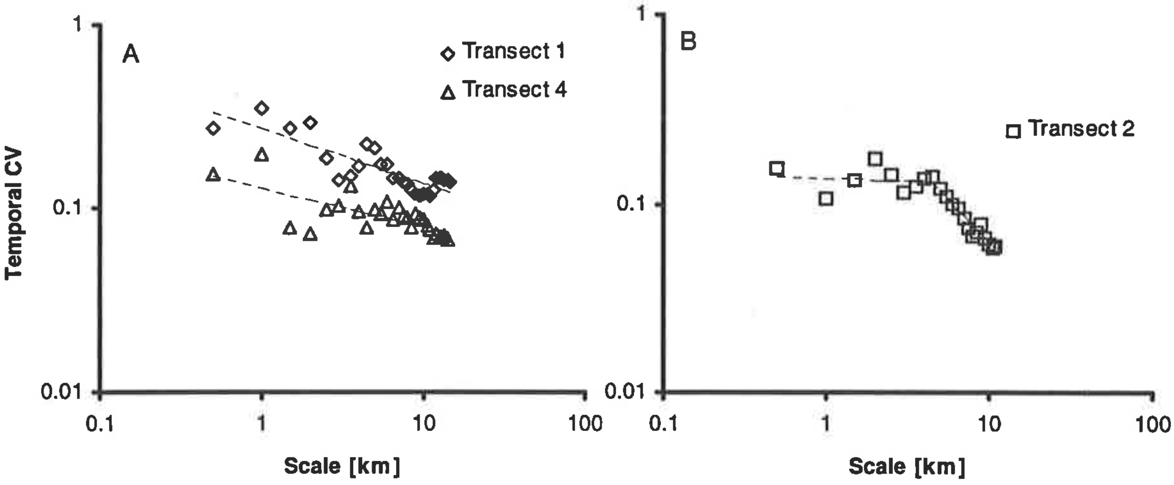

Figure 7.7 Temporal coefficient of variation analysis of the sleepy lizard data. The CV has been calculated over 5 years for each of the three transects. A) Parameters for best fit single lines to transects 1 and 4: Transect 1 $\beta = -0.29$, $a = -1.31$, $SSQ_m = 0.031$ (versus 0.035 for split line), $n = 29$; Transect 4 $\beta = -0.21$, $a = -2.05$, $SSQ_m = 0.034$ (versus 0.037 for split line), $n = 28$. B) Parameters of best fit split line to Transect 3: $\beta_1 = -0.029$, $\beta_2 = -0.94$, $c = 1.5$, $d = -2.04$, $SSQ_m = 0.015$ (versus 0.052 for a straight line), $n = 22$.

The temporal coefficient of variation analysis matches the expected pattern better, especially the pattern for Transect 3. All three transects show a roughly linear decline, with "flat" regions at smaller scales. However, split lines fit only transect 3 significantly better than straight lines, with the break occurring at a scale of 4.5 km. The slope after the break is much less than the expected value of -1/2. The extra variability introduced by the small sample sizes obscures the expected result, but in this case it appears qualitatively similar to what I expected to see.

Discussion

Applying these analyses to empirical data has highlighted an important underlying assumption of both methods. The process generating the patterns, or the variances, must be stationary in space. That is, even if the processes are independent, the processes at different points in space must have the same parameters. This is clearly true for the simulated data; there is no variation in space for the life history parameters. There is no reason to expect that this would be true in reality. The completely unexpected pattern for the Variance Staircase when applied to the lizard population data could be explained by a lack of stationarity in the population processes of the lizards. This assumption may be less critical for the Temporal CV analysis, because the coefficient of variation is a relative measure. The average population density could vary tremendously in space, and the CV could still be the same. However, there are substantial differences between the three transects, and this could be a result of non-stationarity.

Both the computation and the interpretation of these purportedly quantitative methods are very arbitrary. Determining just where along the plot a change of slope occurs is a matter of judgement. O'Neill *et al.* (1991) used an iterative procedure of calculating a regression slope, predicting the next point, and then either adding it in if correctly predicted, or using it as the starting point for a new slope. The statistical validity of this procedure is dubious at best, and I have opted here for being transparent about the arbitrary nature of the interpretation.

Conclusion

The need for explicit, quantitative measures of the characteristic scale, or the scale of variability, in ecosystems has lead to the proposal of a number of methods and concepts. These methods have never been subjected to rigorous testing to determine their sensitivity to patterns, or to violations of their assumptions. In this chapter I have tested two methods for measuring characteristic scales against both a simulated data set, and an empirical data set. These tests highlighted problems with the proposed methods, the Variance Staircase, and the Temporal CV, and with the underlying concept of a characteristic scale.

The results of the empirical tests are interesting for a more general reason than just the differences in analysis. The magnitude of temporal variation in population dynamics across different taxa has been a question of interest to ecologists since Schoener (1985) first noted that lizard populations appear to be less variable through time than mammals. My work here has introduced a hitherto ignored co-variate in the debate: the scale of the analysis relative to dispersal ability or characteristic scales. If lizards have consistently been sampled at larger scales relative to their dispersal ability than other taxa, then they would appear to be less variable with time even though there is no mechanistic reason for it.

Quantifying characteristic scales of ecological processes is an important step towards being able to compare analytical results between different ecosystems (Addicott et al., 1987). I have shown here that two proposed methods of measuring the characteristic scale of an ecosystem are fraught with problems, and pose more problems than they resolve. To answer the question posed in the title of this chapter, characteristic scales in ecology are certainly fiction, possibly fact, and looking for them seems to be futile!

Chapter 8 General Discussion

In this thesis I employed spatially explicit models and computer intensive analysis for two main purposes. First, I explored how processes acting at the individual level scale up to population dynamics when processes are variable in space. Second, I explored the consequences of sampling spatially complex variability for drawing conclusions from the often limited data available to ecologists.

The individual level processes I concentrated on were dispersal and variation in mortality and development. The marsupial model of chapter 2 and 3 was concerned with the consequences of natal dispersal on heterogenous landscapes. Birth and death were also considered at the individual scale, but the primary motivation for this model was the consequences of variation in dispersal. To my knowledge, the population consequences of different dispersal strategies across landscapes have never been compared in a single place. Spatially explicit models incorporating local dispersal normally proceed by chosing a single strategy, and then exploring the consequences of that strategy (eg. Doak et al., 1992; Gustafson & Gardner, 1996). The lesson from this thesis is that using a random walk dispersal behaviour versus a habitat selector or straight line dispersal has significant consequences at the population level. Random walking dispersers achieving higher population sizes than individuals that seek out good habitat for themselves (chapter 2). This population response to the mechanism of dispersal adds another dimension to the observation that errors in the estimation of dispersal parameters propagate through the results of spatially explicit models (Hartway et al., 1998). My model has demonstrated that in addition to mortality rates, incorrectly estimating the kind of directional response individuals make to the landscape during dispersal (ie. random, biased random, or hill climbing) can have significant repercussions.

The marsupial model also demonstrated that correlations between a structural habitat variable (eg. the basal area of acacia trees, or the number of hollow trees) and abundance or occupancy can arise in the absence of active habitat selection. Correlations arise if individuals are restricted to moving locally, and habitat quality is spatially auto-correlated. Thus estimating correlations between abundance and habitat is unlikely to identify the kind of directional response used by a species, in addition to the other failings of such habitat models as discussed in chapter 3.

The tick model has little obvious individual level behaviour, with variable mortality and development being the individual level processes of interest. The model identified fruitful avenues for future research. In particular, understanding the behaviour of hosts towards nocturnal refuge sites is clearly critical to understanding tick population dynamics. The incorporation of spatial and temporal variation into survival and development of ticks clearly demonstrated that using spatiotemporal average rates in the model (ie. ignoring spatialtemporal variability) leads the model to overestimate tick population growth rates.

The second main purpose to my thesis was to use spatially explicit models to understand the observation processes employed by ecologists on spatially complex landscapes. This approach, which I call the "virtual ecologist", is the key to effective use of spatially explicit models in the future (Hartway et al., 1998). I employed this technique in two chapters of this thesis. With the marsupial model I examined the utility of estimating correlations between habitat variables and occupancy. The most interesting conclusion from this approach in this thesis is the observation that probability of occupancy, however estimated, is a surrogate for colonisation rate. This is exciting, because the colonisation rate, a function of dispersal ability, is clearly an important part of understanding and predicting the dynamics of populations for management purposes. Unfortunately, occupancy does not provide information about the other crucial parameter, survival or extinction.

I used the virtual ecologist approach in the tick model to consider the effect of sampling only the proportion of the tick population that is present on lizards on the ability to estimate variation in the tick population as a whole. Because the proportion of the population that is not observable in refuges is highly variable, the number of ticks counted on lizards is a poor indicator of changes in tick abundance.

This thesis has demonstrated that it is possible to go beyond the assumptions of homogeneity, and use spatially explicit models to understand how spatial variability and its interaction with individual level processes influences population dynamics. Finally, this thesis has shown that the "virtual ecologist" is a viable means of improving ecological sampling on spatially complex landscapes. If carefully developed and interpreted, the future of spatially explicit models in applied population management is bright.

Appendix A

The following table presents the citations and classifications for all 173 papers discussed in the introduction and Table 1.1.

Citation	Type	# Species	Scale	Topic
(Cantrell et al., 1996)	General	Multi	Coarse	Persistence
(Rohani & Miramontes, 1995)	General	Multi	Coarse	Persistence
(Auger & Faivre, 1993)	General	Multi	Coarse	Stability
(Bowers & Harris, 1994)	General	Multi	Coarse	Stability
(Comins et al., 1992)	General	Multi	Coarse	Stability
(Goldwasser et al., 1994)	General	Multi	Coarse	Stability
(Hassell et al., 1991)	General	Multi	Coarse	Stability
(Malchow, 1988)	General	Multi	Coarse	Stability
(Malchow, 1995)	General	Multi	Coarse	Stability
(McLaughlin & Roughgarden, 1991)	General	Multi	Coarse	Stability
(McLaughlin & Roughgarden, 1992)	General	Multi	Coarse	Stability
(Murdoch et al., 1992)	General	Multi	Coarse	Stability
(Solé et al., 1992)	General	Multi	Coarse	Stability
(Sugai & Fukao, 1989)	General	Multi	Coarse	Stability
(Colasanti & Grime, 1993)	General	Multi	Coarse	Other
(Hess, 1996)	General	Multi	Coarse	Other
(Holmes et al., 1994)	General	Multi	Coarse	Other
(Veldkamp & Fresco, 1996)	General	Multi	Coarse	Other
(Czaran, 1989)	General	Multi	Fine	Stability
(Lewis, 1994)	General	Multi	Fine	Stability
(McCauley et al., 1993)	General	Multi	Fine	Stability
(Tainaka, 1994)	General	Multi	Fine	Stability
(Tainaka, 1996)	General	Multi	Fine	Stability
(Wilson et al., 1993)	General	Multi	Fine	Stability
(Wilson et al., 1995)	General	Multi	Fine	Stability
(Bartha et al., 1995)	General	Multi	Fine	Other
(Bernstein et al., 1991)	General	Multi	Fine	Other
(Green, 1989)	General	Multi	Fine	Other
(Hendry et al., 1996)	General	Multi	Fine	Other

