The Influence of Habitat Heterogeneity on Patterns of Connectivity among Rabbit Populations in Southern Queensland

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ABSTRACT

Patterns of connectivity among local populations influence the dynamics of regional systems, but most ecological models have concentrated on explaining the effect of connectivity on local population structure using dynamic processes covering short spatial and temporal scales. In this study, a model was developed in an extended spatial system to examine the hypothesis that long term connectivity levels among local populations are influenced by the spatial distribution of resources and other habitat factors.

The habitat heterogeneity model was applied to local wild rabbit populations in the semi-arid Mitchell region of southern central Queensland (the Eastern system). Species' specific population parameters which were appropriate for the rabbit in this region were used. The model predicted a wide range of long term connectivity levels among sites, ranging from the extreme isolation of some sites to relatively high interaction probabilities for others. The validity of model assumptions was assessed by regressing model output against independent population genetic data, and explained over 80% of the variation in the highly structured genetic data set. Furthermore, the model was robust, explaining a significant proportion of the variation in the genetic data over a wide range of parameters.

The performance of the habitat heterogeneity model was further assessed by simulating the widely reported recent range expansion of the wild rabbit into the Mitchell region from the adjacent, panmictic Western rabbit population system. The model explained well the independently determined genetic characteristics of the Eastern system at different hierarchic levels, from site specific differences (for example, fixation of a single allele in the population at one site), to differences between population systems (absence of an allele in the Eastern system which is present in all Western system sites). The model therefore explained the past and long term processes which have led to the formation and maintenance of the highly structured Eastern rabbit population system.

Most animals exhibit sex biased dispersal which may influence long term connectivity levels among local populations, and thus the dynamics of regional systems. When appropriate sex specific dispersal characteristics were used, the habitat heterogeneity model predicted substantially different interaction patterns between female-only and combined male and female dispersal scenarios. In the latter case, model output was validated using data from a bi-parentally inherited genetic marker. Again, the model explained over 80% of the variation in the genetic data.

The fact that such a large proportion of variability is explained in two genetic data sets provides very good evidence that habitat heterogeneity influences long term connectivity levels among local rabbit populations in the Mitchell region for both males and females. The habitat heterogeneity model thus provides a powerful approach for understanding the large scale processes that shape regional population systems in general. Therefore the model has the potential to be useful as a tool to aid in the management of those systems, whether it be for pest management or conservation purposes.

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STATEMENT OF AUTHORSHIP

The work contained in this thesis has not been previously submitted for a degree or diploma at any other higher education institution. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made.

Signed: QUT Verified Signature

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Chapter 1. Factors Affecting Animal Distribution Patterns

1.1 Introduction

Questions regarding regional animal distribution patterns, and the reasons why they exhibit these patterns, are fundamental to the study of ecology. Animals must be able to access food, water, potential breeding partners and other resources that are necessary for long term survival. The heterogenous distribution of such resources across a region is a major factor which is likely to influence animal distributions (Kareiva 1990). Distributions may also be influenced by local and broad scale stochastic effects (Pimm *et al.* 1988, Lande 1993, Halley and Iwasa 1998, Palmqvist and Lundberg 1998), and internal dynamic population processes (May 1986, Hanski 1990, Lawton *et al.* 1994).

An important set of studies have focussed on systems in which a population is composed of interacting subpopulations which are spread out in space (Wright 1931, Gause 1935, Andrewartha and Birch 1954, Huffaker 1958, Erlich and Birch 1967, MacArthur and Wilson 1967, den Boer 1968). In these population systems, dynamics (and thus distribution patterns) are determined at a scale broader than that of the local relatively isolated population (Murdoch 1994). In such a system, local populations may become extinct, and the sites which previously supported a population may be recolonised by limited interactions with neighbouring populations. Such spatial arrangements have the potential therefore to enhance the long term persistence of a population system (Huffaker 1958, den Boer 1968, 1970).

In contrast to earlier theoretical models in which long term persistence was assumed (eg Nicholson 1933), these studies emphasise the ephemeral nature of local populations. Extinctions of local populations may result from localised deterministic and stochastic effects in which extinction probabilities are largely determined by population size, or may result from more broad scale stochastic effects such as drought (see Pimm *et al.* 1988, Lande 1993 and Caughley 1994 for reviews). If a number of local populations are spread out across a region they are likely to experience localised stochastic and deterministic effects differently,

while broad scale abiotic effects are likely to lead to correlations in births and deaths among many local populations (Hanski 1991).

All extant species must at some time have expanded their ranges, either from the original point of speciation, after severe climatic changes (eg ice ages; Hewitt 1996) or as a result of human assisted introductions into new areas (as is the case for many non native species in Australia). For a population system to establish and persist over time, suitable vacant sites must be colonised during a range expansion, or recolonised after local extinction in an established system. Processes which allow the transfer of individuals among sites are thus essential for establishing and maintaining the patterns of distribution of organisms within their ranges (Ims and Yoccoz 1997). What is important therefore is the connectivity among populations, which can be measured as the average number of individuals per generation which move successfully between two populations, through time (after Stacey *et al.* 1997). Alternatively, connectivity can be expressed as the probability of successful transfer of individuals among the populations in question.

Different patterns of population distribution may result from different levels of connectivity. Historical trends in movement among populations may govern spatio-temporal distribution patterns by affecting demographic and genetic parameters in populations which would otherwise be isolated (Kimura and Weiss 1964, Brown and Kodric-Brown 1977, Gilpin 1991, Wu *et al.* 1993). Dispersal is the widely accepted term to describe movement of individuals among populations. It is comprised of at least three processes, emigration (the one-way movement of individuals from their home range), travel (the movement of individuals between populations), and immigration (the assimilation of those individuals into new populations). Dispersal has the capacity to increase the size of populations (Lidicker and Stenseth 1992) and thus alter their persistence times (Brown and Kodric-Brown 1977, Schoener 1991), and to modify genetic variation within the recipient population (Hedrick and Gilpin 1997). These three processes are also known as transfer processes (Ims and Yoccoz 1997). Transfer processes can also lead to the colonisation of new patches or the recolonisation of vacant patches, which were previously occupied by populations

driven to extinction (Lande 1993). The successful limited movement of propagules (which may include groups or individuals) among populations therefore has the potential to augment the persistence of individual populations, and hence the system of which they are a part (Hansson 1991, Adler and Nuernberger 1994).

Alternatively, a high degree of interaction may lead to synchronous population dynamics which are likely to decrease the persistence time of population systems (Harrison and Quinn 1989, Palmqvist and Lundberg 1998). Understanding transfer processes, and the factors which affect them, thus has important implications for understanding and manipulating the distribution patterns of organisms, including conservation biology (Hof and Flather 1996), epidemiology (Earn *et al.* 1998) and pest management (Stenseth 1981). If connectivity can be determined directly, it may allow us to correlate the historical pattern of these processes with environmental (resource) factors and therefore potentially determine the critical environmental factors which have given rise to the interaction pattern over time.

1.2 Models of Distribution Patterns

The concept of a population is central to ecological and genetic studies. In ecology, populations were been viewed as collections in the same space and time of homogenous individuals (Cole 1957). The limits of a population under this definition had considerable lattitude, since the scale at which a population was considered was defined by the question of interest. Mathematical models have often been used to infer connectivity levels within population systems, generally under the assumption that a population is continuously distributed across a landscape, or that a population is comprised of semi-discrete subpopulations (Slatkin 1985), also known as local populations (Hanski and Gilpin 1997). While these conceptualisations of a population are based on interaction levels, the dynamics of individual populations may also be important (eg source-sink populations, Pulliam 1988). Differences in definitions of a population has led to confusion (Thomas and Kunin 1999). It has been recently suggested that it is the

processes that occur within (births and deaths) and among (immigration and emigration) populations that should be fundamental to the classification of populations and the systems within which they interact (Thomas and Kunin 1999).

In many ecological studies in the past dispersal was viewed solely as the movement of individuals, although now it is acknowledged that successful dispersal involves reproduction (and thus gene flow) to recipient populations (Lidicker and Stenseth 1992). This idea is fundamental to genetic models since the reproduction of immigrants is essential for the transfer of genes among populations (Slatkin 1985). Although the spatial extent of populations and population interactions have become popular topics in ecological studies in recent decades (see Hanski and Gilpin 1991 for review), the evolutionary implications of interactions within a subdivided population were considered some time before (Wright 1931). For this purpose, Wright (1931) employed a model of a subdivided population known as the island model (later renamed the infinite- or n- island model, Slatkin 1985). In this model, a population is subdivided into an infinite number of subgroups, each breeding at random within itself except for a proportion of migrants drawn at random from other subpopulations. Since equal connectivity among subpopulations is assumed, and the average properties of the system do not change due to the assumption of an infinite number of subpopulations, the characteristics of a single subpopulation are equivalent to all others. Local genetic drift in each subpopulation, which is caused by the random sampling of genes at the time of gamete formation, will lead to genetic differentiation in the absence of some level of gene flow (Slatkin 1985).

One important characteristic of this early model is that it shows no explicit spatial structure (connectivity among all subpopulations is equal). This occurs because it is assumed that the contribution of individuals from a subpopulation to any other subpopulation is equal irrespective of their relative spatial relationship. Although this assumption ensured analytical tractability, and the model continues to be used as a theoretical extreme of the long distance transfer of individuals,

the lack of a definable spatial element means that few real populations are likely to exhibit such a structure (Harrison 1991).

Levins' (1970) classical metapopulation model can be considered one class of island model. Levins described an idealised population system in which a large number of identical patches were embedded in an inhospitable matrix (habitat unable to support a population), internal patch dynamics were ignored and patches could only exist in one of two states at any one time, vacant or occupied. Recolonisation of an empty patch assumed successful dispersal to and reproduction within the patch. The classical metapopulation model has been criticised for restrictive assumptions, which include correlated dynamics and the equal size and quality of all patches (which implies identical carrying capacities in each patch) (Harrison 1991, Hastings and Harrison 1994). Additionally, the assumption of equal connectivity among all patches discounts any effects of distance or other factors which may affect the interchange of individuals among patches and so, like the island model, the classical metapopulation model does not define explicitly spatial structure. For these reasons, few real populations have been found which conform to this model (Harrison 1991).

The stepping stone model (Kimura and Weiss 1964) describes the effect of spatially limited dispersal among populations, and was one of the earliest models to recognise explicitly the effect of space. In this model, a finite number of contiguous subpopulations have fixed spatial coordinates in one, two or three dimensions, with exchange of individuals occurring exclusively among adjacent subpopulations. While the direct exchange of individuals is limited to neighbouring populations, gene flow can eventually occur between non-neighbouring subpopulations in a number of sequential steps via the subpopulations that connect them (Neigel 1997). Although in the original model the degree of connectivity is equal between each set of neighbouring subpopulations, the model allows for the possibility that patch characteristics vary (such as size or quality) and therefore allows for differences in connectivity because patches can be identified uniquely (Kareiva 1990). From a theoretical genetic perspective, the stepping stone model and island models can be considered the extremes in short and long distance connectivity.