(Lhotka, 1994)	General	Multi	Fine	Other
(Neubert et al., 1995)	General	Multi	Fine	Other
(Claessen & De Roos, 1995)	General	Multi	Medium	Stability
(Rees & Long, 1992)	General	Multi	----	Persistence
(Wood & Thomas, 1996)	General	Multi	----	Persistence
(Hassell et al., 1994)	General	Multi	----	Stability
(Smith, 1991)	General	Multi	----	Stability
(Szymanski & Caraco, 1994)	General	Multi	----	Stability
(Halley et al., 1994)	General	Multi	----	Other
(Laval, 1996)	General	Multi	----	Other
(Olson & Sequeira, 1995)	General	Multi	----	Other
(Onstad et al., 1990)	General	Multi	----	Other
(Ruardij et al., 1995)	General	Multi	----	Other
(Wilhoit, 1991)	General	Multi	----	Other
(Adler & Nuernberger, 1994)	General	Single	Coarse	Persistence
(Fahrig & Merriam, 1994)	General	Single	Coarse	Persistence
(Fahrig, 1997)	General	Single	Coarse	Persistence
(Pease et al., 1989)	General	Single	Coarse	Persistence
(Perry & Gonzalez Andujar, 1993)	General	Single	Coarse	Persistence
(Possingham & Davies, 1995)	General	Single	Coarse	Persistence
(Wu et al., 1993)	General	Single	Coarse	Persistence
(Doak et al., 1992)	General	Single	Coarse	Spread
(Lewis & Kareiva, 1993)	General	Single	Coarse	Spread
(Ruxton, 1996)	General	Single	Coarse	Stability
(Solé & Valls, 1992)	General	Single	Coarse	Stability
(Cavalli Sforza & Feldman, 1990)	General	Single	Coarse	Other
(Hof et al., 1994)	General	Single	Coarse	Other
(Sato & Iwasa, 1993)	General	Single	Coarse	Other
(Harada et al., 1995)	General	Single	Fine	Persistence
(Gibson & Austin, 1996)	General	Single	Fine	Spread
(Hara, 1994)	General	Single	Fine	Stability
(Hara & Wyszomirski, 1994)	General	Single	Fine	Stability
(Molofsky, 1994)	General	Single	Fine	Stability
(Bonan, 1991)	General	Single	Fine	Other

(Bonan, 1993)	General	Single	Fine	Other
(Ferriere & Michod, 1996)	General	Single	Fine	Other
(Hutson & Vickers, 1995)	General	Single	Fine	Other
(Iwasa et al., 1991)	General	Single	Fine	Other
(Kenkel, 1991)	General	Single	Fine	Other
(Lavorel et al., 1995)	General	Single	Fine	Other
(Sipper, 1994)	General	Single	Fine	Other
(Wallinga, 1995)	General	Single	Fine	Other
(Fahrig, 1992)	General	Single	----	Persistence
(Van Den Bosch et al., 1990)	General	Single	----	Spread
(Andersen, 1991)	General	Single	----	Stability
(Bascompte & Solé, 1994)	General	Single	----	Stability
(Cantrell & Cosner, 1991)	General	Single	----	Stability
(Goldstein & Holsinger, 1992)	General	Single	----	Other
(Sato, 1995)	General	Single	----	Other
(Vickers, 1989)	General	Single	----	Other
(Vickers et al., 1993)	General	Single	----	Other
(Zhylyayev, 1991)	General	Single	----	Other
(Hochberg et al., 1994a)	Specific	Multi	Coarse	Persistence
(Barlow, 1993)	Specific	Multi	Coarse	Spread
(Dale et al., 1991)	Specific	Multi	Coarse	Spread
(Reyes et al., 1994)	Specific	Multi	Coarse	Spread
(Wollkind et al., 1991)	Specific	Multi	Coarse	Stability
(Baretta et al., 1995)	Specific	Multi	Coarse	Other
(Broekhuizen et al., 1995)	Specific	Multi	Coarse	Other
(Bryant et al., 1995)	Specific	Multi	Coarse	Other
(De Wit et al., 1995)	Specific	Multi	Coarse	Other
(Garnier et al., 1995)	Specific	Multi	Coarse	Other
(Kumar et al., 1991)	Specific	Multi	Coarse	Other
(Malanson & Cairns, 1995)	Specific	Multi	Coarse	Other
(Malanson, 1996)	Specific	Multi	Coarse	Other
(Moloney et al., 1992)	Specific	Multi	Coarse	Other
(Moloney & Levin, 1996)	Specific	Multi	Coarse	Other
(Real & McElhany, 1996)	Specific	Multi	Fine	Spread
(Czaran & Bartha, 1989)	Specific	Multi	Fine	Other
(Fahrig et al., 1994)	Specific	Multi	Fine	Other

(Hoy et al., 1990)	Specific	Multi	Fine	Other
(Morris, 1993)	Specific	Multi	Fine	Other
(Pacala et al., 1996)	Specific	Multi	Fine	Other
(Turner et al., 1994)	Specific	Multi	Fine	Other
(Wilson et al., 1991)	Specific	Multi	Fine	Other
(White & Harris, 1995)	Specific	Multi	Medium	Spread
(Gibbs, 1993)	Specific	Multi	----	Persistence
(Murray & Seward, 1992)	Specific	Multi	----	Spread
(Okubo et al., 1989)	Specific	Multi	----	Spread
(Smith & Harris, 1991)	Specific	Multi	----	Spread
(Gaedke & Ebenhoeh, 1991)	Specific	Multi	----	Stability
(Rees et al., 1996)	Specific	Multi	----	Other
(Schneider, 1992)	Specific	Multi	----	Other
(Botsford et al., 1994)	Specific	Single	Coarse	Persistence
(Day & Possingham, 1995)	Specific	Single	Coarse	Persistence
(Gotelli, 1991)	Specific	Single	Coarse	Persistence
(Hanski et al., 1994)	Specific	Single	Coarse	Persistence
(Hanski & Thomas, 1994)	Specific	Single	Coarse	Persistence
(Kindvall & Ahlen, 1992b)	Specific	Single	Coarse	Persistence
(Kmet & Holcik, 1994)	Specific	Single	Coarse	Persistence
(Lamberson et al., 1994)	Specific	Single	Coarse	Persistence
(Lebreton, 1996)	Specific	Single	Coarse	Persistence
(Lindenmayer & Possingham, 1995a)	Specific	Single	Coarse	Persistence
(Lindenmayer & Possingham, 1995b)	Specific	Single	Coarse	Persistence
(Lindenmayer & Possingham, 1996)	Specific	Single	Coarse	Persistence
(Southgate & Possingham, 1995)	Specific	Single	Coarse	Persistence
(Topping & Sunderland, 1994)	Specific	Single	Coarse	Persistence
(Deriso et al., 1991)	Specific	Single	Coarse	Spread
(Matis et al., 1994)	Specific	Single	Coarse	Spread
(Mullen, 1989)	Specific	Single	Coarse	Spread
(Polymenopoulos & Long, 1990)	Specific	Single	Coarse	Spread
(Baker, 1993)	Specific	Single	Coarse	Other

(Collie & Walters, 1991)	Specific	Single	Coarse	Other
(Fiksen et al., 1995)	Specific	Single	Coarse	Other
(Fletcher, 1992)	Specific	Single	Coarse	Other
(Flinn et al., 1992)	Specific	Single	Coarse	Other
(Fulton, 1991)	Specific	Single	Coarse	Other
(Hilborn, 1990)	Specific	Single	Coarse	Other
(Pet et al., 1996)	Specific	Single	Coarse	Other
(Possingham & Roughgarden, 1990)	Specific	Single	Coarse	Other
(Rijnsdorp & Pastoors, 1995)	Specific	Single	Coarse	Other
(Zuidema et al., 1994)	Specific	Single	Coarse	Other
(Arnold & Holford, 1995)	Specific	Single	Fine	Spread
(Black & Moran, 1991)	Specific	Single	Fine	Spread
(Hochberg et al., 1994b)	Specific	Single	Fine	Spread
(Korzukhin & Porter, 1994)	Specific	Single	Fine	Spread
(Schotzk & Knudsen, 1992)	Specific	Single	Fine	Spread
(Turchin, 1991)	Specific	Single	Fine	Spread
(With & Crist, 1995)	Specific	Single	Fine	Spread
(During, 1995)	Specific	Single	Fine	Stability
(Hermann et al., 1996)	Specific	Single	Fine	Stability
(Batchelder & Williams, 1995)	Specific	Single	Fine	Other
(Britton et al., 1996)	Specific	Single	Fine	Other
(Cain et al., 1995)	Specific	Single	Fine	Other
(Crist & Wiens, 1995)	Specific	Single	Fine	Other
(Knudsen & Schotzko, 1991)	Specific	Single	Fine	Other
(Lovvorn & Gillingham, 1996)	Specific	Single	Fine	Other
(Mason & Brandt, 1996)	Specific	Single	Fine	Other
(Milne et al., 1992)	Specific	Single	Fine	Other
(Williams et al., 1992)	Specific	Single	Fine	Other
(Akcakaya et al., 1995)	Specific	Single	Medium	Persistence
(Doak, 1989)	Specific	Single	Medium	Persistence
(McCarthy, 1996)	Specific	Single	Medium	Persistence
(Akcakaya & Baur, 1996)	Specific	Single	----	Persistence
(Kenney et al., 1995)	Specific	Single	----	Persistence
(Pulliam et al., 1992)	Specific	Single	----	Persistence
(Thomas, 1996)	Specific	Single	----	Persistence

(Atzeni et al., 1994)	Specific	Single	----	Spread
(Berg & Hamrick, 1995)	Specific	Single	----	Other
(Gonzalez Andujar & Perry, 1995)	Specific	Single	----	Other
(Madenjian et al., 1995)	Specific	Single	----	Other
(Rose et al., 1993)	Specific	Single	----	Other
(Simmonds & Fryer, 1996)	Specific	Single	----	Other
(Wiles et al., 1992)	Specific	Single	----	Other

Literature Cited

Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S. & Soluk, D. A. (1987). Ecological neighborhoods: scaling environmental patterns. *Oikos* **49**, 340-346.

Adler, F. R. & Nuernberger, B. (1994). Persistence in patchy irregular landscapes. *Theoretical Population Biology* **45**, 41-75.

Akcakaya, H. R. & Baur, B. (1996). Effects of population subdivision and catastrophes on the persistence of a land snail metapopulation. *Oecologia* **105**, 475-483.

Akcakaya, H. R., McCarthy, M. A. & Pearce, J. L. (1995). Linking landscape data with population viability analysis: Management options for the helmeted honeyeater Lichenostomus melanops cassidix. *Biological Conservation* **73**, 169-176.

Allaine, D., Rodrigue, I., Berre, M. L. & Ramousse, R. (1994). Habitat preferences of alpine marmots, Marmota marmota. *Canadian Journal of Zoology* **72**, 2193-2198.

Allen, T. F. H. & Starr, T. B. (1982). *Hierarchy: perspecitves for ecological complexity.* Chicago: University of Chicago Press.

Andersen, M. (1991). Properties of some density-dependent integrodifference equation population models. *Mathematical Biosciences* **104**, 135-157.

Anderson, M. J. & Gribble, N. A. (1998). Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Australian Journal of Ecology* **23**, 158-167.

Anderson, R. M. & Gordon, D. M. (1982). Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology* **85**, 373-398.

Andrewartha, H. G. & Birch, L. C. (1954). *The distribution and abundance of animals.* Chicago: University of Chicago Press.

Andrews, R. H., Petney, T. N. & Bull, C. M. (1982). Reproductive interference between 3 parapatric species of reptile tick. *Oecologia* **52**, 281-286.

Arnold, G. P. & Holford, B. H. (1995). A computer simulation model for predicting rates and scales of movement of demersal fish on the European continental shelf. *ICES Journal of Marine Science* **52**, 981-990.

Atzeni, M. G., Mayer, D. G., Spradbery, J. P., Anaman, K. A. & Butler, D. G. (1994). Comparison of the predicted impact of a screwworm fly outbreak in Australia using a growth index model and a life-cycle model. *Medical and Veterinary Entomology* **8**, 281-291.

Auger, P. & Faivre, B. (1993). Propagation of extinction waves in spatial models of interspecific competition and selective predation. *Acta Oecologica* **14**, 781-805.

Augustin, N. H., Muggleston, M. A. & Buckland, S. T. (1996). An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology* **33**, 339-347.

Austin, M. P., Meyers, J. A. & Doherty, M. D. (1994). Data capability, sub-project 3. Modelling of landscape patterns and processes using biological data. Canberra, Division of Wildlife and Ecology, CSIRO.

Austin, M. P., Nicholls, A. O. & Margules, C. R. (1990). Measurement of the realised qualitative niche: environmental niches of five *Eucalyptus* species. *Ecological Monographs* **60**, 161-177.

Commonwealth of Australia (1992). National Forest Policy Statement.

Baker, W. L. (1993). Spatially heterogeneous multi-scale response of landscapes to fire suppression. *Oikos* **66**, 66-71.

Baretta, J. W., Ebenhoeh, W. & Ruardij, P. (1995). The European regional seas ecosystem model, a complex marine ecosystem model. *Netherlands Journal of Sea Research* **33**, 233-246.

Barlow, N. D. (1993). A model for the spread of bovine Tb in New Zealand possum populations. *Journal of Applied Ecology* **30**, 156-164.

Bartha, S., Czaran, T. & Oborny, B. (1995). Spatial constraints masking community assembly rules: A simulation study. *Folia Geobotanica et Phytotaxonomica* **30**, 471-482.

Bascompte, J. & Solé, R. V. (1994). Spatially induced bifurcations in single-species population dynamics. *Journal of Animal Ecology* **63**, 256-264.

Batchelder, H. P. & Williams, R. (1995). Individual-based modelling of the population dynamics of Metridia lucens in the North Atlantic. *ICES Journal of Marine Science* **52**, 469-482.

Baur, A. & Baur, B. (1993). Daily movement patterns and dispersal in the land snail Arianta arbustorum. *Malacologia* **35**, 89-98.

Berg, E. E. & Hamrick, J. L. (1995). Fine-scale genetic structure of a turkey oak forest. *Evolution* **49**, 110-120.

Bernstein, C., Kacelnik, A. & Krebs, J. R. (1991). Individual decisions and the distribution of predators in a patchy environment: II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology* **60**, 205-226.

Berryman, A. A. (1991). Stabilization or regulation: what it all means! *Oecologia* **86**, 140-143.

Biggins, D. E., Miller, B. J., Hanebury, L. R., Oakleaf, B., Farmer, A. H., Crete, R. & Dood, A. (1993). A Technique for evaluating black-footed ferret Habitat. *U. S. Fish and Wildlife Service Biological Report* **93**, 73-88.

Black, K. P. & Moran, P. J. (1991). Influence of hydrodynamics on the passive dispersal and initial recruitment of larvae of Acanthaster planci (Echinodermata: Asteroidea) on the Great Barrier Reef. *Marine Ecology Progress Series* **69**, 55-65.

Block, W. M. & Brennan, L. A. (1993). The habitat concept in ornithology: theory and applications. In: *Current Ornithology, Volume 11.* (Power, D. M. ed. pp. 35-91. New York: Plenum Press.

Bonan, G. B. (1991). Density effects on the size structure of annual plant populations: An indication of neighbourhood competition. *Annals of Botany* **68**, 341-348.

Bonan, G. B. (1993). Analysis of neighborhood competition among annual plants: Implications of a plant growth model. *Ecological Modelling* **65**, 123-136.

Bonsall, M. B., Jones, T. H. & Perry, J. N. (1998). Determinants of dynamics: population size, stability, and persistence. *Trends in Ecology and Evolution* **13**, 174-176.

Botsford, L. W., Moloney, C. L., Hastings, A., Largier, J. L., Powell, T. M., Higgins, K. & Quinn, J. F. (1994). The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. *Deep Sea Research Part II Topical Studies in Oceanography* **41**, 107-145.

Bowers, M. A. & Harris, L. C. (1994). A large-scale metapopulation model of interspecific competition and environmental change. *Ecological Modelling* **72**, 251-273.

Bradbury, R. H., Reichelt, R. E. & Green, D. G. (1984). Fractrals in ecology: methods and interpretation. *Marine Ecology Progress Series* **14**, 295-296.

Braithwaite, L. W., Dudzinski, M. L. & Turner, J. (1983). Studies on the Arboreal marsupial fauna of eucalypt forest being harvested for woodpulp at Eden, NSW. II. Relationship between the fauna density, richness and diversity, and measured variables of the habitat. *Australian Wildlife Research* **10**, 231-247.

Brandt, C. A., Parrish, J. K. & Hodges, C. N. (1995). Predictive approaches to habitat quantification: Dark-rumped petrels on Haleakala, Maui. *Auk* **112**, 571-579.

Britton, N. F., Partridge, L. W. & Franks, N. R. (1996). A mathematical model for the population dynamics of army ants. *Bulletin of Mathematical Biology* **58**, 471-492.

Broekhuizen, N., Heath, M. R., Hay, S. J. & Gurney, W. S. C. (1995). Modelling the dynamics of the North Sea's mesozooplankton.*Netherlands Journal of Sea Research* **33**, 381-406.

Brooker, L., Brooker, M. & Cale, P. (1999). Animal dispersal in fragmented habitat: measuring habitat connectivity, corridor use, and dispersal

mortality. *Conservation Ecology [online]* **3**, 4.

Bryant, A. D., Heath, M. R., Broekhuizen, N., Ollason, J. G., Gurney, W. S. C. & Greenstreet, S. P. R. (1995). Modelling the predation, growth and population dynamics of fish within a spatially-resolved shelf-sea ecosystem model. *Netherlands Journal of Sea Research* **33**, 407-421.

Buckland, S. T. & Elston, D. A. (1993). Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology* **30**, 478-495.

Buckland, S. T., Elston, D. A. & Beaney, S. J. (1996). Predicting distributional change, with application to bird distributions in northeast Scotland. *Global Ecology and Biogeography Letters* **5**, 66-84.

Bull, C. M. (1988). Mate fidelity in an Australian lizard Trachydosaurus rugosus. *Behavioral Ecology and Sociobiology* **23**, 45-50.

Bull, C. M. (1990). Comparisons of displaced and retained partners in a monogamous lizard. *Australian Wildlife Research* **17**, 135-140.

Bull, C. M. (1995). Population ecology of the sleepy lizard, Tiliqua rugosa, at Mt. Mary, South Australia. *Australian Journal of Ecology* **20**, 393-402.

Bull, C. M. & Baghurst, B. C. (1998). Home range ovelap between mothers and their offspring in the sleepy lizard, Tiliqua rugosa. *Behavioural Ecology and Sociobiology* **42**, 357-362.

Bull, C. M. & Burzacott, D. (1993). The impact of tick load on the fitness of their lizard hosts. *Oecologia* **96**, 415-419.

Bull, C. M., Burzacott, D. & Sharrad, R. D. (1989). No competition for resources between two tick species at their parapatric boundary. *Oecologia* **79**, 558-562.

Bull, C. M., Chilton, N. B. & Sharrad, R. D. (1988). Risk of predation for two reptile tick species. *Experimental & Applied Acarology* **5**, 93-100.

Bull, C. M., Cooper, S. J. B. & Baghurst, B. C. (1998). Social monogamy and extra-pair fertilization in an Australian lizard, Tiliqua rugosa. *Behavioural Ecology and Sociobiology* **44**, 63-72.

Bull, C. M. & Freake, M. J. (in press). Home range fidelity in the Australian sleepy lizard, Tliqua rugosa. *Wildlife Research.*

Bull, C. M. & King, D. R. (1981). A parapatric boundary between 2 species of reptile ticks in the Albany area, Western Australia. *Transactions of the Royal Society of South Australia* **105**, 205-208.

Bull, C. M., McNally, A. & Dubas, G. (1991). Asynchronous seasonal activity of male and female sleepy lizards, Tiliqua rugosa. *Journal of Herpetology* **25**, 436-441.

Bull, C. M. & Possingham, H. (1995). A model to explain ecological parapatry. *American Naturalist* **145**, 935-947.

Bull, C. M. & Smyth, M. (1973). The distribution of three species of reptile ticks, *Aponomma hydrosauri* (Denny), *Amblyomma albolimbatum* Neumann, and *Amb.limbatum*Neumann. II. Water balance of nymphs and adults in relation to distribution. *Australian Journal of Zoology* **21**, 103-110.

Bulmer, M. G. (1975). The statistical analysis of density dependence. *Biometrics* **31**, 901-911.

Cain, M. L., Pacala, S. W., Silander, J. A., Jr. & Fortin, M. J. (1995). Neighborhood models of clonal growth in the white clover Trifolium repens. *American Naturalist* **145**, 888-917.

Cantrell, R. S. & Cosner, C. (1991). The effects of spatial heterogeneity in population dynamics. *Journal of Mathematical Biology* **29**, 315-338.

Cantrell, R. S., Cosner, C. & Hutson, V. (1996). Spatially explicit models for the population dynamics of a species colonizing an island. *Mathematical Biosciences* **136**, 65-107.

Caswell, H. (1989). *Matrix Population Models*. Sunderland, MA: Sinauer Associates.

Cavalli Sforza, L. L. & Feldman, M. W. (1990). Spatial subdivision of populations and estimates of genetic variation. *Theoretical Population Biology* **37**, 3-25.

Chesson, P. (1978). Predator-prey theory and variability. *Annual review of ecology and systematics* **9**, 323-347.

Chesson, P. L. (1981). Models for spatially distributed populations: The effect of within-patch variability. *Theoretical Population Biology* **19**, 288-325.

Chesson, P. L. (1990). Geometry, heterogeneity and competition in variable environments. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **330**, 165-173.

Chesson, P. L. & Warner, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* **117**, 923-943.