The stepping stone model was an important advance from the island model as it allowed for a more explicit explanation of the problem of isolation by distance (Wright 1943), in which the transfer of individuals (or genes) among populations is spatially dependent. Such a situation requires the recognition of a spatial element to explain the distribution pattern of genes which would result from restrictions in connectivity. For instance, in a population system which can be described by a stepping stone model in one dimension, the level of gene flow will show an inverse relationship with geographic distance (and therefore, measures of genetic differentiation will increase with geographic distance) (Slatkin 1993). In this model, distance acts as an isolating factor among populations.

A number of ecological models exhibit features of the stepping stone model because they identify particular patches and thus allow for variation in the characteristics of those patches. The source-sink model (Pulliam 1988) describes a stable population system with asymmetrical connectivity between two contiguous populations, such that a one way transfer of individuals occurs from the source to the sink population. In this model the quality of resources in the source patch leads to a greater number of births than deaths (thereby leading to a larger population and increased persistence times). In contrast, sink populations occupy patches in which inferior resource quality leads to mortality outweighing within-habitat reproduction (Pulliam 1988), thereby decreasing persistence times regardless of patch size.

Several metapopulation models include the potential for variability in both the size and quality of patches (eg Hanski and Gyllenberg 1993, Bowers and Harris 1994, Day and Possingham 1995), thereby allowing for variation in the degree of interactions among populations. However these models assume that local population extinctions are mainly driven by population size (which is represented by patch area) and that connectivity is related to the geographical distance among patches. These assumptions may be legitimate in those systems in which local populations tend to be small and in which habitable patches can be clearly delineated within a matrix unsuitable for the establishment of local populations.

In many population systems however, patch area *per se* may not provide the best explanation for local population dynamics, particularly in systems that experience substantial environmental variability (Fleishman *et al.* 2002). Indeed, even within an established metapopulation framework, habitat quality can affect the dynamics of real population systems (Harrison *et al.* 1988, Hanski and Gilpin 1991, Thomas *et al.* 1996, Boughton 1999). In population systems which undergo regional or catastrophic extinctions (Hanski 1991) many local populations will be affected simultaneously and extinction probabilities will show a limited relationship with population size (Harrison 1991). Here, the quality of resources that affect the growth and survival of local populations may be a better determinant of population system dynamics than patch size.

Another confounding effect in metapopulation models is that for simplicity, they normally consider a spatial structure in which local populations occupy resource patches in a matrix of relatively unsuitable habitat. As a result of this simplification, isolation between populations in these systems is considered to be a simple function of distance. Terrestrial systems typically do not exhibit such a binary characteristic, and biological and physical features are more likely to be distributed heterogeneously in space and time (Wiens 1997). Distance may therefore not be the only, or even the most important factor which isolates populations (Fleishmann *et al.* 2002). Metapopulation models ignore environmental and behavioural factors which may affect connectivity between populations, such as geographical barriers (eg mountains, rivers), behavioural barriers (eg an aversion to a particular vegetation type such as dense forest), or the heterogenous distribution of resources which may be necessary to sustain life during dispersal (eg water).

One further limitation of current ecological models is that they assume that transfers among populations are achievable by individuals. Their application is therefore limited if the processes which determine the spatial distribution of a species occur at a scale broader than that which can be achieved by individual movement. Connectivity may need to be considered in a broader spatial context, in which the descendants of the individuals which leave a donor population, rather than the individuals themselves, bring about the recolonisation or augment

the persistence of populations which are widely spaced. Such a case, in which populations in a region saturated by patches affect the demographic characteristics and persistence times of non-neighbouring populations over time, is perhaps more correctly viewed as a stepping stone model. Although many studies consider the genetic implications of gene flow in metapopulations over broad temporal and spatial scales, the potential for one population to influence a distant population has not been considered from an ecological perspective.

1.3 Processes Which Determine Connectivity

Theoretical models highlight the importance of broad scale processes, particularly dispersal, in determining the persistence and therefore the distribution pattern of species within their range. Dispersal has been defined as the movement an animal makes from its home range to the place where it reproduces (Lidicker and Stenseth 1992). While this definition implies a single process, dispersal is perhaps more correctly viewed as the end point of three distinct processes: leaving (emigration), travelling (movement between the individuals home range and its destination patch) (Ims and Yoccoz 1997) and arriving (immigration and reproductive incorporation into an existing population or colonisation of a new patch) (Lidicker and Stenseth 1992). Although often not stated explicitly, successful dispersal by an individual can be interrupted during any one of these processes, and therefore together they will determine the degree of isolation (or connectivity) among populations.

An animal that emigrates leaves a familiar territory in which potential sources of food and shelter (both from predators and from abiotic elements) are known. There are risks inherent in emigrating, since mortality may be higher in dispersers than in residents (Gaines and McClenaghan 1980, Hansson 1991), successful mating in a new territory may not occur, and immigrant fecundity may be lower than that of philopatric individuals (those animals that remain within their natal home range) (Krohne and Burgin 1987, Massot *et al.* 1994). From an evolutionary perspective, emigration is worthwhile if on average, individuals produce a larger number of viable offspring over the course of their lives after leaving their home territory than if they stayed (Lemel *et al.* 1997).

Dispersal tends to be male-biased in mammals and female-biased in birds (Greenwood 1980, Wolff 1994, Clarke *et al.* 1997). Numerous hypotheses have been proposed to explain sex related dispersal behaviours. Most of these hypotheses centre around the advantages in competition for resources (mates or other breeding resources) conferred on the philopatric sex, or on the fecundity costs of dispersal (Greenwood 1980, Johnson 1986, Pusey 1987, Wolff and Plissner 1998).

The population genetic consequences of sex-biased dispersal have recently attracted much attention (see Prugnolle and de Meeus 2002 for review). While there have been theoretical treatments examining population dynamic consequences of sex-biased dispersal (Ruxton 1995, Doebeli 1996, 1997, Lindstrom and Kokko 1998), these have implicitly focused on isolated populations (Ranta *et al.* 1999). There have been relatively few studies examining the population dynamic consequences of sex specific dispersal behaviour within subdivided populations (although see Efford 1998, Aars and Ims 2000). Ecological models have generally tended to ignore dispersal differences between the sexes, although some recent simulation models have employed sex specific dispersal rates (eg Gaona *et al.* 1998). Successful colonisation will tend to be constrained by dispersal of the more philopatric sex. It may therefore be important to assess any differences in the dispersal potential of males and females when examining dispersal among local populations within a subdivided population system.

If an emigrant does not become a member of a breeding population after leaving it's home range it is irrelevant from a genetic and demographic perspective (Stacey *et al.* 1997). Immigration tends to enhance the persistence of local populations in fluctuating environments, leading to greater population system persistence (Hastings 1982, Hastings 1991, Doebeli 1995, Hanski and Zhang 1993, Hof and Flather 1996, Murdoch *et al.* 1996, Rohani *et al.* 1996, Peltonen and Hanski 1991, Hill *et al.* 1996, Holyoak and Lawler 1996). If immigration occurs before the target population goes to extinction, the demographic and genetic contribution of immigrants may bring about a "rescue effect" (Brown and Kodric-Brown, 1977). Immigration therefore can buffer populations from

adverse demographic, genetic or abiotic effects (Stacey *et al.*, 1997). Immigration can be detrimental, since immigrants may introduce disease into a population (Hess 1996). In pest populations, diseases have been introduced deliberately in the past in an effort to control the size and distribution of pest populations (eg the release of myxomatosis into the Australian wild rabbit population, Fenner and Fantini 1999). While the positive effects of connectivity on population or system persistence usually requires reproduction of immigrants within the recipient population, the transmission of a disease may not require sexual contact if the disease is not sexually transmitted. Contact between individuals or even proximity to transmission vectors (eg Spanish fleas for myxomatosis, Fenner and Fantini 1999), may be sufficient to spread a disease from a new immigrant to a recipient population.

When local populations are driven to extinction by natural or anthropogenic influences, dispersal may bring about the colonisation of habitable patches within a population system. Successful colonisations may form viable populations which produce more emigrants. Repetitions of this process lead to the establishment of new population systems during range expansion (Sakai *et al.* 2001) and ensure that the persistence of existing population systems is greater than that of individual populations. Colonisation of extinct patches may provide the major mechanism for gene flow in some systems (Slatkin 1985, Fuller *et al.* 1996).

After emigration from a donor population, and before immigrating into a recipient population, individuals must negotiate an array of spatial, physical and resource factors in the intervening habitat. Any factor which impedes or promotes travel will, in conjunction with factors which affect immigration, determine the degree to which one (donor) population can influence the genetic and demographic parameters of another (recipient) population and so affect both its genetic constitution and persistence. Geographical distance and barriers (including inhospitable matrix) have been traditionally considered as major factors which limit dispersal. More recently it has been recognised that 'viscous' landscape elements may restrict dispersal without necessarily acting as absolute barriers (Wiens *et al.* 1997).

Although ecological studies have considered the influence of populations on the dynamic parameters and persistence of other populations, these studies are considered at a relatively restricted scale in which individuals can disperse between populations. Such influence may occur at broader spatial and temporal scales which have in the past been examined in population genetic studies (stepping stone models). Systems are likely to exist in which ecological processes occur at this broader scale, and so an extended perspective of connectivity needs to be developed. For instance, the distance between populations may be so great that it is unlikely that an individual is physiologically capable of travelling between donor and recipient patches. Conversely, if the individual is capable of traversing the geographic distance, it may be behaviourally unlikely to do so if adequate habitat patches which could be colonised intervene (adequate patches are those patches in which breeding could take place but have a high extinction tendency due to poor resource quality or quantity). In such a setting over time, individuals may emigrate from a relatively temporally stable donor population to fill adjacent unstable habitats. Populations in these intervening populations may persist long enough to produce a propagule of emigrants which move to an adjacent patch, with successive generations of descendants utilising habitat patches between donor and recipient populations.

Although it has not been considered in traditional ecological models, this scenario would allow the influence of a donor population on a distant recipient population to be quantified. This model bears similarities to a stepping stone model, however previous models have considered the effects of gene flow only via temporally stable populations. Connectivity between patches in this spatially extended ecological model is likely to be a function of the characteristics of intervening patches such as resource quality (Pulliam 1988), since this will determine the demographic capacity of populations in intervening populations to provide emigrants. Any historical isolation between populations in this model would thus be due to patch quality which would affect the probability of successful colonisation between the donor patch and the recipient patch.