Chilton, N. B. (1989). Life cycle adaptations and their implications in the distribution of two parapatric species of tick. Bull, C. M. Flinders University, South Australia.

Chilton, N. B. & Bull, C. M. (1996). Can predators maintain parapatry? Ant distribution across a tick parapatric boundary in South Australia. *Australian Journal of Ecology* **21**, 410-417.

Chilton, N. B., Bull, C. M. & Andrews, R. H. (1992). Niche segregation in reptile ticks: Attachment sites and reproductive success of females. *Oecologia* **90**, 255-259.

Claessen, D. & De Roos, A. M. (1995). Evolution of virulence in a host-pathogen system with local pathogen transmission. *Oikos* **74**, 401-413.

Colasanti, R. L. & Grime, J. P. (1993). Resource dynamics and vegetation processes: A deterministic model using two- dimensional cellular automata. *Functional Ecology* **7**, 169-176.

Collie, J. S. & Walters, C. J. (1991). Adaptive management of spatially replicated groundfish populations. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1273-1284.

Collins, E. I. & Lichvar, R. W. (1986). Vegetation inventory of current and historic black-footed ferret (Mustela nigripes) habitat in Wyoming (USA). *Great Basin Naturalist Memoirs* **8**, 85-93.

Comins, H. N., Hassell, M. P. & May, R. M. (1992). The spatial dynamics of host-parasitoid systems. *Journal of Animal Ecology* **61**, 735-748.

Cowles, H. C. (1899). The ecological relations of the vegetation on the sand dunes of Lake Michigan. *The Botanical Gazette* **27**, 95-391.

Cressie, N. A. C. (1993). *Statistics for spatial data*. New York: Wiley.

Crist, T. O. & Wiens, J. A. (1995). Individual movements and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). *Journal of Animal Ecology* **64**, 733-746.

Crofton, H. D. (1971). A quantitative approach to parasitism. *Parasitology* **62**, 179-194.

Crowley, P. H. (1977). Spatially distributed stochasticity and the constancy of ecosystems. *Bulletin of Mathematical Biology* **39**, 157-166.

Czaran, T. (1989). Coexistence of competing populations along an environmental gradient: A simulation study. *Coenoses* **4**, 113-120.

Czaran, T. & Bartha, S. (1989). The effect of spatial pattern on community dynamics: A comparison of simulated and field data. *Vegetatio* **83**, 229-240.

Dale, V. H., Gardner, R. H., Deangelis, D. L., Eagar, C. C. & Webb, J. W. (1991). Elevation-mediated effects of balsam woolly adelgid on southern Appalachian spruce-fir forests. *Canadian Journal of Forest Research* **21**, 1639-1648.

Davey, S. M. (1989). Thoughts towards a forest wildlife management strategy.*Australian Forestry* **52**, 56-67.

Davidson, J. & Andrewartha, H. G. (1948). The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology* **17**, 200-222.

Day, J. R. & Possingham, H. P. (1995). A Stochastic Metapopulation Model with Variability in patch Size and Position. *Theoretical Population Biology* **48**, 333-360.

De Roos, A. M., McCauley, E. & Wilson, W. G. (1991). Mobility versus density-limited predator-prey dynamics on different spatial scales.*Proceedings of the Royal Society of London Series B* **246**, 117-122.

De Wit, R., Van Den Ende, F. P. & Van Gemerden, H. (1995). Mathematical simulation of the interactions among cyanobacteria, purple sulfur bacteria and chemotropic sulfur bacteria in microbial mat communities. *FEMS Microbiology Ecology* **17**, 117-135.

DeAngelis, D. L. & Gross, L. J. (1991). *Individual-based models and approaches in ecology: Populations, communities, and ecosystems*. New York: Chapman and Hall.

den Boer, P. J. (1981). On the survival of populations in a heterogeneous and variable environment. *Oecologia* **50**, 39-45.

den Boer, P. J. (1991). Seeing the trees for the wood: random walks or bounded fluctuations of population size. *Oecologia* **86**, 484-491.

Deriso, R. B., Punsly, R. G. & Bayliff, W. H. (1991). A Markov movement model of yellowfin tuna in the Eastern Pacific Ocean and some analyses for international management. *Fisheries Research* **11**, 375-396.

Diekmann, O., Metz, J. A. & Sabelis, M. W. (1988). Mathematical Models of Predator/Prey/Plant Interactions in a Patch Environment. *Experimental and Applied Acarology* **5**, 319-342.

Dizij, A. & Kurtenbach, K. (1995). Clethrionomys glareolus, but not Apodemus flavicollis, acquires resistance to Ixodes ricinus L., the main European vector of Borrelia burgdorferi. *Parasite Immunology* **17**, 177-183 *LHM: Locally held journal. Check the catalogue for specific issue details and location.

Doak, D. (1989). Spotted owls and old growth logging in the Pacific Northwest (USA). *Conservation Biology* **3**, 389-396.

Doak, D. F., Marino, P. C. & Kareiva, P. M. (1992). Spatial scale mediates the influence of habitat fragmentation on dispersal success: Implications for conservation. *Theoretical Population Biology* **41**, 315-336.

Doherty, P. & Fowler, A. (1994). Demographic consequences of variable recruitment to coral reef fish populations: A congeneric comparison of two damselfishes. *Bulletin of Marine Science* **54**, 297-313.

Donald, P. F., Hines, P., Jackson, P., Dustow, J., Hepburn, I., Albon, G. F. & Jervis, S. (1996). Numbers, distribution and habitat associations of corn buntings on the Outer Hebrides and Tiree in 1995. *Scottish Birds* **18**, 170-181.

Doyle, C. J. (1991). Mathematical models in weed management. *Crop protection* **10**, 432-444.

During, H. J. (1995). Population regulation in tuber-bearing mosses: A simulation model. *Lindbergia* **20**, 26-34.

Durrett, R. & Levin, S. A. (1994). Stochastic spatial models: A user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **343**, 329-350.

Esch, G. W. & Fernández, J. C. (1993). *A function biology of parasitism: ecological and evolutionary implications*. London: Chapman and Hall.

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

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

Fahrig, L., Coffin, D. P., Lauenroth, W. K. & Shugart, H. H. (1994). The advantage of long-distance clonal spreading in highly disturbed habitats. *Evolutionary Ecology* **8**, 172-187.

Fahrig, L. & Merriam, G. (1994). Conservation of fragmented populations. *Conservation Biology* **8**, 50-59.

Fahrig, L. & Paloheimo, J. (1988). Determinants of local population size in patchy habitats. *Theoretical Population Biology* **34**, 194-213.

Ferriere, R. & Michod, R. E. (1996). The evolution of cooperation in spatially heterogeneous populations. *American Naturalist* **147**, 692-717.

Fiedler, P. C. & Reilly, S. B. (1994). Interannual variability of dolphin habitats in the eastern tropical Pacific. II. Effects on abundances estimated from tuna vessel sightings, 1975-1990. *U S National Marine Fisheries Service Fishery Bulletin* **92**, 451-463.

Fiksen, O., Giske, J. & Slagstad, D. (1995). A spatially explicit fitness-based model of capelin migrations the Barents Sea. *Fisheries Oceanography* **4**, 193-208.

Fletcher, W. J. (1992). Use of a spatial model to provide initial estimates of stock size for a purse seine fishery on pilchards (Sardinops sagax neopilchardus) in Western Australia. *Fisheries Research* **14**, 41-57.

Flinn, P. W., Hagstrum, D. W., Muir, W. E. & Sudayappa, K. (1992). Spatial model for simulating changes in temperature and insect population dynamics in stored grain. *Environmental Entomology* **21**, 1351-1356.

Fretwell, S. D. & Lucas Jr, H. L. (1970). On territorial behaviour and other factors indluencing habitat distribution in birds. I. Theoretical Development. *Acta Biotheoretica* **19**, 16-36.

Fritz, R. (1979). Consequences of insular population structure: distribution and extinction of spruce grouse populations. *Oecologia* **42**, 57-65.

Fulton, M. R. (1991). A computationally efficient forest succession model: Design and initial tests. *Forest Ecology and Management* **42**, 23-34.

Gaedke, U. & Ebenhoeh, W. (1991). Predator-mediated coexistence of calanoid copepods in a spatially heterogeneous environment: A numerical simulation model. *Ecological Modelling* **56**, 267-290.

Garnier, J., Bellen, G. & Coste, M. (1995). Seasonal succession of diatoms and Chlorophyceae in the drainage network of the Seine River: Observations and modeling. *Limnology and Oceanography* **40**, 750-765.

Gibbs, J. P. (1993). Importance of small wetlands for the persistence of local populations of wetland- associated animals. *Wetlands* **13**, 25-31.

Gibson, G. J. & Austin, E. J. (1996). Fitting and testing spatio-temporal stochastic models with application in plant epidemiology. *Plant Pathology* **45**, 172-184.

Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**, 7-26.

Goater, C. P. (1992). Experimental population dynamics of Rhabdias bufonis (Nematoda) in toads (Bufo bufo): Density-dependence in the primary infection. *Parasitology* **104**, 179-187.

Goldstein, D. B. & Holsinger, K. E. (1992). Maintenance of polygenic variation in spatially structured populations: Roles for local mating and genetic redundancy. *Evolution* **46**, 412-429.

Goldwasser, L., Cook, J. & Silverman, E. D. (1994). The effects of variability of metapopulation dynamics and rates of invasion. *Ecology* **75**, 40-47.

Gonzalez Andujar, J. L. & Perry, J. N. (1995). Models for the herbicidal control of the seed bank of Avena sterilis: The effects of spatial and temporal heterogeneity and of dispersal. *Journal of Applied Ecology* **32**, 578-587.

Gotelli, N. J. (1991). Demographic models for Leptogorgia virgulata, a shallow-water gorgonian. *Ecology* **72**, 457-467.

Gotelli, N. J. & Kelley, W. G. (1993). A general model of metapopulation dynamics. *Oikos* **68**, 36-44.

Green, D. G. (1989). Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics. *Vegetatio* **82**, 139-153.

Green, D. G. (1997). Complexity in ecological systems. In: *Frontiers in Ecology: Building the Links*. (Klomp, N. & Lunt, I. eds). Oxford: Elsevier Science.

Green, D. G., Bradbury, R. H. & Reichelt, R. E. (1987). Patterns of predictability in coral reef community structure. *Coral Reefs* **6**, 27-34.

Grieg-Smith, P. (1979). Pattern in vegetation. *Journal of Ecology* **67**, 755-779.

Gurney, W. S. C., Nisbet, R. M. & Blythe, S. P. (1986). The systematic formulation of models of stage-structured populations. In: *The dynamics of physiologically structured populations*. (Metz, J. A. J. & Diekmann, O. eds). Heidelberg: Springer-Verlag.

Gustafson, E. J. & Gardner, R. H. (1996). The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* **77**, 94-107.

Guyatt, H. L., Bundy, D. A., Medley, G. M. & Grenfell, B. T. (1990). The relationship between the frequency distribution of Ascaris lumbricoides and the prevalence and intensity of infection in human communities. *Parasitology* **101**, 139-144.

Haas, C. A. (1995). Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* **9**, 845-854.