1.4 Modelling Connectivity

In regions where resource patches are contiguous and a patch becomes filled after colonisation, the travel component of dispersal occurs only across patch boundaries and so can be ignored (except in patches where populations cannot establish and thus the patch must be traversed). When dispersal occurs in the stepwise fashion as described above, dispersal is unlikely to be impeded during emigration or immigration into the (vacant) recipient patch. If so, factors which might inhibit emigration and immigration can be largely ignored and the level of influence that one population exerts on another will be a function of the dispersal flow through intervening patches. In this scenario, factors affecting population size in each intervening temporally unstable patch, such as species specific resources required for successful reproduction and population growth, will ultimately limit connectivity by determining the size of the emigrant flow from each patch. If the species specific habitat attributes which enable populations to reproduce and grow can be determined and averaged over time, and appropriate numerical values applied to them, mathematical combination of these values should allow for the development of a quantitative model of relative connectivity based on habitat heterogeneity. In this model the relative long term isolation among populations will be related to the spatial heterogeneity of resources within a region.

The general applicability of any mathematical model is limited without reference to independent empirical data to test the veracity of model assumptions (eg Gotelli and Kelly 1993). Validation of a model requires the application of a data set which is independent, both of the assumptions and of the operation of the model. Testing the veracity of the tentative isolation by habitat heterogeneity model therefore requires the existence of techniques to measure the relative level of dispersal of organisms over long time spans (greater than several generations), between distant donor and recipient patches, through an environment saturated with resource patches in a temporally unstable environment. One reason that such broad scale spatial and temporal processes have not been considered in ecological studies may be that ecological methods for measuring dispersal apply only to the time and space over which observations are made (Neigel 1997).

1.5 Measuring Connectivity

Ecologists have relied predominantly on variations of a single technique to directly measure the transfer of individuals from one location to another. Mark recapture methods, in which animals which are caught in one site are marked, released, and potentially trapped again at other sites, have traditionally been used to infer the existence and level of dispersal processes among populations. This technique is flexible and can allow for the information regarding specific events to be determined, such as the life history stage at which dispersal occurs or the ecological conditions which favour dispersal (Slatkin 1994). However mark recapture techniques can only demonstrate dispersal within generations. In systems which exhibit extinctions, recolonisations and the influence of populations on the persistence of others over a broad region, such a technique precludes the observation of potentially important connectivity effects over larger spatial and temporal scales.

This broader view is encompassed in indirect measures of effective gene flow, which estimate the long term effects of gene flow over a large range of temporal and spatial scales (Neigel 1997). In population systems where long term connectivity among demes is high, local populations will tend to show population genetic similarities (Slatkin 1985). In contrast, population genetic differentiation will occur when local populations are isolated. The level of population genetic differentiation among local populations has been frequently assessed by the estimation of F statistics, particularly F_{ST} (Wright 1951).

F_{ST} can be interpereted as the standardised variance in the frequency of an allele among populations (Wright 1951), and can be used to indirectly estimate gene flow (Slatkin 1994). Indirect genetic methods produce estimates of the average level of gene flow with reference to a mathematical distribution model (often the island model), and include the interaction of gene flow and other factors to predict how much gene flow must have been occurring over time in order for observed population genetic patterns to be present (Slatkin, 1994).

Any technique used to estimate dispersal levels must be relatively insensitive to factors other than gene flow which might affect allele frequencies. Significant variations in the distribution pattern of sampled populations from the island model may introduce some degree of error, although such errors are unlikely to be large (Slatkin and Barton, 1989). Similarly, in populations not at equilibrium, such as large populations (particularly those with low levels of gene flow), and systems which exhibit large fluctuations in subpopulation size over a relatively short temporal scale, F_{ST} results must be treated with caution, and are unlikely to give precise estimates of the numbers of migrants per generation (Slatkin and Barton, 1989). Even in non-equilibrial systems, however, large differences in F_{ST} values among local populations are likely to reflect underlying dispersal trends. Since the levels of differentiation among local populations will be strongly influenced by long term patterns of connectivity, F_{ST} estimates based on population genetic data can be used to infer relative levels of connectivity among populations.

As well as an appropriate mathematical technique for estimating gene flow, an appropriate genetic marker must be used to determine genetic variation for use in calculations. Although a variety of genetic markers exist, mitochondrial (mt) DNA has proven invaluable for use in many population systems (Neigel 1997). While double stranded, the haploid mtDNA genome does not undergo recombination, and is inherited maternally in most animal species. Because of this, the effective population size of mtDNA genes is approximately one quarter that of nuclear genes, which allows population subdivision to be detected in mtDNA sequences at a level of gene flow at which nuclear genes are panmictic (Birky *et al.* 1983). Also, mutation rates are often higher in some animal mtDNA genes than equivalent nuclear sequences, potentially allowing for greater variation to be detected (Neigel 1997). mtDNA is therefore an appropriate choice of marker in populations which exhibit significant levels of gene flow, including those which are subject to large fluctuations in population size.

Since mtDNA is maternally inherited, frequency based data may be confounded by any sex related biases in dispersal. It may therefore be appropriate in addition to employ a biparentally inherited genetic marker. For this purpose, Amplified

Fragment Length Polymorphisms (AFLPs) are being used more frequently, since they provide a relatively cheap and reliable means for analysing population structure and can be used to calculate F_{ST} analogs (Mueller and Wolfenbarger 1999). As a nuclear marker, AFLPs provide information regarding combined male and female gene flow but due to a larger effective population size are unlikely to be as sensitive as mtDNA to population subdivision (Birky *et al.* 1983).

Analyses of inbreeding coefficients (eg F_{ST}) are robust and can be used to infer historical trends in dispersal among populations, even when the populations undergo large size fluctuations. Inbreeding coefficients can therefore be used to infer connectivity among spatially structured populations. This approach can be used to generate a data set independent from the assumptions and the operation of the habitat heterogeneity model, and so provides a means of validation of the model.

1.6 The European Rabbit in Australia as a Model Species

Several criteria are desirable in the selection of a model species with which to test the tentative model of isolation by habitat heterogeneity. Populations of the species should be affected by relatively few, well known habitat attributes (to limit possible interactions among attributes) and be spread widely across a region which exhibits a range of variations in resource levels (which, if the model is accurate, will create variations in connectivity among populations through time).

In Australia, these criteria are ideally met by the wild rabbit (*Oryctolagus cuniculus*). The first recorded release of wild rabbits in Australia was in Geelong, Victoria in 1859 (Stodart and Parer 1988). Although only a few (between 15 and 24) rabbits were released, the species is now widely distributed and constitutes a major pest species in Australia. Rabbits cause significant damage to native flora and fauna, and estimated damage to agricultural systems of $A60-90 million annually (Wilson *et al.* 1992). Rabbits expanded their range rapidly through Australia, and this has been attributed to their prolific reproductive and dispersal capacities, good competitive ability and the absence

of significant natural predators and parasites in Australia (Rural Lands Protection Board 1987), although human assisted translocations may have also played a role in their spread (Stodart and Parer 1988, Wilson *et al.* 1992).

Rabbits evolved in a mediterranean climate, and northern limits to their geographical range are likely due to an interaction between temperature, day length and pasture growth occurring in response to summer rainfall (Cooke 1977). Within this broad geographical range, rabbit population distribution patterns have been shown to be influenced by ecological factors including soil type, surface cover, altitude and water distribution (Parer 1987). As a fossorial species, the success of local populations is closely tied to the availability of suitable burrowing habitat in arid and semi-arid environments (Myers 1958). Rabbits exhibit a preference for sandy soils (Myers and Parker 1965, Parker *et al.* 1976, Parer and Libke 1985, Parer 1987, although see Hall and Myers 1978), as it is easily dug, has good drainage (which decreases the risk of a warren being flooded), and the flora associated with this soil type responds quickly to rain. Sandy soils exist at one end of a continuum of soil type suitability which is determined by clay content, with heavy cracking clays being most unsuitable. Soil type is thus highly suitable for consideration as a habitat attribute which is likely to influence connectivity among rabbit populations.

The success of rabbits as a pest species in Australia is well illustrated by their capacity to attain high densities even in arid regions in which large suitable soil patches exist next to patches which are unsuitable for burrowing (Fuller *et al.* 1996). During long periods of drought, most rabbits will die, with a few surviving in only the most favourable areas (Myers and Parker 1975a, 1975b). In such catastrophic systems it is highly likely that extinctions and recolonisations play a major role in establishing long term regional rabbit distributions. Traditionally, the success of recolonisation after local extinctions would be considered to be affected by the distance between refuge populations and suitable empty sites, and/or the presence of geographic barriers to dispersal among sites.

Fuller *et al.* (1996) have shown that rabbit populations are panmictic over a large area in western Queensland. This may be an effect of a relatively promiscuous

mating system in resource rich areas, and of a high level of extinctions and recolonisations in response to recurrent episodes of drought. In contrast, analysis of mtDNA haplotype frequencies of rabbit populations in a more eastern semi-arid region (the Mitchell region) showed that populations were highly structured (Wilson *et al.* 2002). The Mitchell region is characterised by a range of soil types, from suitable to less suitable, although few areas would be unable to sustain a population. While potential geographic barriers may exist (eg the Maranoa River which flows seasonally), this is not reflected in the pattern of haplotype frequencies (Wilson *et al.* 2002). Furthermore, isolation among populations in the eastern system is not a function of the distance between them (Wilson *et al.* 2002).

The current genetic structure of local rabbit populations within the Mitchell region may be related in part to recent range expansion in addition to within system interactions. If habitat heterogeneity has the capacity to influence dispersal processes in the long term it should also have influenced the initial genetic constitution of local rabbit populations within this region.

Rabbit populations in the semi-arid region of Queensland present as excellent candidates on which to test a tentative model of habitat heterogeneity. Determining relative connectivity levels in this region may allow for a better understanding of the dynamics of local populations within this system. An added benefit of such knowledge would be that local and broad scale control programs could be more specifically targeted.

This study has been designed to consider the effect of habitat heterogeneity on population system dynamics in a extended spatial framework. The specific objectives of the study were to:

1. develop a mathematical model in which relative long term connectivity among local populations within a population system is determined by the spatial distribution of resources.

2. test the model using regionally appropriate parameters for the wild rabbit in the Mitchell region based on empirical data, and to validate the model using independent population genetic data.

3. employ a stochastic enhancement of the model to simulate a range expansion into the Mitchell region in order to determine the historical and long term contribution of habitat heterogeneity to connectivity among local wild rabbit populations.

4. use the model to assess any differences between male and female patterns of long term connectivity among local rabbit populations in the Mitchell region.

Chapter 2. A Model of Isolation Due to Habitat Heterogeneity

2.1 Introduction

For many years, populations of plants and animals were considered to be a well-mixed collection of individuals occupying a space that was usually arbitrarily defined by the bounds of the question of interest (Elton 1927, Cole 1957). It is now recognised that even at the local level of scale, resources upon which individuals depend for survival and reproduction tend to be distributed heterogeneously in space (Karieva 1990). It follows that the spatial distribution of local populations will reflect this resource distribution (Andrewartha and Birch 1954, den Boer 1968, Levins 1969), and that the relative levels of demographic and genetic differentiation among spatially distinct populations within a system will be a function of the long term connectivity among those local populations (Slatkin 1985, Hansson 1991, Harrison and Hastings 1996).

Models that view connectivity as a fundamental characteristic of animal and plant population systems have evolved, and have tended to grow in complexity (Karieva 1990). While early models (Levins 1970) postulated equal connectivity among all local populations, later models considered that differences in connectivity could exist among populations due to geographical distance (eg. Hanski 1991, Kozakiewicz 1993, Adler and Nuernberger 1994, Hanski 1994) or to barriers to dispersal (Lidicker 1975, Slatkin 1985, Kozakiewicz 1993). Recent studies suggest that social systems may also play a role in determining connectivity among local populations (Cowan and Garson 1985, Brandt 1992, Surridge *et al.* 1999).

The relative levels of connectivity within a population system may also be affected by differences in the quality of resources within habitat patches (Pulliam 1988, Pulliam & Danielson 1991, Pulliam *et al.* 1992). The source-sink model of Pulliam (1988) examined a system of interacting populations in which the quality of patch resources affected both the dynamics of populations within patches and patch-to-patch interactions.

While differences in resource quality in this model were extreme, numerous species occupy a local range in which resource quality varies less drastically (Caughley *et al.* 1988). In these situations, interactions between spatially disjunct local populations may occur in a "stepping stone" fashion via populations occupying intervening resource patches, with the dynamics of these intervening populations being affected by the quality of the resources in the patches that they occupy. The possibility therefore exists that relative differences in long term connectivity among spatially distinct local populations within these population systems may ultimately be related to the quality of resources within intervening patches.

While a number of models have examined the effects of resource heterogeneity on population systems (see Dias 1996 for review), few have considered broad scale, long term spatial processes such as connectivity that may influence population structure. Fewer still have been validated using independent empirical data (Karieva 1990). In addition, these models are often based on moving cohorts through time, for example discrete time models.

The current structure and functioning of any population system is a consequence of the long term sum of individual events affecting each of its constituent populations. An alternative approach to modelling the spatial distribution of population structure within such systems is to base a model on long term mean summary variables which reflect the long term impact of these processes, rather than cohort based variables. An advantage of modelling long term connectivity among populations using mean, long term summary variables is that model validation can be carried out using independent population genetic data. Such data are the consequence of the long term sum of individual events, as any mechanism that causes differential levels of connectivity within a population system can result in genetic structuring among local populations (Wright 1951, Kimura and Weiss 1964, Ims and Andreassen 1999).

This chapter develops a general model of long term relative connectivity due to the spatial heterogeneity of resources within a system comprised of resource patches of varying quality. A simple extension of the model allows for the

incorporation of patches containing landscape elements which impede dispersal. The usefulness of the habitat heterogeneity model is then demonstrated by applying it to a spatially structured rabbit population system in central southern Queensland, for which independent genetic data on population structure are available. The specific aim of the rabbit case study is to determine if population structuring within the system can be explained by differences in long term connectivity among sites, due to the distribution of a major resource (soil type) and a landscape element which impedes dispersal (dense forest).

2.2 Model Development

Assume a vacant landscape consisting of contiguous resource patches, where resources are defined as factors essential for survival and reproduction of the species of interest. The level of scale at which the landscape is partitioned is determined by its constituent patches, which are defined as the minimum area within which the relative quality of identified resources can be considered homogenous. Also assume that when occupied, a patch contains a single population. Further assume that maximum population growth will occur in patches in which resource quality is optimal and that the effect of suboptimal resources within a patch will be to modify population growth downwards from optimal. Given this assumption, it is practical to index the level of each resource in a patch relative to the best quality of that resource in the system. Since patches are delineated by resource quality, contiguous patches will differ in the quality of at least one resource. In order to calculate the relative long term connectivity in a population system within the landscape, it is necessary to first determine the degree of interaction between each of the constituent populations.

Consider the long term potential for interaction between a population in an originating patch and the population in a distant destination patch. If the landscape is initially vacant, a seeding propagule introduced into the originating patch (patch 1) will experience growth as determined by a maximum growth factor which is modified by the relative quality of resources available in the patch. A proportion of the final population will then disperse and colonise the next patch (patch 2). This process of colonisation, growth and dispersal will

occur from patch to patch in a stepwise fashion until a dispersing propagule colonises the destination patch. The mode of movement between origin and destination patches (for instance, a random walk or a straight line) is immaterial to the structure of the model but may be important in interpreting outcomes when applying the model to a specific system.

It is important to note that growth and dispersal are not used here as descriptors of individual annual cyclic events. It is assumed that, in each patch, the growth variable represents the long term mean of all population growth events in that patch. Similarly, the dispersal variable represents the long term mean proportion of the population that has dispersed. Thus a single series of growth and dispersal steps along a path between an originating and a destination patch can be used to represent the long term sum of processes affecting connectivity along that path.

For each resource identified in the system, an index of quality for the resource in any patch (R) can be defined as the quality of that resource in the patch (r_p) relative to the optimal quality of the resource in the system (r_{opt}). In a system with a single resource in a specified patch:

$$R_1 = r_1 / r_{opt} \quad (1)$$

However a species may be dependent upon a number of resources within a region. In a system of m resources the overall relative patch resource index (R_p) for any patch can be determined as the product of each individual resource index within the patch, and so for a multiple resource system:

$$R_p = \prod_{i=1}^{m} R_i \quad (2)$$

The relative resource index in a patch acts as a reducing fraction on growth in that patch. The size of the propagule immigrating into the second patch (N_2) can therefore be calculated as:

$$N_2 = N_1 G_1 R_1 d_1 \quad (3)$$

where:

N_1 = the size of the propagule seeding the originating patch

G_1 = the long term mean growth factor in the originating patch

d_1 = the long term mean proportion of individuals dispersing from the originating population to the next patch

R_1 = the resource quality index in the originating patch

The process of colonisation, growth and dispersal is repeated from patch to patch along a dispersal path from the originating to the destination patch, and so the size of a propagule emigrating from the last patch on the dispersal path (p) and immigrating into the destination patch is given by:

$$N_{p+1} = N_1 \prod_{i=1}^{p} (G_i d_i R_i) \quad (4)$$

Even in population systems that experience considerable environmental stochasticity on a regional scale, the long term variation in growth and dispersal among patches may be low. If so, the model can be simplified by considering G and d as system constants rather than patch constants and Equation 4 can be simplified as:

$$N_{p+1} = N_1 [Gd]^p \prod_{i=1}^{p} R_i \quad (5)$$

Equation 5 allows for the size of a propagule entering any destination patch via a specified path from an originating patch to be calculated. To determine the total number of immigrants into the patch, this equation is applied for each dispersal path which enters the patch and the results summed.

Consider now the relative long term connectivity among n local populations within specific patches in a system. The connectivity (C) of a local population, α, results from the mean of all two way interactions between α and the n-1 other distant populations. As connectivity within a system can be considered a relative measure, this mean can be indexed relative to the total interactions within the system:

$$C\alpha = \left(\sum_{i=1}^{n-1} N\alpha(in)_i + \sum_{i=1}^{n-1} N\alpha(out)_i \right) \Big/ 2\left(\sum_{i=1}^{n} N(tot)_i \right) \quad (6)$$

Where:

$\sum_{i=1}^{n-1} N\alpha(in)_i$ = the sum of all propagules colonising patch population α from the (n-1) other local patch populations

$\sum_{i=1}^{n-1} N\alpha(out)_i$ = the sum of all propagules from patch population α colonising the (n-1) other local patch populations

$\sum_{i=1}^{n} N(tot)_i$ = the sum of all propagules colonising all patches

For the model to be useful, it is necessary to further define relative resource quality. The quality of a resource may vary as a gradient, a step function or a binary condition, for instance the presence or absence of the resource in a patch. Even if resource quality varies as a continuous gradient it may be reasonable to describe variations in quality with a limited number of categories. For instance, a gradient function of a resource in the system may still be categorised as having three relative levels of quality - optimal, intermediate or poor. From experimental evidence the relative effect of these different qualities of the resource on population growth within the system can then be indexed.

In some population systems, the relative levels of long term connectivity among local populations can also be affected by patches which include geographical barriers, or certain landscape elements which are resistant to dispersal or "viscous" (eg Wiens *et al.* 1997, Roland *et al.* 2000, Ferreras 2001). Geographical barriers can easily be incorporated into the model by considering that population growth is not possible in these patches. Resource quality would therefore be indexed as zero preventing further dispersal along that path. If the patch contains a viscous landscape element, population growth is again not supported and the probability of successful dispersal through the patch will relate to the geographical distance of the dispersal path through the landscape element. Relative resource quality in such patches would again be indexed as zero, but a dispersal resistance function based on dispersal distance through the patch is applied. All of the factors which have the potential to affect long term connectivity among local populations within a system (spatial heterogeneity in

the distribution of patch resources of different quality, and the spatial distribution of viscous landscape elements or geographical barriers) can be considered under the term habitat heterogeneity.