Halley, J. M., Comins, H. N., Lawton, J. H. & Hassell, M. P. (1994). Competition, succession and pattern in fungal communities: Towards a cellular automaton model. *Oikos* **70**, 435-442.

Hanski, I. (1994). Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* **9**, 131-135.

Hanski, I., Foley, P. & Hassell, M. P. (1996). Random walks in a metapopulation: how much density dependence is necessary for long-term persistence? *Journal of Animal Ecology* **65**, 274-282.

Hanski, I., Kuussaari, M. & Nieminen, M. (1994). Metapopulation structure and migration in the butterfly Melitaea cinxia. *Ecology* **75**, 747-762.

Hanski, I. & Thomas, C. D. (1994). Metapopulation dynamics and conservation: A spatially explicit model applied to butterflies. *Biological Conservation* **68**, 167-180.

Hara, T. (1994). Growth and competition in clonal plants-persistence of shoot populations and species diversity. *Folia Geobotanica et Phytotaxonomica* **29**, 181-202.

Hara, T. & Wyszomirski, T. (1994). Competitive asymmetry reduces spatial effects on size-structure dynamics in plant populations. *Annals of Botany* **73**, 285-297.

Harada, Y., Ezoe, H., Iwasa, Y., Matsuda, H. & Sato, K. (1995). Population persistence and spatially limited social interaction. *Theoretical Population Biology* **48**, 65-91.

Hartway, C., Ruckelshaus, M. & Kareiva, P. (1998). The challenge of applying spatially explicit mmodels to a world or sparse and messy data. In: *Modeling spatiotemporal dynamics in ecology*. (Bascompte, J. & Solé, R. V. eds). Berlin: Springer Verlag.

Hassell, M. P. (1987). Detecting regulation in patchily distributed animal populations. *Journal of Animal Ecology* **56**, 705-713.

Hassell, M. P., Comins, H. N. & May, R. M. (1991). Spatial structure and chaos in insect population dynamics. *Nature* **353**, 255-258.

Hassell, M. P., Comins, H. N. & May, R. M. (1994). Species coexistence and self-organizing spatial dynamics. *Nature* **370**, 290-292.

Hassell, M. P., Latto, J. & May, R. M. (1989). Seeing the wood for the trees: detecting density dependence from existing life-table studies. *Journal of Animal Ecology* **58**, 883-892.

Hassell, M. P., Southwood, T. R. E. & Reader, P. M. (1987). The dynamics of the viburnum whitefly (*Aleurotrachelus jelinekii*): a case study of population regulation. *Journal of Animal Ecology* **56**, 283-300.

Hayward, G. D., Hayward, P. H. & Garton, E. O. (1993). Ecology of boreal owls in the northern Rocky Mountains, USA. *Wildlife Monographs* **124**, 1-59.

Hendry, R. J., McGlade, J. M. & Weiner, J. (1996). A coupled map lattice model of the growth of plant monocultures. *Ecological Modelling* **84**, 81-90.

Hermann, A. J., Hinckley, S., Megrey, B. A. & Stabeno, P. J. (1996). Interannual variability of the early life history of walleye pollock near Shelikof Strait as inferred from a spatially explicit, individual-based model. *Fisheries Oceanography* **5**, 39-57.

Hess, G. (1996). Disease in metapopulation models: Implications for conservation. *Ecology* **77**, 1617-1632.

Hilborn, R. (1990). Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 635-643.

Hilborn, R. & Mangel, M. (1997). *The Ecological Detective: Confronting Models with Data.* Princeton, NJ: Princeton University Press.

Hochberg, M. E., Clarke, R. T., Elmes, G. W. & Thomas, J. A. (1994a). Population dynamic consequences of direct and indirect interactions involving a large blue butterfly and its plant and red ant hosts. *Journal of Animal Ecology* **63**, 375-391.

Hochberg, M. E., Menaut, J. C. & Gignoux, J. (1994b). The influences of tree biology and fire in the spatial structure of the West African savannah. *Journal of Ecology* **82**, 217-226.

Hof, J., Bevers, M., Joyce, L. & Kent, B. (1994). An integer programming approach for spatially and temporally optimizing wildlife populations. *Forest Science* **40**, 177-191.

Hogle, J. S., Wesche, T. A. & Hubert, W. A. (1993). A test of the precision of the habitat quality index model II. *North American Journal of Fisheries Management* **13**, 640-643.

Holekamp, K. E. (1984). Natal dispersal in Belding's ground squirrel (*Spermophilus beldingi*). *Behavioral Ecology and Sociobiology* **16**, 21-30.

Holmes, E. E., Lewis, M. A., Banks, J. E. & Veit, R. R. (1994). Partial differential equations in ecology: Spatial interactions and population dynamics. *Ecology* **75**, 17-29.

Homer, C. G., Jr, T. C. E., Ramsey, R. D. & Price, K. P. (1993). Use of remote sensing methods in modelling sage grouse winter habitat. *Journal of Wildlife Management* **57**, 78-84.

Hood, G. M. (1997). Spatial structure in a host-pathogen system. In: *Frontiers in Ecology: Building the Links*. (Klomp, N. & Lunt, I. eds). Oxford: Elsevier Science.

Houston, B. R., Clark, T. W. & Minta, S. C. (1986). Habitat suitability index model for the black-footed ferret: (Mustela nigripes) a method to locate transplant sites. *Great Basin Naturalist Memoirs* **8**, 99-114.

How, R. (1983). Mountain Brushtail Possum. In: *Complete Book of Australian Mammals*. (Strahan, R. ed. pp. 147-148. Sydney: Angus and Robertson.

Hoy, C. W., McCulloch, C. E., Sawyer, A. J., Shelton, A. M. & Shoemaker, C. A. (1990). Effect of intraplant insect movement on economic thresholds. *Environmental Entomology* **19**, 1578-1596.

Hughes, G. (1996). Incorporating spatial pattern of harmful organisms into crop loss models. *Crop Protection* **15**, 407-421.

Hume, I. D., Foley, W. J. & Chilcott, M. J. (1984). Physiological mechanisms of foliage digestion in the greater glider and the ringtail possum (Marsupialia: Pseudocheiridae). In: *Possums and Gliders*. (Smith, A. P. & Hume, I. D. eds). pp. 247-251. Sydney: Surrey Beatty.

Husband, B. C. & Barrett, S. C. H. (1996). A metapopulation perspective in plant population biology. *Journal of Ecology* **84**, 461-469.

Hutson, V. C. L. & Vickers, G. T. (1995). The spatial struggle of tit-for-tat and defect. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **348**, 393-404.

Iwasa, Y., Sato, K. & Nakashima, S. (1991). Dynamic modeling of wave regeneration (Shimagare) in subalpine Abies forests. *Journal of Theoretical Biology* **152**, 143-158.

Johnson, A. R., Wiens, J. A., Milne, B. T. & Crist, T. O. (1992). Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* **7**, 63-75.

Johnson, C. R. (1997). Self-organising in spatial competition systems. In: *Frontiers in Ecology: Building the Links*. (Klomp, N. & Lunt, I. eds). Oxford: Elsevier Science.

Jones, R. E. (1977). Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* **46**, 195.

Kareiva, P. (1990). Population dynamics in spatially complex environments: Theory and data. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **330**, 175-190.

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

Kareiva, P. M. & Shigesada, N. (1983). Analyzing insect movement as a correlated random walk. *Oecologia* **56**, 234-238.

Keast, A. (1968). *Evolution of mammals on southern continents : IV. Australian*

mammals: zoogeography and evolution. Stony Brook, NY: Department of Biological Sciences, State University of New York.

Keitt, T. H. & Johnson, A. R. (1995). Spatial heterogeneity and anomalous kinetics: emergent patterns in diffusion-limited Predatory-Prey interaction. *Journal of Theoretical Biology* **172**, 127-139.

Kenkel, N. C. (1991). A weighted tesselation model for studying plant population dynamics. *Coenoses* **6**, 143-149.

Kenney, J. S., Smith, J. L. D., Starfield, A. M. & McDougal, C. W. (1995). The long-term effects of tiger poaching on population viability. *Conservation Biology* **9**, 1127-1133.

Kindvall, O. & Ahlen, I. (1992a). Geometrical factors and metapopulation dynamics of the bush cricket, *Metrioptera bicolor* Philipi (Orthoptera: Tettigonidae). *Conservation Biology* **6**, 520-529.

Kindvall, O. & Ahlen, I. (1992b). Geometrical factors and metapopulation dynamics of the bush cricket, Metrioptera bicolor Philippi (Orthoptera: Tettigoniidae). *Conservation Biology* **6**, 520-529.

Kmet, T. & Holcik, J. (1994). The diffusive Lotka-Volterra model as applied to the population dynamics of the German carp and predator and prey species in the Danube River basin. *Ecological Modelling* **74**, 277-285.

Knudsen, G. R. & Schotzko, D. J. (1991). Simulation of Russian wheat aphid movement and population dynamics on preferred and non-preferred host plants. *Ecological Modelling* **57**, 117-132.

Korzukhin, M. D. & Porter, S. D. (1994). Spatial model of territorial competition and population dynamics in the fire ant Solenopsis invicta (Hymenoptera: Formicidae). *Environmental Entomology* **23**, 912-922.

Krebs, C. J. (1989). *Ecological Methodology*. Cambridge: Harper and Row.

Krebs, C. J. (1995). Two paradigms of population regulation. *Wildlife Research* **22**, 1-10.

Kretzschmar, M. & Adler, F. R. (1993). Aggregated distributions in models for patchy populations. *Theoretical Population Biology* **43**, 1-30.

Kumar, S. K., Vincent, W. F., Austin, P. C. & Wake, G. C. (1991). Picoplankton and marine food chain dynamics in a variable mixed-layer: A reaction-diffusion model. *Ecological Modelling* **57**, 193-220.

Lamberson, R., Noon, B. R., Voss, C. & McKelvey, K. S. (1994). Reserve design for territorial species: The effects of patch size and spacing on the viability of the northern spotted owl. *Conservation Biology* **8**, 185-195.

Lampo, M. & Bayliss, P. (1996). The impact of ticks on Bufo marinus from native habitats. *Parasitology* **113**, 199-206.

Laval, P. (1996). The representation of space in an object-oriented computational pelagic ecosystem. *Ecological Modelling* **88**, 113-124.

Lavorel, S., Gardner, R. H. & V, O. N. R. (1995). Dispersal of annual plants in hierarchically structured landscapes. *Landscape Ecology* **10**, 277-289.

Lebreton, J. D. (1996). Demographic Models for Subdivided Popualtions: The Renewal Equation Approach. *Theoretical Population Biology* **49**, 291-313.

Leirs, H., Stenseth, N. C., Nichols, J. D., Hines, J. E., Verhagen, R. & Verheyen, W. (1997). Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature* **389**, 176-180.

Letcher, B. H., Priddy, J. A., Walters, J. R. & Crowder, L. B. (1998). An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. *Biological Conservation* **86**, 1-14.

Levin, S. A. (1974). Dispersion and population interactions. *American Naturalist* **108**, 207-208.