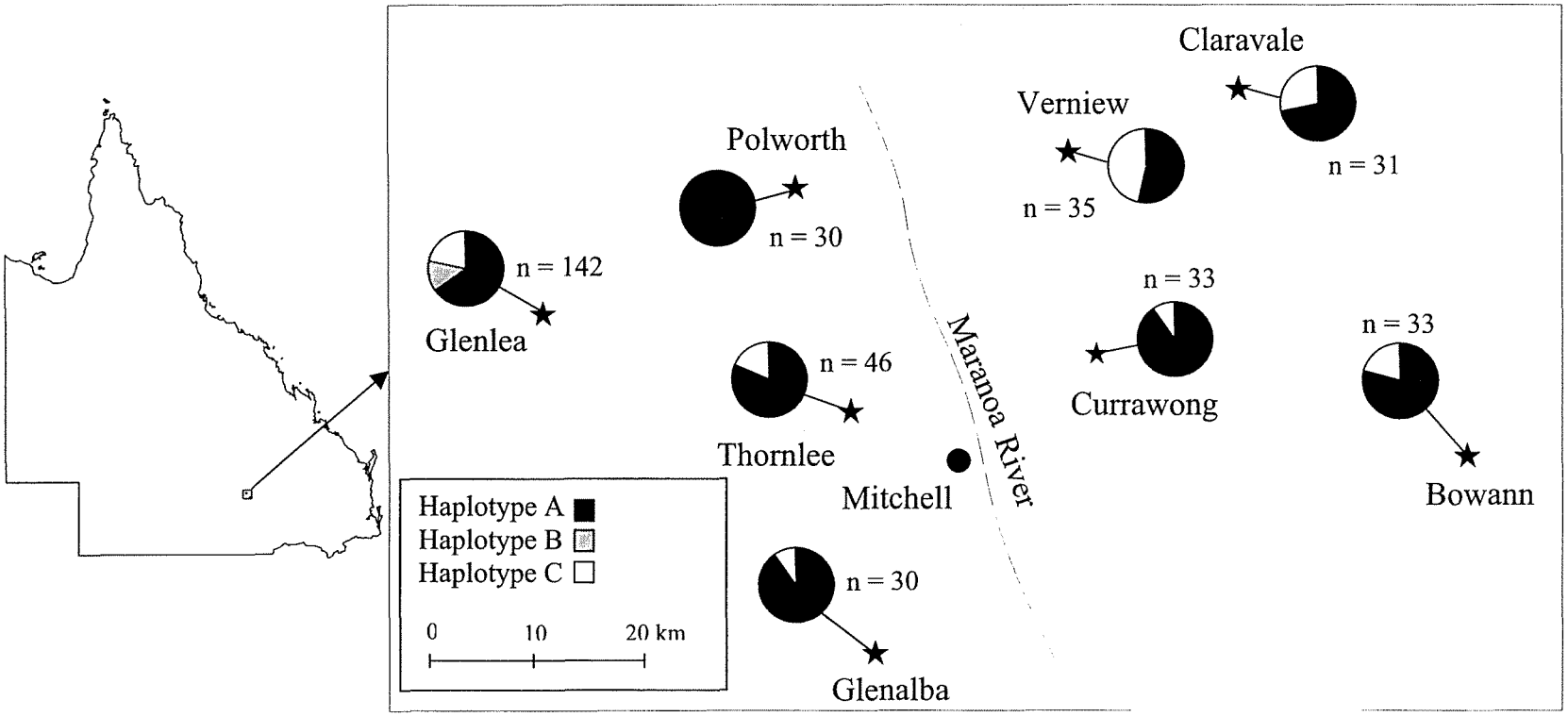
2.3 Model Application

To apply the model to a particular species in a specific population system, it is necessary to identify the resources upon which the species depends, and to map the spatial variation in quality of these resources within the system. It is then necessary to obtain empirical data on the effect of the variations in resource quality on population growth together with estimates of long term mean growth and dispersal. To determine the usefulness of the model in a given system, model output (relative connectivity indices) can be compared to an appropriate, independent estimator of long term connectivity. Population genetic data are particularly useful for this role, as population genetic structuring will occur largely in response to the long term level of gene flow between each local population and the remainder of the system (Slatkin 1985).

The wild rabbit *Oryctolagus cuniculus* L. is an appropriate species with which to demonstrate the utility of the model. The wild rabbit is one of the most damaging pests in Australia (Williams *et al.* 1995). Due to its pest status, research on aspects of wild rabbit population dynamics in Australia has been conducted for over 50 years, and the resources upon which rabbit populations depend are well documented. In addition, Wilson *et al.* (2002) provide population genetic data for eight wild rabbit populations in the semi-arid Mitchell region of central southern Queensland (Figure 2.1). These data show a high degree of population structuring that could not be explained by geographic distance among sites or by potential geographic barriers to dispersal such as topographic discontinuities or rivers.

It is well recognized that soil type is a major resource that affects rabbit survival and reproduction (Myers and Parker 1965, Myers 1970, Myers and Parker 1975b, Parker *et al.* 1976). The effect of soil type on population success is well documented, with rabbit populations in Australia (Myers and Parker 1965, Myers

Figure 2.1. Location of the Mitchell region in central southern Queensland (inset), with mitochondrial haplotype frequencies at study sites (★). (source: Wilson *et al.* 2002). Glenlea haplotype frequencies are the sum of frequencies of four populations occurring on the same large resource patch. There was no significant difference in haplotype frequencies among the four populations ($\chi^2_{(6)} = 10.4$, p=0.11).



1970, Myers and Parker 1975, Parker *et al.* 1976, Parer and Libke 1985), England (Trout and Smith 1995), France (Rogers *et al.* 1994) and Spain (Soriguer and Rogers 1981) attaining different densities in patches of different soil types.

Myers (1970) estimated rabbit density in semi-arid New South Wales over six years on each of three soil types similar to those found in the Mitchell region. A mean density was calculated for each soil type, and then mean densities were indexed relative to the optimal soil type (the soil type on which mean rabbit density was greatest). This resulted in indices of 1, 0.61, 0.31 for optimal, intermediate and poor soils respectively. Soil patches in the Mitchell area were then defined using a 1:500 000 soil map (Gallowway *et al.* 1974), and the appropriate soil index applied to each patch.

No long term rabbit population growth data are available for the Mitchell region, however over 19 years of growth data were available for two study sites in the arid zone of South Australia (B. Cooke, pers. comm; a shorter section of the data is available in Cooke (1974)). These data allowed a long term mean growth factor to be determined by averaging population increases from trough to peak density. The resulting long term mean growth factor of 7.88 (S.E.=1.61) agreed well with the maximum observed annual finite rate of increase of 7.85 calculated for rabbits in Australia by Hone (1999).

Two studies of rabbit dispersal have been conducted over different periods at a study site in southern New South Wales (Daly 1979, Parer 1982). Parer (1982) determined numbers of male and female rabbits which dispersed to non-natal warrens in each of five years which included years of high and very low rainfall (Table 3 in Parer 1982) and calculated survivorship curves for rabbits known to be alive. From these data, and given that rabbits are known to have a 1:1 sex ratio (Myers and Poole 1963), the proportion of females dispersing was calculated as 0.24. Daly (1979) also presented data on dispersal over a two year period. From these data, female dispersal was calculated to be 0.32 and 0.31. From the Parer (1982) and Daly (1979) studies, the long term mean dispersal factor used here was calculated as 0.29 (S.E.=0.03). For comparison, Dunsmore

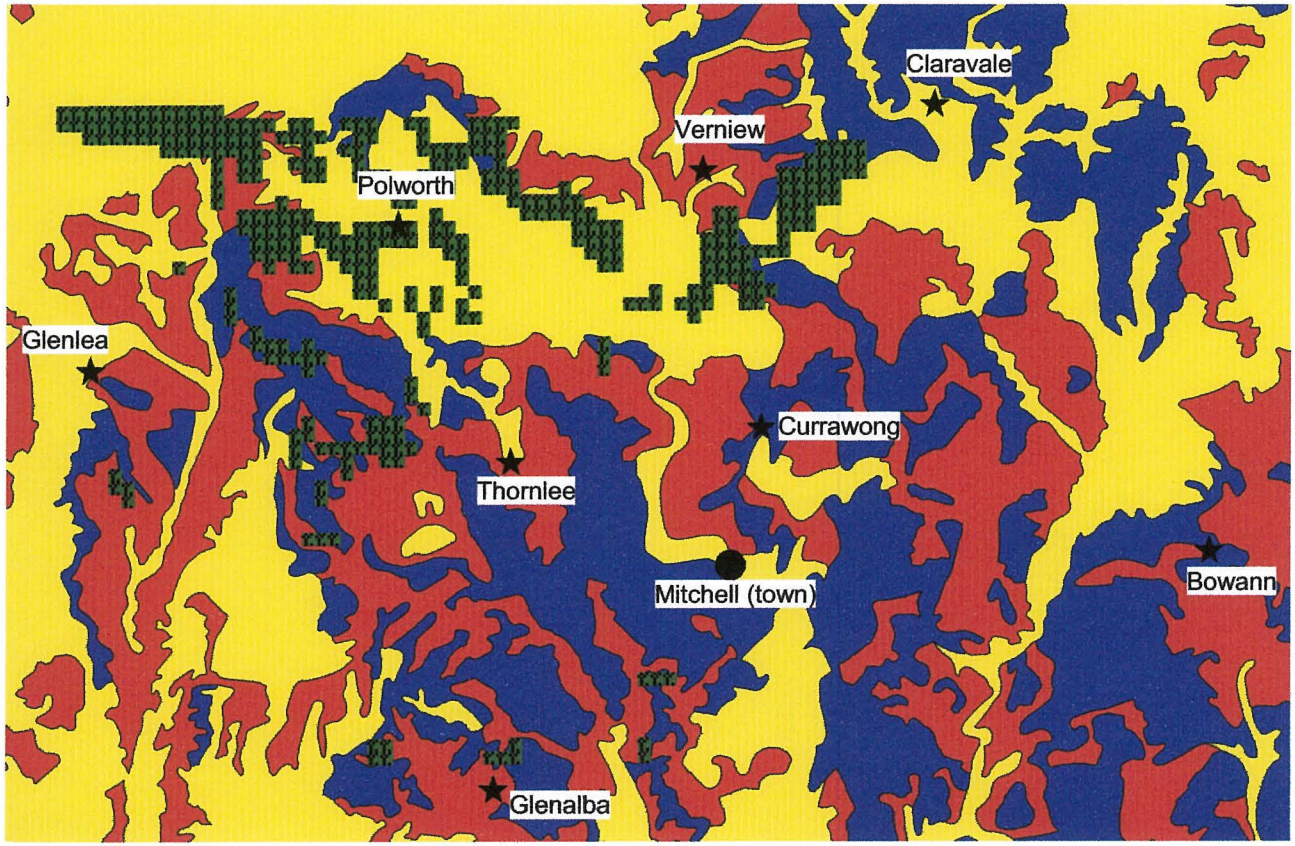
(1974) calculated female dispersal as 0.26, however large differences in the landscape and environment of his study area and the Mitchell region precluded inclusion of this estimate into the calculation of the long term mean dispersal factor.

Dense forests impede rabbit dispersal (Ratcliffe 1959, Stodart and Parer 1988, Myers *et al.*1994) but the nature of this resistance has not been quantified. Available data suggest that the mean maximum distance over which individual rabbits can disperse successfully through vegetation types other than dense forest is 1.5 km (Parer 1982). Rabbits are unlikely to be able to disperse as freely through dense forest, and so this distance serves as a conservative indication of dispersal potential through dense forests. For modelling purposes it was assumed that resistance to dispersal through dense forest follows a logarithmic form, with 100% of a propagule able to disperse successfully through linear distances of less than 1.5 km, 10% of a propagule able to move through linear distances of 1.5 to 3 km, and 1% of a propagule able to disperse greater than 3 km. This dispersal resistance function was employed in the model when a propagule reached a patch of dense forest (a patch in which resources were indexed as 0).

In summary, the following parameters were used as inputs to the model for this system: a long term mean growth factor (G) of 7.88, a long term mean dispersal factor (d) of 0.29, soil resource indices of 1, 0.61 and 0.31 for optimal, intermediate and poor soils respectively, and a resource index of 0 for dense forests with a dispersal resistance function of 1, 0.1 and 0.01 at less than 1.5 km, 1.5 to 3 km and greater than 3 km respectively.