Levin, S. A. & Buttel, L. (1986). Measures of patchiness in ecological systems. Cornell University, Ithaca, Ecosystem Research Center.

Lewis, M. A. (1994). Spatial coupling of plant and herbivore dynamics: The contribution of herbivore dispersal to transient and persistent "waves" of damage. *Theoretical Population Biology* **45**, 277-312.

Lewis, M. A. (1994). Spatial coupling of plant and herbivore dynamics: The contribution of herbivore dispersal to transient and persistent "waves" of damage. *Theoretical Population Biology* **45**, 277-312.

Lewis, M. A. & Kareiva, P. (1993). Allee dynamics and the spread of invading organisms. *Theoretical Population Biology* **43**, 141-158.

Lhotka, L. (1994). Implementation of individual-oriented models in aquatic ecology. *Ecological Modelling* **74**, 47-62.

Lindenmayer, D. B. (1997). Differences in the biology and ecology of arboreal marsupials in forests of southeastern Australia. *Journal of Mammology* **78**, 1117-1127.

Lindenmayer, D. B., Burgman, M. A., Akcakaya, H. R., Lacy, R. C. & Possingham, H. P. (1995a). A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife metapopulations. *Ecological Modelling* **82**, 161-174.

Lindenmayer, D. B., Cunningham, R. B., Donnelly, C. F., Triggs, B. E. & Belvedere, M. (1995b). Factors influencing the occurrence of mammals in retained linear strips (wildlife corridors) and contiguous stands of montane ash forest in the central highlands of Victoria, southeastern Australia. *Forest Ecology and Managment* **67**.

Lindenmayer, D. B., Cunningham, R. B., Donnelly, C. F., Triggs, B. J. & Belvedere, M. (1994). The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-eastern Australia: Patterns of use and the microhabitat requirements of the mountain brushtail possum Trichosurus caninus Ogilby in retained linear habitats (wildlife corridors). *Biological Conservation* **68**, 43-51.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Nix, H. A. & Smith, A. P. (1991). The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, South East Australia: III The habitat requirements of Leadbeater's Possum *Gymnobelideus leadbeateri* and models of the diversity and abundance of arboreal marsupials. *Biological Conservation* **56**, 295-315.

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Smith, A. P. & Nix, H. A. (1990). Habitat requirements of the mountain brushtail possum and the greater glider in the montane ash-type eucalypt forests of the central highlands of Victoria.*Australian Wildlife Research* **17**, 467-478.

Lindenmayer, D. B. & Possingham, H. P. (1995a). Modelling the impacts of wildfire on the viability of metapopulations of the endangered Australian species of arboreal marsupial, Leadbeater's possum.*Forest Ecology and Management* **74**, 197-222.

Lindenmayer, D. B. & Possingham, H. P. (1995b). Modelling the viability of metapopulations of the endangered Leadbeater's possum in south-eastern Australia.*Biodiversity and Conservation* **4**, 964-1018.

Lindenmayer, D. B. & Possingham, H. P. (1996). Ranking conservation and timber management options for Leadbeater's possum in southeastern Australia using population viability analysis. *Conservation Biology* **10**, 235-251.

Lindquist, J. L., Rhode, D., Puettmann, K. J. & Maxwell, B. D. (1994). The influence of plant population spatial arrangement on individual plant yield. *Ecological Applications* **4**, 518-524.

Lippman, S. A. & McCall, J. J. (1977). The economics of job search: a survey. *Economic Inquiry* **14**, 155-189.

Loehle, C. (1990). Home range: a fractal approach. *Landscape Ecology* **5**, 39-52.

Logan, J. A., Wollkind, D. J., Hoyt, S. C. & Tanigoshi, L. K. (1976). An analytic model for description of temperature dependent rate phenomena in arthropods. *Environmental Entomology* **5**, 1133-1140.

Lovvorn, J. & Gillingham, M. P. (1996). Food dispersion and foraging energetics: A mechanistic synthesis for field studies of avian benthivores. *Ecology* **77**, 435-451.

Lubchenco, J., Olson, A. M., Brubaker, L. B., Carpenter, S. R., Holland, M. M., Hubbell, S. P., Levin, S. A., MacMahon, J. A., Matson, P. A., Melillo, J. M., Mooney, H. A., Peterson, C. H., Pulliam, H. R., Real, L. A., Regal, P. J. & Risser, P. G. (1991). The sustainable biosphere initiative: an ecological research agenda. *Ecology* **72**, 371-412.

Mac Nally, R. & Watson, D. M. (1997). Distinguishing area and habitat heterogeneity effects on species richness: Birds in Victorian buloke remnants. *Australian Journal of Ecology* **22**, 227-232.

Madenjian, C. P., Whittle, D. M., Elrod, J. H., R, O. G. & Owens, R. W. (1995). Use of a simulation model to reconstruct PCB concentrations in prey of Lake Ontario lake trout. *Environmental Science & Technology* **29**, 2610-2615.

Malanson, G. P. (1996). Effects of dispersal and mortality on diversity in a forest stand model. *Ecological Modelling* **87**, 103-110.

Malanson, G. P. & Cairns, D. M. (1995). Effects of increase cloud-cover on a montane forest landscape. *Ecoscience* **2**, 75-82.

Malchow, H. (1988). Spatial patterning of interacting and dispersing populations. *Memoirs Of The Faculty Of Science Kyoto University Series.*

Malchow, H. (1995). Flow- and locomotion-induced pattern formation in nonlinear population dynamics. *Ecological Modelling* **82**, 257-265.

Mangel, M. & Tier, C. (1994). Four facts every conservation biologist should know about persistence. *Ecology* **75**, 607-614.

Maron, J. L. & Harrison, S. (1997). Spatial pattern formation in an insect host-parasitoid system. *Science* **278**, 1619-1621.

Marquez, A. L., Real, R., Vargas, J. M. & Salvo, A. E. (1997). On identifying common distribution patterns and their causal factors: a probabilistic method applied to petidophytes in the Iberian Peninsula. *Journal of Biogeography* **24**, 613-631.

Marsh, L. M. & Jones, R. E. (1988). The form and consequences of random walk movement models. *Journal of Theoretical Biology* **133**, 113-131.

Mason, D. M. & Brandt, S. B. (1996). Effects of spatial scale and foraging efficiency on the predictions made by spatially-explicit models of fish growth rate potential. *Environmental Biology of Fishes* **45**, 283-298.

Matis, J. H., Kiffe, T. R. & Otis, G. W. (1994). Use of birth-death-migration processes for describing the spread of insect populations. *Environmental Entomology* **23**, 18-28.

Maurer, B. A. (1986). Predicting habitat quality for grassland birds using density-habitat correlations. *Journal of Wildlife Management* **50**, 556-566.

May, R. M. (1974). *Stability and complexity in model ecosystems.* Princeton, NJ: Princeton University Press.

May, R. M. (1975). Biological populations obeying difference equations: stable points, stable cycles, and chaos. *Journal of Theoretical Biology* **51**, 511-524.

Maynard-Smith, J. (1982). *Evolution and the theory of games.* Cambridge: Cambridge University Press.

McCarthy, M. A. (1996). Extinction dynamics of the helmeted honeyeater: effects of demography, stochasticity, inbreeding and spatial structure. *Ecological Modelling* **85**, 151-163.

McCarthy, M. A. (1997). Competition and dispersal from multiple nests. *Ecology* **78**, 873-883.

McCarthy, M. A., Franklin, D. C. & Burgman, M. A. (1994). The importance of demographic uncertainty: An example from the helmeted honeyeater Lichenostomus melanops cassidix. *Biological Conservation* **67**, 135-142.

McCauley, E., Wilson, W. G. & De Roos, A. M. (1993). Dynamics of age-structured and spatially structured predator-prey interactions: Individual-based models and population-level formulations. *American Naturalist* **142**, 412-442.

McCullagh, P. & Nelder, J. A. (1983). *Generalized Linear Models.* London: Chapman and Hall.

McLaughlin, J. F. & Roughgarden, J. (1991). Pattern and stability in predator-prey communities: How diffusion in spatially variable environments affects the Lotka-Volterra model. *Theoretical Population Biology* **40**, 148-172.

McLaughlin, J. F. & Roughgarden, J. (1992). Predation across spatial scales in heterogeneous environments. *Theoretical Population Biology* **41**, 277-299.

Meents, J. K., Rice, J., Anderson, B. W. & Ohmart, R. D. (1983). Nonlinear relationships between birds and vegetation. *Ecology* **64**, 1022-1027.

Merendino, M. T. & Ankney, C. D. (1994). Habitat use by mallards and American black ducks breeding in central Ontario. *Condor* **96**, 411-421.

Merriam, G. & Lanoue, A. (1990). Corridor use by small mammals: field measurement for three experimental types of *Peromyscus leucopus. Landscape Ecology* **4**, 123-131.

Milne, B. T., Johnston, K. M. & Forman, R. T. T. (1989). Scale-dependent proximity of wildlife habitat in a spatially-neutral bayesian model. *Landscape Ecology* **2**, 101-110.

Milne, B. T., Turner, M. G., Wiens, J. A. & Johnson, A. R. (1992). Interactions between the fractal geometry of landscapes and allometric herbivory. *Theoretical Population Biology* **41**, 337-353.

Molofsky, J. (1994). Population dynamics and pattern formation in theoretical populations. *Ecology* **75**, 30-39.

Moloney, K. A. & Levin, S. A. (1996). The effects of disturbance architecture on landscape-level population dynamics. *Ecology* **77**, 375-394.

Moloney, K. A., Levin, S. A., Chiariello, N. R. & Buttel, L. (1992). Pattern and scale in a serpentine grassland. *Theoretical Population Biology* **41**, 257-276.

Morris, W. F. (1993). Predicting the consequences of plant spacing and biased movement for pollen dispersal by honey bees. *Ecology* **74**, 493-500.

Morrison, M. L., Marcot, B. G. & Mannan, R. W. (1992). *Wildlife habitat relationships: concepts and applications.* Madison: University of Wisconsin Press.

Mullen, A. J. (1989). Aggregation of fish through variable diffusivity. *U S National Marine Fisheries Service Fishery Bulletin* **87**, 353-362.

Murdoch, W. W., Briggs, C. J., Nisbet, R. M., Gurney, W. S. C. & Stewart Oaten, A. (1992). Aggregation and stability in metapopulation models. *American Naturalist* **140**, 41-58.

Murray, J. D. & Seward, W. L. (1992). On the spatial spread of rabies among foxes with immunity. *Journal of Theoretical Biology* **156**, 327-348.

Mysterud, A. & Ims, R. A. (1998). Functional responses in habitat use: availability influences relatiove use in trade-off situations. *Ecology* **79**, 1435-1441.

Nams, V. O. (1996). The VFractal: A new estimator for fractal dimension of animal movement paths. *Landscape Ecology* **11**, 289-297.

Neave, H. M., Cunningham, R. B., Norton, T. W. & Nix, H. A. (1996). Biological inventory for conservation evaluation III. Relationships between birds, vegetation and environmental attributes in southern Australia. *Forest Ecology and Management* **85**, 197-218.