Eight local patch populations (sites) in the landscape were selected to coincide with the populations sampled by Wilson *et al.* (2002). For modelling purposes it was assumed that these populations are fixed in space, were relatively resistant to extinction, and were initially the only populations within the study area. The area between these sites was mapped as a series of patches based on soil and vegetation type (Figure 2.2), and a resource index determined for each patch. A computer program was developed to simulate the movement of propagules

Figure 2.2. The spatial relationship among sites (★), dense forests ■ and optimal □ , intermediate ■, and poor ■ quality soil patches in the Mitchell region.



through patches between all combinations of any two sites (Appendix 1). To assess the effect of spatial heterogeneity on the system, propagules were moved along five predetermined paths between all combinations of site pairs. This was achieved by considering each site as a circle with a radius of 6 km from the centre of the site, with five linear dispersal paths drawn between different points on the circles of the selected site pairs. This method of moving propagules is simplistic and is presented only to demonstrate the utility of the model. A random walk through patches between sites may be appropriate for more extensive simulation studies.

As site connectivity indices are relative, the size of seeding propagules was arbitrary, and the simulation program was seeded with 100 individuals at each of the 8 sites. The total number of successful colonists arriving at each site resulting from travel through patches along each of the five paths from each other site was recorded and relative connectivity indices calculated (Table 2.1). As Table 2.1 shows, there is substantial variation in long term connectivity among sites. The differences in connectivity among sites are fully apparent when viewed spatially as connectivity isoclines. Isoclines were formed by categorising site - pair connectivity (Table 2.1) as high, intermediate or low in relation to the total connectivity within the system, and constructing a polygon to join sites within the same category (Figure 2.3). Bowann, Claravale, Currawong, Glenalba and Thornlee exhibited relatively high levels of connectivity, Glenlea showed a low level of interaction, whilst Polworth and Verniew were effectively isolated from each other and the rest of the system.

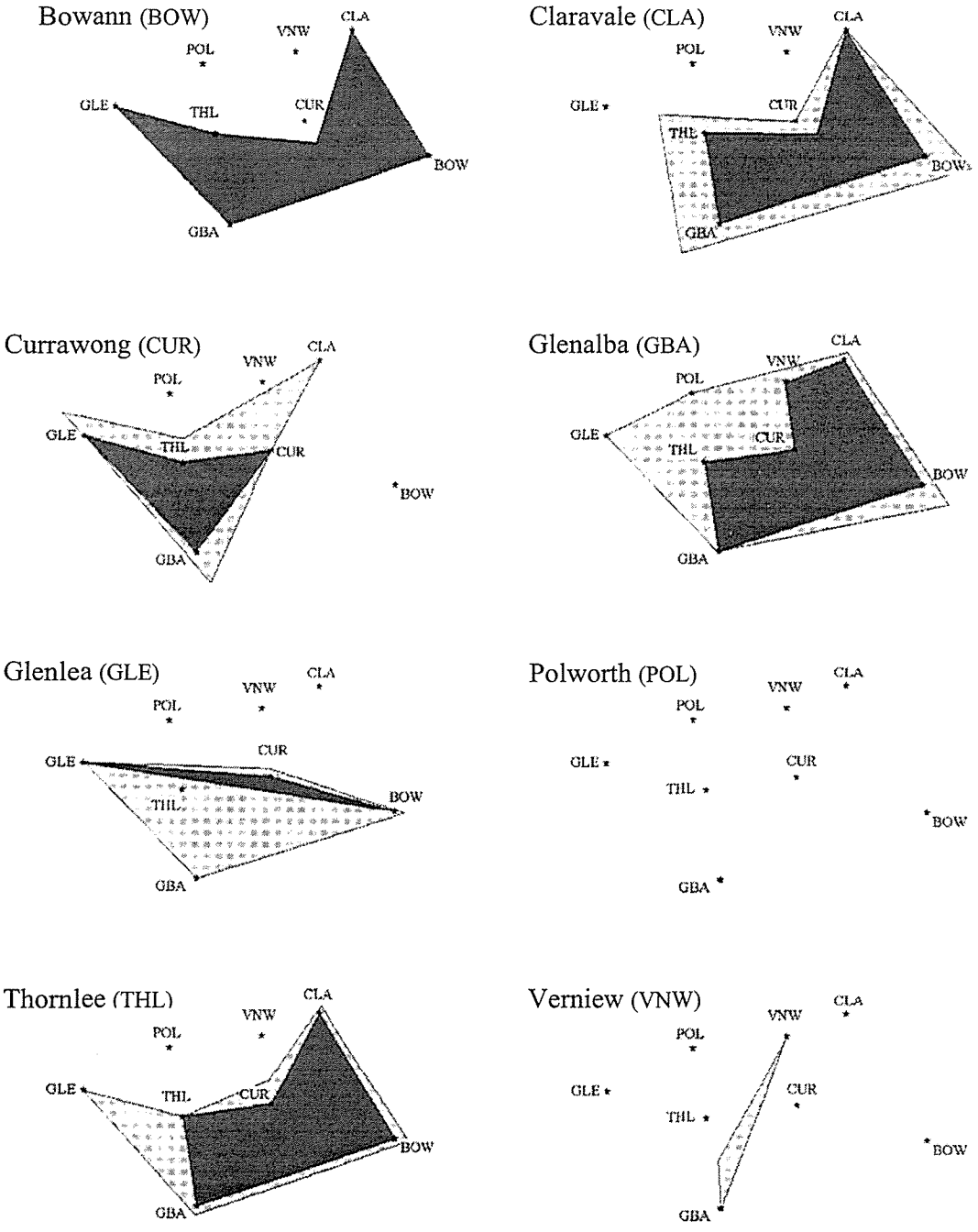
2.4 Model Validation

The mitochondrial haplotype frequency data of Fuller *et al.* (1997) and Wilson *et al.* (2002) were used to provide an independent assessment of the degree of isolation among eight sites based on differences in genetic population structure. Pairwise F_{ST} distances were estimated using Arlequin (Schneider *et al.* 2000) and the mean of pairwise F_{ST} estimates between each site and all other sites was

Table 2.1. Model output matrix: Number of successful colonisers and relative connectivity indices for eight sites within the Mitchell region.

		Contribution from system to site								
		Bowann	Claravale	Currawong	Glenalba	Glenlea	Polworth	Thornlee	Verniew	**System to site index**
	Bowann	0	12955	1402	4087	4446	42	3740	57	0.151
	Claravale	24136	0	3096	10006	960	162	5074	894	0.25
Contribution	Currawong	1069	931	0	4193	9109	8	2706	614	0.105
from site	Glenalba	6676	6073	8278	0	3391	392	3294	2666	0.17
to system	Glenlea	2982	276	9126	1689	0	50	1203	0	0.086
	Polworth	130	133	24	638	139	0	63	0	0.006
	Thornlee	10580	5089	8876	5485	3929	68	0	497	0.195
	Verniew	182	899	2018	2188	0	0	495	0	0.033
Site to system index		0.258	0.149	0.185	0.160	0.124	0.004	0.094	0.027	
Mean relative connectivity index		0.205	0.199	0.145	0.167	0.105	0.005	0.144	0.03	

Figure 2.3. Spatial configuration of site-system interactions for sites within the Mitchell region. Connectivity between sites is ranked as high (>3% of total interactions within the system)■, moderately high (1-3%)□ and low (<1%)□ .



calculated to determine the relative level of differentiation between each site and the remainder of the system (Table 2.2).

Table 2.2. Mean of pairwise F_{ST} estimates for each site and all remaining sites with standard errors of the mean (s.e.m).

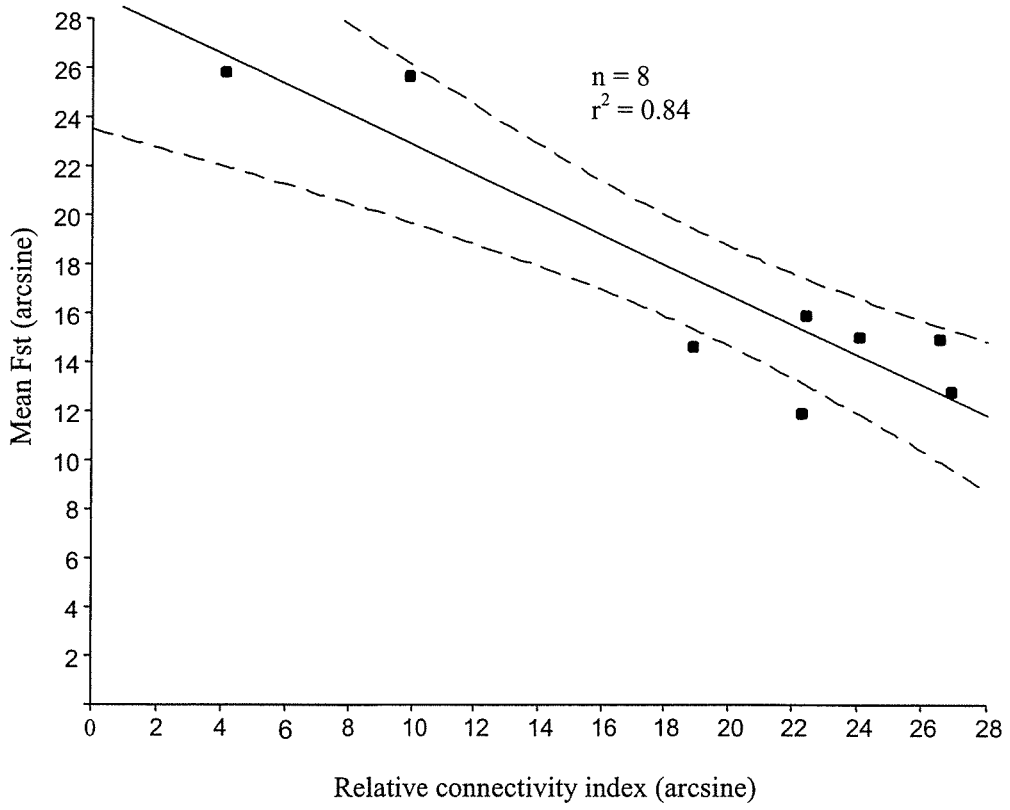
Site	**F_{ST}**	**s.e.m**
Bowann	0.04891	0.024
Claravale	0.06691	0.033
Currawong	0.07507	0.032
Glenalba	0.06755	0.033
Glenlea	0.06394	0.019
Polworth	0.18978	0.045
Thornlee	0.04294	0.024
Verniew	0.18770	0.049

The mean F_{ST} index was regressed with the independently constructed long term relative connectivity index (Figure 2.4). As the indices of both genetic differentiation and connectivity are bounded between 0 and 1, all data were arcsine transformed. A large proportion of the variation in the genetic structure was accounted for by the relative connectivity index derived from the habitat heterogeneity model (r^2=0.84, p= 0.001). The negative relationship between the variables shows that the Fst estimate for a site is higher (the site is more genetically differentiated) for isolated sites than for highly connected sites.

2.5 Sensitivity Analysis

The calculated relative connectivity indices for the Eastern rabbit population system account for a large proportion of the variability in the validation data. This provides strong support for the model, however this support is thus far limited to a single system. It is therefore important to assess the performance of the habitat heterogeneity model under a variety of conditions in order to confirm its robustness.

Figure 2.4. The relationship between population genetic structure (mean of pairwise F_{ST}) and relative connectivity indices, with 95% pointwise confidence intervals (---). F_{ST} and connectivity indices are bounded between 0 and 1, and have been arcsine transformed



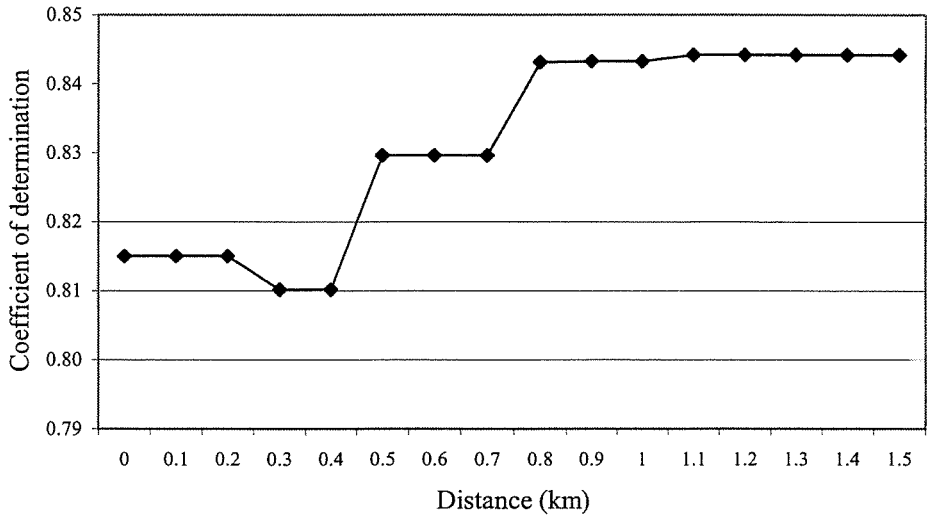
2.5.1 Dense forests

There are two components to the model of long term connectivity in this system (spatial heterogeneity in soil quality and the resistance of dense forest to dispersal by rabbits). To determine the contribution of dispersal resistance through dense forest, resource quality was removed from the model by ignoring spatial variations in soil quality (that is, considering all patches optimal), and combining all adjacent patches except for dense forest. Dispersal resistance through dense forests accounted for a large proportion of the variation in the population genetic data (r^2= 0.71, p= 0.008), but gave a poorer fit than the complete model that included spatial resource heterogeneity (r^2= 0.84, p= 0.001).

Given the large contribution of dispersal resistance through dense forests to the fit of the model to the validation data, further analyses were conducted to determine the effect of changing the distance through dense forests at which the dispersal resistance indices were applied, and changing the form of the dispersal resistance indices. For clarity, the values used for all parameters as described above (section 2.3) will be identified as standard parameter values.

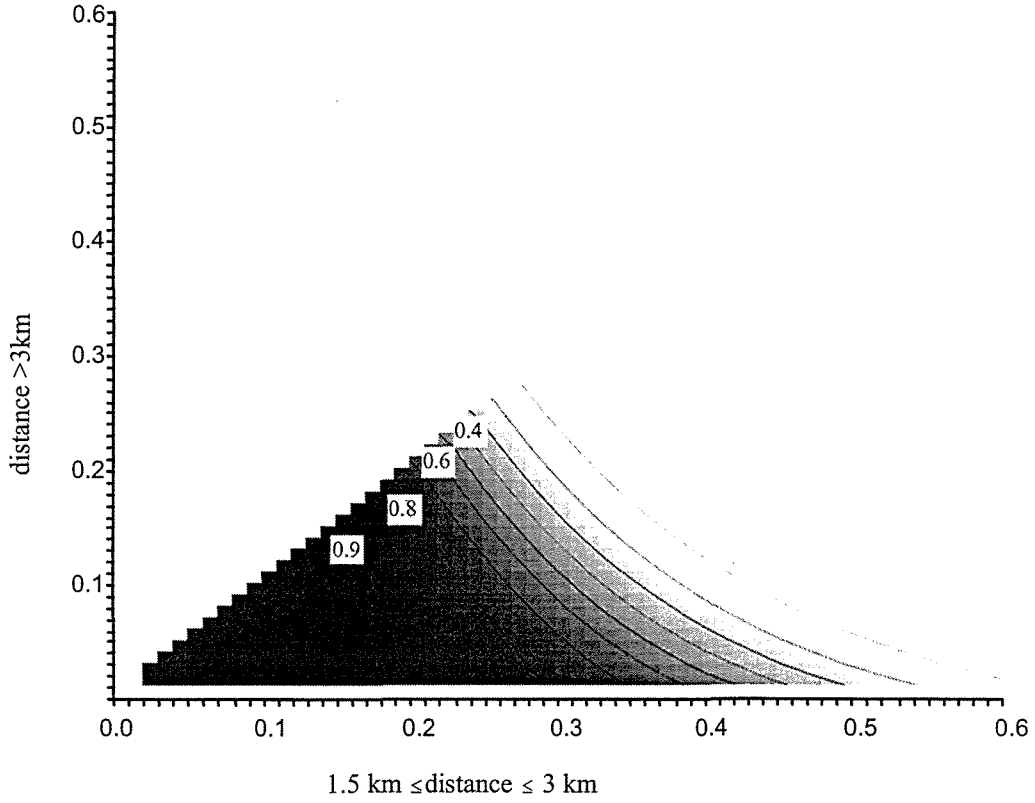
It was assumed above that rabbits can freely disperse through dense forests up to a distance of 1.5km, with reductions in the number of dispersers occurring thereafter. This distance was based on empirical estimates of dispersal through vegetation types other than dense forests, and thus can reasonably be considered conservative. Dense forests may provide a greater impediment to rabbit dispersal, and reductions in the number of dispersers could begin closer to the forest edge than 1.5km. To assess this, the distance at which the dispersal resistance indices were applied was varied (from the edge of a forest patch up to a maximum of 1.5 km). The model was run using all other standard parameter values. The fit of the model output to population genetic data was insensitive to the distance at which dispersal indices were applied (Figure 2.5).

Figure 2.5. Variation in the fit of model output to population genetic data when the distance at which the dispersal resistance function is applied is changed.



The dispersal resistance function determines the number of dispersers that successfully traverse a dense forest patch, and thus has the potential to affect the isolation of particular sites. To assess the effect of the relationship on model performance, the proportion of a dispersing propagule that successfully traversed a dense forest patch was varied. Since the model output is relatively insensitive to the distance at which the indices were applied, the standard parameter values were used for distance at which indices were applied and for all other parameters. The fit of the model is strongly affected by the proportion of disperses which successfully traverse dense forest patches (Figure 2.6).

Figure 2.6. Two dimensional contour graph showing the distribution of coefficients (r^2) obtained from regression of connectivity indices (model output) against population genetic data when the dispersal resistance function is varied. Contour lines indicate regression coefficient isoclines (labelled with regression coefficient values).



Model output is affected by both dispersal resistance indices, but is most strongly affected by the proportion of dispersers that successfully traverse dense forest distances of greater than 3km. This suggests that the difficulty in traversing a dense forest patch increases substantially with the linear distance throught the dense forest patch. This is biologically reasonable, since the rabbit is not a forest dwelling species (Myers *et al.* 1994).

2.5.2 Population parameters

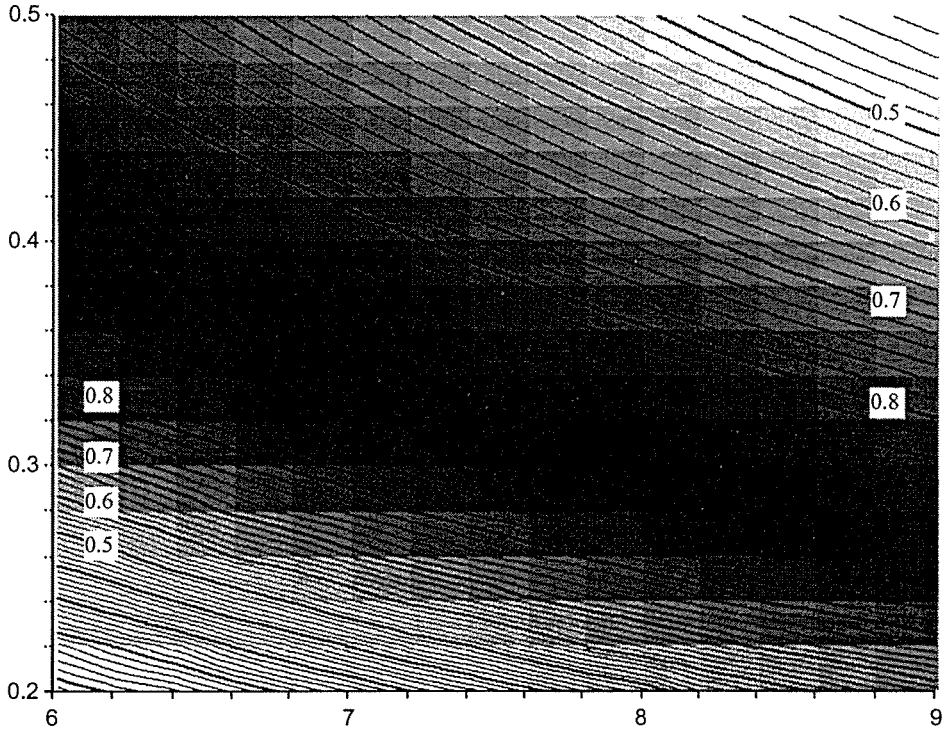
To further test the robustness of the habitat heterogeneity model, simulations were run keeping resource and dispersal resistance indices constant but using a range of growth and dispersal values which are consistent with those found for the wild rabbit in Australia (Hone 1999, Daly 1979, Parer 1982). For each simulation run, connectivity indices were calculated and regressed against the independent population genetic data set (Table 2.2) in the manner described above. The model output explains most of the variation in the population genetic data across a wide range of population parameter combinations (Figure 2.7).

The sensitivity of the model output to intial population size in each patch was also assessed, by varying initial population size at each source patch between 10 and 1000 individuals using all other standard parameter values. Model output was largely insensitive to initial population size. The coefficient of variation decreased smoothly from 0.87 (N_I=10) to 0.83 (N_1=1000).

2.5.3 Dispersal paths

Dispersal paths between sites were chosen to provide an appropriate sample of habitat heterogeneity within the Mitchell region. The output from the model could be influenced by the choice of paths if particular path combinations strongly overrepresented or underrepresented the heterogeneity between site pairs. The model was therefore adapted to allow dispersal between site pairs along a single dispersal path only, with random selection of this path between each site pair. The model was run for 1000 simulations using standard parameter

Figure 2.7. Two dimensional contour graph showing the distribution of coefficients (r^2) obtained from regression of connectivity indices (model output) against population genetic data for a range of dispersal and growth parameter combinations. Contour lines indicate regression coefficient isoclines (labelled with regression coefficient values).