Nelson, M. E. (1993). Natal dispersal and gene flow in white-tailed deer in northeastern minnesota. *Journal of Mammology* **74**, 316-322.

Neubert, M. G., Kot, M. & Lewis, M. A. (1995). Dispersal and pattern Formation in a Discrete-Time Predator-Prey Model. *Theoretical Population Biology* **48**, 7-43.

Nicholson, A. J. & Bailey, V. A. (1935). The Balance of Animal Populations, Part I. *Proceedings of the Zoological Society, London* **3**, 551-598.

NPWS (1994a). Fauna of north-east NSW forests, NSW National Parks and Wildlife Service.

NPWS (1994b). Flora of north-east NSW forests, NSW National Parks and Wildlife Service.

Okubo, A. (1980). *Diffusion and Ecological Problems: Mathematical Models*. Berlin: Springer Verlag.

Okubo, A., Maini, P. K., Williamson, M. H. & Murray, J. D. (1989). On the spatial spread of the gray squirrel in Britain (UK). *Proceedings of the Royal Society of London B Biological Sciences* **238**, 113-126.

Olson, R. L. & Sequeira, R. A. (1995). An emergent computational approach to the study of ecosystem dynamics. *Ecological Modelling* **79**, 95-120.

O'Neill, R. V., Gardner, R. H., Milne, B. T., Turner, M. G. & Jackson, B. (1991). Heterogeneity and Spatial Hierarchies. In: *Ecological Heterogeneity*. (Kolasa, J. & Pickett, S. T. A. eds). New York: Springer Verlag.

Onstad, D. W., Maddox, J. V., Cox, D. J. & Kornkven, E. A. (1990). Spatial and temporal dynamics of animals and the host-density threshold in epizootiology. *Journal of Invertebrate Pathology* **55**, 76-84.

Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Jr., Kobe, R. K. & Ribbens, E. (1996). Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs* **66**, 1-43.

Paradis, E. & Croset, H. (1995). Assessment of habitat quality in the Mediterranean pine vole (Microtus duodecimcostatus) by the study of survival rates. *Canadian Journal of Zoology* **73**, 1511-1518.

Parma, A., Amarasekare, P., Mangel, M., Moore, J., Murdoch, W. W., Noonburg, E., Pascual, M. A., Possingham, H. P., Shea, K., Wilcox, C. & Yu, D. (1998). What can adaptive management do for our fish, forests, food, and biodiversity. *Integrative Biology* **1**, 16-26.

Pearce, J. L., Burgman, M. A. & Franklin, D. C. (1994). Habitat selection by Helmeted Honeyeaters. *Wildlife Research* **21**, 53-63.

Pease, C. M., Lande, R. & Bull, J. J. (1989). A model of population growth, dispersal and evolution in a changing environment. *Ecology* **70**, 1657-1664.

Pedlar, J. H., Fahrig, L. & Merriam, H. G. (1997). Raccoon habitat use at 2 spatial scales. *Journal of Wildlife Management* **61**, 102-112.

Peet, R. K. (1991). Lessons from nature: case studies in natural systems. In: *Foundations of ecology: classic papers with commentaries.* (Real, L. A. & Brown, J. A. eds). Chicago: University of Chicago Press.

Perry, J. N. (1982). Fitting split-lines to ecological data. *Ecological Entomology* **7**, 421-436.

Perry, J. N. & Gonzalez Andujar, J. L. (1993). Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. *Journal of Ecology* **81**, 453-463.

Pet, J. S., Machiels, M. A. M. & Van Densen, W. L. T. (1996). A size-structured simulation model for evaluating management strategies in gillnet fisheries exploiting spatially differentiated populations. *Ecological Modelling* **88**, 195-214.

Petney, T. N. & Bull, C. M. (1984). Microhabitat selection by 2 reptile ticks at their parapatric boundary. *Australian Journal of Ecology* **9**, 233-240.

Pietsch, R. S. (1995). The fate of Common Brushtail Possums translocated to sclerophyll forest. In: *Reintroduction biology of Australasian fauna.* (Serena, M. ed. pp. 239-246. Chipping Norton, Australia: Surrey Beatty and Sons.

Platt, T. & Denman, K. L. (1975). Spectral analysis in ecology. *Annual review of ecology and systematics* **6**, 189-210.

Pollard, E., Lakhani, K. H. & Rothery, P. (1987). The detection of density-dependence from a series of annual censuses. *Ecology* **68**, 2046-2055.

Polymenopoulos, A. D. & Long, G. (1990). Estimation and evaluation methods for population growth models with spatial diffusion: Dynamics of mountain pine beetle. *Ecological Modelling* **51**, 97-122.

Possingham, H. P. & Davies, I. (1995). ALEX: A model for the viability analysis of spatially structured populations. *Biological Conservation* **73**, 143-150.

Possingham, H. P., Lindenmayer, D. B. & Norton, T. W. (1993). The role of PVA in endangered species management. *Pacific Conservation Biology* **1**, 39-45.

Possingham, H. P., Lindenmayer, D. B., Norton, T. W. & Davies, I. (1994a). Metapopulation viability analysis of the greater glider *Petauroides volans* in a wood production area. *Biological Conservation* **70**, 227-236.

Possingham, H. P. & Roughgarden, J. (1990). Spatial population dynamics of a marine organism with complex life cycle. *Ecology* **71**, 973-985.

Possingham, H. P., Tuljapurkar, S., Wilks, M. & Roughgarden, J. (1994b). Population cycling in space-limited organisms subject to density-dependent predation. *American Naturalist* **143**, 642-661.

Prescott, D. R. C. & Collister, D. M. (1993). Characteristics of occupied and unoccupied loggerhead shrike territories in southeastern alberta. *Journal of Wildlife Management* **57**, 346-352.

Press, W. H., Teukolsky, S. A., Vetterling, W. T. & Flannery, B. P. (1992). *Numerical Recipes in C.* Cambridge: Cambridge University Press.

Pressey, R. L., Possingham, H. P. & Margules, C. R. (1996). Optimality in reserve selection algorithms: When does it matter and how much? *Biological Conservation* **76**, 259-267.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist* **132**, 652-661.

Pulliam, H. R., Dunning, J. B. J. & Liu, J. (1992). Population dynamics in complex landscapes: A case study. *Ecological Applications* **2**, 165-177.

Quintana-Ascencio, P. F. & Menges, E. S. (1995). Inferring metapopulation dynamics from patch-level incidence of florida scrub plants. *Conservation Biology* **10**, 1210-1219.

Ranta, E., Kaitala, V. & Lundberg, P. (1997). The spatial dimension in population fluctuations. *Science* **278**.

Ray, C. & Hastings, A. (1996). Density dependence: are we searching at the wrong spatial scale? *Journal of Animal Ecology* **65**, 556-566.

Real, L. A. (1991). Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. *American Naturalist* **138**, 901-917.

Real, L. A. & McElhany, P. (1996). Spatial pattern and process in plant-pathogen interactions. *Ecology* **77**, 1011-1025.

Reddingius, J. (1990). Models for testing: a secondary note. *Oecologia* **83**, 50-52.

Rees, M., Grubb, P. J. & Kelly, D. (1996). Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *American Naturalist* **147**, 1-32.

Rees, M. & Long, M. J. (1992). Germination biology and the ecology of annual plants. *American Naturalist* **139**, 484-508.

Reyes, E., Sklar, F. H. & Day, J. W. (1994). A regional organism exchange model for simulating fish migration. *Ecological Modelling* **74**, 255-276.

Rijnsdorp, A. D. & Pastoors, M. A. (1995). Modelling the spatial dynamics and fisheries of North Sea plaice (Pleuronectes platessa L.) based on tagging data. *ICES Journal of Marine Science* **52**, 963-980.

Rohani, P. & Miramontes, O. (1995). Host-parasitoid metapopulations: The consequences of parasitoid aggregation on spatial dynamics and searching efficiency. *Proceedings of the Royal Society of London Series B Biological Sciences* **260**, 335-342.

Roitberg, B. D. & Mangel, M. (1997). Individuals on the landscape: behavior can mitigate landscape differences among habitats. *Oikos* **80**, 234-240.

Roitberg, B. D., Mangel, M. & Tourigny, G. (1990). The density dependence of parasitism by tephritid fruit flies. *Ecology* **71**, 1871-1885.

Rose, K. A., Christensen, S. W. & Deangelis, D. L. (1993). Individual-based modeling of populations with high mortality: A new method based on following a fixed number of model individuals. *Ecological Modelling* **68**, 273-292.

Rotenberry, J. T. & Wiens, J. A. (1998). Foraging patch selection by shrubsteppe sparrows. *Ecology* **79**, 1160-1173.

Ruardij, P., Baretta, J. W. & Baretta Bekker, J. G. (1995). Sesame, a software environment for simulation and analysis of marine ecosystems. *Netherlands Journal of Sea Research* **33**, 261-270.

Ruxton, G. D. (1996). Dispersal and chaos in spatially structured models: Individual-level approach. *Journal of Animal Ecology* **65**, 161-169.

Sato, K. (1995). Lattice models in ecology: Usefulness of pair approximation. *Japanese Journal of Ecology* **45**, 247-258.

Sato, K. & Iwasa, Y. (1993). Modeling of wave regeneration in subalpine Abies forests: Population dynamics with spatial structure. *Ecology* **74**, 1538-1550.

Saupe, D. (1988). Algorithms for random fractals. In: *The science of fractal images*. (O, P. H. & D, S. eds). New York: Springer Verlag.

Schneider, D. C. (1992). Thinning and clearing of prey by predators. *American Naturalist* **139**, 148-160.

Schneider, D. C. (1994). *Quantitative Ecology: Spatial and Temporal Scaling*. San Diego: Academic Press.

Schoener, T. W. (1985). Are lizard population sizes unusually constant through time? *American Naturalist* **126**, 633-641.

Schotzk, D. J. & Knudsen, G. R. (1992). Use of geostatistics to evaluate a spatial simulation of Russian wheat aphid (Homoptera: Aphididae) movement behavior on preferred and nonpreferred hosts. *Environmental Entomology* **21**, 1271-1282.

Scott, M. E. (1987). Temporal changes in aggregation: a laboratory study. *Parasitology* **94**, 583-595.

Sharrad, R. D. (1979). Studies of the factors which determine the distribution of three species of South Australian ticks. University of Adelaide, South Australia.

Shigesada, N., Kawasaki, K. & Takeda, Y. (1995). Modeling stratified diffusion in biological invasions. *American Naturalist* **146**, 229-251.

Simmonds, E. J. & Fryer, R. J. (1996). Which are better, random or systematic acoustic surveys? A simulation using North Sea herring as an example. *ICES Journal of Marine Science* **53**, 39-50.

Sipper, M. (1994). Studying artificial life using a simple, general cellular model. *Artificial Life* **2**, 1-35.

Skellam, J. G. (1951). Random dispersal in theoretical populations. *Biometrika* **38**, 346.

Smith, A. T. & Peacock, M. M. (1990). Conspecific attraction and the determination of metapopulatio colonization rates. *Conservation Biology* **4**, 320-323.

Smith, G. (1994). Parasite population density is regulated. In: *Parasitic and Infectious Diseases: Epidemiology and Ecology*. (Scott, M. E. & Smith, G. eds). San Diego: Academic Press.

Smith, G. C. & Harris, S. (1991). Rabies in urban foxes (Vulpes vulpes) in Britain: The use of a spatial stochastic simulation model to examine the pattern of spread and evaluate the efficacy of different control regimes. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **334**, 459-479.

Smith, H. F. (1938). An empirical law describing heterogeneity in the yields of agricultural crops. *Journal of Agricultural Science* **28**, 1-23.

Smith, M. (1991). Using massively-parallel supercomputers to model stochastic spatial predator-prey systems. *Ecological Modelling* **58**, 347-368.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. New York: W. H. Freeman and Company.

Solé, R. V., Bascompte, J. & Valls, J. (1992). Stability and complexity of spatially extended two-species competition. *Journal of Theoretical Biology* **159**, 469-480.

Solé, R. V. & Valls, J. (1992). On structural stability and chaos in biological systems. *Journal of Theoretical Biology* **155**, 87-102.

Solow, A. R. (1990). Testing for density dependence: a cautionary note. *Oecologia* **83**, 47-49.

Solow, A. R. & Steele, J. H. (1990). On sample size, statistical power, and the detection of density dependence. *Journal of Animal Ecology* **59**, 1073-1076.

Southgate, R. & Possingham, H. (1995). Modelling the reintroduction of the greater bilby Macrotis lagotis using the metapopulation model analysis of the likelihood of extinction (ALEX). *Biological Conservation* **73**, 151-160.

Srividya, A., Krishnamoorthy, K., Sabesan, S., Panicker, K. N., Grenfell, B. T. & Bundy, D. A. P. (1991). Frequency distribution of Brugia malayi microfilariae in human populations. *Parasitology* **102**, 207-212.

Stacey, P. B. & Taper, M. (1992). Environmental variation and the persistence of small populations. *Ecological Applications* **2**, 18-29.

Steele, J. H. & Henderson, E. W. (1979). Spatial patterns in North Sea plankton. *Deep Sea Research* **26**, 955-964.

Stenseth, N. C. & Lidicker Jr., W. Z. (1992). The study of dispersal: a conceptual guide. In: *Animal Dispersal: Small Mammals as a Model.* (Stenseth, N. C. & Lidicker Jr., W. Z. eds). pp. 1-20. London: Chapman and Hall.

Stiling, P. (1988). Density-dependent processes and key factors in insect populations. *Journal of Animal Ecology* **57**, 581-594.

Stiling, P., Throckmorton, A., Silvanima, J. & Strong, D. R. (1991). Does spatial scale affect the incidence of density dependence? A field test with insect parasitoids. *Ecology* **72**, 2143-2154.

Strong, D. R. (1989). Density independence in space and inconsistent temporal relationships for host mortality caused by a fairyfly parasitoid. *Journal of Animal Ecology* **58**, 1065-1076.

Stuart, A. (1984). *The ideas of sampling*. New York: Macmillan.

Sugai, Y. & Fukao, T. (1989). Spatial Lattice Habitat Preference Model: Pattern formation of population. *International Journal of Systems Science* **20**, 1891-1908.

Sutcliffe, O., Thomas, C. D., Yates, T. J. & Greatorex-Davies, J. N. (1997). Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia* **109**, 235-241.

Szymanski, B. & Caraco, T. (1994). Spatial analysis of vector-borne disease: A four-species model. *Evolutionary Ecology* **8**, 299-314.

Tainaka, K. I. (1994). Intrinsic uncertainty in ecological catastrophe. *Journal of Theoretical Biology* **166**, 91-99.

Tainaka, K. I. (1996). Uncertainty in ecological catastrophe. *Ecological Modelling* **86**, 125-128.

Taylor, A. D. (1998). Environmental Variability and the persistence of parasitoid-host metapopulation models. *Theoretical Population Biology* **53**, 98-107.

Temple, S. A. & Cary, J. R. (1988). Modelling dynamics of habitat interior bird populations in fragmented landscapes. *Conservation Biology* **2**, 340-347.

Thomas, L. (1996). Monitoring long-term population change: Why are there so many analysis methods? *Ecology* **77**, 49-58.

Topping, C. J. & Sunderland, K. D. (1994). A spatial population dynamics model for Lepthyphantes tenuis (Araneae: Linyphiidae) with some simulations of the spatial and temporal effects of farming operations and land-use. *Agriculture Ecosystems & Environment* **48**, 203-217.

Turchin, P. (1991). Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**, 1253-1266.

Turner, M. G., Arthaud, G. J., Engstrom, R. T., Hejl, S. J., Liu, J., Loeb, S. & McKelvey, K. (1995). Usefulness of spatially explicit population models in land management. *Ecological Applications* **5**, 12-16.

Turner, M. G., Wu, Y., Wallace, L. L., Romme, W. H. & Brenkert, A. (1994). Simulating winter interactions among ungulates, vegetation and fire in Northern Yellowstone Park. *Ecological Applications* **4**, 472-496.

Turner, S. J., O'Neill, R. V., Conley, W., Conley, M. R. & Humphries, H. C. (1991). Pattern and Scale: Statistics for Landscape Ecology. In: *Quantitative Methods in Landscape Ecology*. (Turner, S. J. & Gardner, R. H. eds). New York: Springer Verlag.

Tyre, A. J., Possingham, H. P. & Lindenmayer, D. (1997). Spatially explicit ecological models: population consequences of individual habitat selection mechanisms. In: *MODSIM 97 International Congress on modelling and Simulation, Proceedings*. (McDonald, A. D. & McAleer, M. eds): Modelling and Simulation Society of Australia.

Tyre, A. J., Possingham, H. P. & Lindenmayer, D. L. (1998). Modelling dispersal behaviour on a fractal landscape. *Environmental Modelling and Software* **14**, 103-113.

Vail, S., Smith, G. & Lord, C. (1994). Population biology of *Ixodes scapularis*, the vector of lyme disease in the eastern and north central United States. In: *Parasitic and infectious diseases: epidemiology and ecology*. (Scott, M. E. & Smith, G. eds). pp. 263-278. San Diego: Academic Press.

Vail, S. G. & Smith, G. (1997). Density-dependent seasonal dynamics of blacklegged tick (Acari: Ixodidae) nymphs. *Journal of Medical Entomology* **34**, 301-306 *LHM: Locally held journal. Check the catalogue for specific issue details and location.

Van Den Bosch, F., Metz, J. A. J. & Diekmann, O. (1990). The velocity of spatial population expansion. *Journal of Mathematical Biology* **28**, 529-566.

van Dijk, T. S. & den Boer, P. J. (1992). The life histories and population dynamics of two carabid species on a Dutch heathland. 1. Fecundity and the mortality of immature stages. *Oecologia* **90**, 340-352.

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

Varley, G. C., Gradwell, G. R. & Hassell, M. P. (1973). *Insect population ecology*. Oxford: Blackwell.

Veldkamp, A. & Fresco, L. O. (1996). CLUE: A conceptual model to study the conversion of land use and its effects. *Ecological Modelling* **85**, 253-270.

Venables, W. N. & Ripley, B. D. (1994). *Modern Applied Statistics with S-Plus*. New York: Springer-Verlag.

Verhulst, S., Perrins, C. M. & Riddington, R. (1997). Natal dispersal of great tits in a patchy environment. *Ecology* **78**, 864-872.

Vickers, G. T. (1989). Spatial patterns and ESS's.*Journal of Theoretical Biology* **140**, 129-136.

Vickers, G. T., Hutson, V. C. L. & Budd, C. J. (1993). Spatial patterns in population conflicts. *Journal of Mathematical Biology* **31**, 411-430.

Wallinga, J. (1995). The role of space in plant population dynamics: Annual weeds as an example. *Oikos* **74**, 377-383.

White, P. C. L. & Harris, S. (1995). Bovine tuberculosis in badger (Meles meles) populations in southwest England: An assessment of past, present and possible future control strategies using simulation modelling. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **349**, 415-432.

Wiens, J. A., Crist, T. O., With, K. A. & Milne, B. T. (1995). Fractal patterns of insect movement in microlandscape mosaics. *Ecology* **76**, 663-666.

Wiens, J. A., Rotenberry, J. T. & Van Horne, B. (1987). Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* **48**, 132-147.

Wiles, L. J., Wilkerson, G. G., Gold, H. J. & Coble, H. D. (1992). Modeling weed distribution for improved postemergence control decisions. *Weed Science* **40**, 545-553.

Wilhoit, L. R. (1991). Modelling the population dynamics of different aphid genotypes in plant variety mixtures. *Ecological Modelling* **55**, 257-284.

Williams, B., Dransfield, R. & Brightwell, R. (1992). The control of tsetse flies in relation to fly movement and trapping efficiency.*Journal of Applied Ecology* **29**, 163-179.

Wilson, E. A., Powell, E. N. & Ray, S. M. (1991). The effects of host density and parasite crowding on movement and patch formation of the ectoparasitic snail, Boonea impressa: Field and modelling results. *Journal of Animal Ecology* **60**, 779-804.

Wilson, W. G., De Roos, A. M. & McCauley, E. (1993). Spatial instabilities within the diffusive Lotka-Volterra system: Individual-based simulation results. *Theoretical Population Biology* **43**, 91-127.

Wilson, W. G., McCauley, E. & De Roos, A. M. (1995). Effect of dimensionality on Lotka-Volterra predator-prey dynamics: Individual based simulation results.*Bulletin of Mathematical Biology* **57**, 507-526.

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

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

With, K. A. & King, A. W. (1997). The use and misuse of neutral landscape models in ecology. *Oikos* **79**, 219-229.

Woiwod, I. P. & Hanski, I. (1992). Patterns of density dependence in moths and aphids. *Journal of Animal Ecology* **61**, 619-629.

Wolda, H. (1989). The equilibrium concept and density dependence tests. What does it all mean? *Oecologia* **81**, 430-432.

Wolfenbarger, D. O. (1946). Dispersion of small organisms. *The American Midland Naturalist* **35**, 1-152.

Wollkind, D. J., Collings, J. B. & Barba, M. C. B. (1991). Diffusive instabilities in a one-dimensional temperature-dependent model system for a mite predator-prey interaction on fruit trees: Dispersal motility and aggregative prey taxis effects. *Journal of Mathematical Biology* **29**, 339-362.

Wood, S. N. & Thomas, M. B. (1996). Space, time and persistence of virulent pathogens. *Proceedings of the Royal Society of London Series B Biological Sciences* **263**, 673-680.

Wu, J., Vankat, J. L. & Barlas, Y. (1993). Effects of patch connectivity and arrangement on animal metapopulation dynamics: A simulation study. *Ecological Modelling* **65**, 221-254.

Zhylyayev, H. H. (1991). Problems of determining spatiotemporal boundaries of plant populations. *Ukrayins'Kyi Botanichnyi Zhurnal* **48**, 35-38.

Zuidema, G., Van Den Born, G. J., Alcamo, J. & Kreileman, G. J. J. (1994). Simulating changes in global land cover as affected by economic and climatic factors. *Water Air and Soil Pollution* **76**, 163-198.