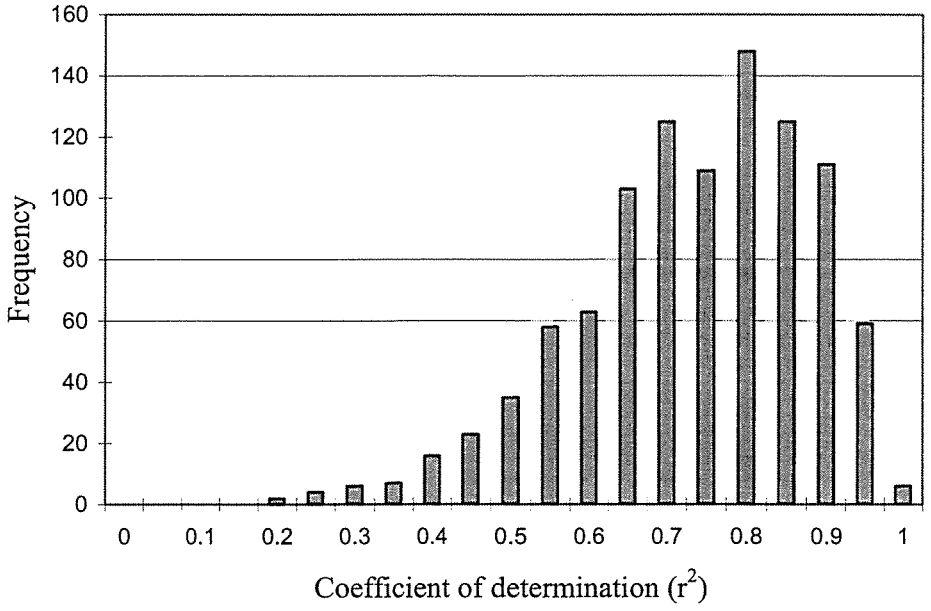


values. For each simulation run, connectivity indices were calculated and regressed against the independent population genetic data set (Table 2.2) in the manner described above. Of the 1000 runs, 942 produced connectivity indices that explained more than 50% of the variability in the population genetic data (Figure 2.8). The mean coefficient of determination across all runs was 0.71.

The model is relatively insensitive to intial starting conditions (initial population size) and other population parameters, dispersal path combinations between sites and the distance at which dispersal resistance indices are applied within dense forest. The model is thus extremely robust to variations in most parameters. However, since the model is designed to test the hypothesis that habitat heterogeneity affects connectivity, connectivity indices should show marked

changes in response to variation in habitat heterogeneity variables such as the dispersal resistance index. Model output is sensitive to the choice of dispersal resistance index chosen between 1.5km and 3km, but particularly to the index chosen for tracts of forest of greater than 3km. This is consistent with a scenario where extensive tracts of forest provide a substantial impediment to rabbit movement, and consequently this analysis supports the logarithmic form of the dispersal resistance function.

Figure 2.8. Distribution of coefficients of determination (r^2) when using a single randomly selected path between each site pair combination over 1000 simulations.



The model explains a large proportion of genetic structure in the Eastern system across a wide range of parameters. This indicates the very strong influence of habitat heterogeneity on the pattern of connectivity among wild rabbit populations within this region. Any effects of other processes which might potentially influence connectivity (such as social behaviour or isolation by distance) are therefore likely to be minor in comparison. This is consistent with the analysis of Wilson et al (2002) who found that the population genetic structuring within this region could not be explained by isolation by distance.

This also confirms that the observed genetic structure of local populations in this system is highly likely to be a consequence of the long term connectivity among sites, which in turn is determined by the combined effect of heterogeneity in the spatial distribution of soil quality and dense forests.

2.6 Discussion

Results of the simulation model show that habitat heterogeneity has the capacity to substantially influence long term mean connectivity levels among local rabbit populations in the study region. The spatial configuration of soil patches of different quality and of dense forests led to a wide range of predicted interaction probabilities among local populations. Bowann, Claravale, Currawong, Glenalba and Thornlee form a group where long term connectivity levels were not only high but similar among sites, with connectivity indices ranging between 0.144 and 0.205. These results are in accordance with the population genetic data of Wilson *et al* (2002) that show this subset of sites to be panmictic.

Predicted long term connectivity indices for Verniew and Polworth were very low in comparison to this group (0.03 and 0.005 respectively), suggesting that habitat heterogeneity has led to the isolation of these populations from the remainder of the system. Population genetic data show the strong divergence of these local populations from other populations within the study region (Table 2.2), confirming their relative isolation.

Most ecological models to date have highlighted the significance of geographical distance or geographical barriers as factors which isolate populations. As shown here, within some systems the possibility also exists that differences in long term connectivity among local populations may be related to the spatial distribution of resources, in addition to landscape elements which inhibit dispersal. It is highly probable that differences in long term connectivity among local populations within the rabbit population system of southern central Queensland are related to the spatially heterogeneous distribution of resources (soils and vegetation) and dense forests.

In this case study the habitat heterogeneity model was validated with population genetic data and accounted for over 80% of the variability in population structure. Furthermore, the model is very robust, accounting for a significant proportion of the variability in population structure over a wide range of parameter values. This

strongly suggests that the habitat heterogeneity model incorporates the major processes which have brought about variations in connectivity among local wild rabbit populations within the Mitchell region, and thus provides a clear indication of the usefulness of the model as a tool for understanding the processes underlying regional dynamics.

Long term connectivity levels can provide an indication of the probability of recolonisation after local population extinctions. The Mitchell region is semi-arid, and so the probability extinction of local rabbit populations is likely to be considerable. Alternatively, extinctions may occur in response to control strategies. When an extinction occurs at a highly connected site, it is likely to be rapidly recolonised by interactions with extant local populations at other highly connected sites. Conversely, the probability of recolonisation at isolated sites (such as Polworth or Verniew) after a local population extinction is likely to be much lower.

It is also possible to use a habitat heterogeneity model to assess interaction probabilities of a single extant population and several vacant sites in the region. This situation may mimic the range expansion of a species into a new area or the reintroduction of a species into a region after a broad scale (regional) extinction (eg due to bushfire, drought or anthropogenic influences). Such modelling would allow for the evaluation of the probability of colonisation of particular sites from an extant population (whose genetic composition is known) under a scenario of range expansion.

Extending the habitat heterogeneity model in this way provides an avenue for exploring the possibility that two adjacent rabbit population systems in Queensland were formed and persist as a result of habitat heterogeneity. The Western rabbit population system is genetically panmictic and covers a vast area of Western Queensland (Fuller *et al.*1996). This system is contiguous with the highly structured Eastern rabbit population system (Wilson *et al.* 2002), however differences in population genetic structure between the two systems cannot be explained by geographical distance or topographical barriers (Wilson *et al.* 2002).

The population genetic characteristics of the Glenlea site place this local population within the Western system, while all other sites included in the case study form part of the Eastern system (Wilson *et al.* 2002). The predicted connectivity index for Glenlea (0.105) showed that the overall interaction of this site with the Eastern system was low. While it is likely that strong isolation of a site due to habitat heterogeneity will bring about local population genetic differences within a population system (such as at Polworth and Verniew), less severe isolating mechanisms might also influence the population genetic characteristics of a system when a species expands its range. Since the range of the wild rabbit in Queensland expanded from west to east (Stodart and Parer 1988) it is reasonable to consider a site such as Glenlea, which is in the west and immediately adjacent to the Eastern system, as a possible colonising source for this system. The genetic characteristics of a system which would result from the colonisation of the Mitchell region from Glenlea given the spatial distribution of soil quality and dense forests is considered in the next chapter.

Chapter 3. Range Expansion of the Wild Rabbit into the Mitchell Region

3.1 Introduction

The wild rabbit is a relatively recent arrival to Australia, and its introduction and subsequent rapid spread have been well documented (Stodart and Parer 1988). While it seems highly probable that long term connectivity levels among rabbit populations within the Eastern system are related to the quality and spatial distribution of soils and of dense forests, it is important to note that the current population genetic structure within any population system can be related to both historical and contemporary processes (Slatkin 1985). This may be viewed as an interaction between the original genetic structure of populations when they were newly colonised and subsequent gene flow among populations within the system after colonisation. Given the recent range expansion by rabbits on the Australian continent, both colonisation and subsequent interactions among populations may well be relevant for interpreting processes which gave rise to the observed population structure within the Eastern system.

If a range expansion progresses as a wave of advance, with a closed front and short dispersal distances (eg Fisher 1937, Skellam 1951, van den Bosch *et al.* 1988), new colonies would be expected to show little divergence from more established populations. However spatial limitations in connectivity can lead to population structuring during a range expansion (eg Ibrahim *et al.* 1996, Le Corre and Kremer 1998). If the spatial distribution of resource quality does act in the long term to lead to variations in connectivity among populations (and thus variations in gene flow) as was seen in Chapter 2, it may also influence colonisation dynamics of a species expanding its range. Using the model of habitat heterogeneity to simulate a range expansion of a species into a region allows predictions to be made regarding the state of the system both after colonisation, and after subsequent interactions among newly established local populations. Comparing these predictions with independent genetic data allows for further verification of the assumptions underlying the habitat heterogeneity model.

It is well known that the wild rabbit spread through the south western corner of Queensland and continued east into and beyond the Mitchell region (Stodart and

Parer 1988). This is of particular interest, given the substantial population genetic differences between the Western (panmictic) system and the Eastern (highly structured) system (Wilson *et al.* 2002). Colonisation of the Eastern system is hypothesised to have occurred during a wave of expansion of rabbits from the west to the east, followed by successive waves of interaction among the sites within the system during expansionary phases related to sporadic favourable environmental conditions. Under this scenario, it is possible to extend the model of habitat heterogeneity presented in the previous chapter to simulate a range expansion of the wild rabbit into the Eastern system, with subsequent population interactions, using mtDNA data.

The specific aims of these simulations were to:

1. use the habitat heterogeneity model to simulate a range expansion into the Mitchell region from a putative colonising Western system local population (Glenlea); and

2. simulate the influence of long term interactions within the Eastern system following a range expansion.

3.2 Model Extension

The underlying structure of the simulation model of habitat heterogeneity was maintained as a series of growth and dispersal events across a landscape (Appendix 2), and model parameters were identical to those used in the previous chapter. During the colonisation phase in these simulations the Eastern region was considered vacant and Glenlea was chosen as a point of entry into the Eastern region. This site sits on a very large soil patch which abuts the Mitchell region from the north to the south. Using Glenlea as an entry point to the Mitchell region thus conforms to the known pattern of spread of rabbits from west to east. The genetic constitution of the populations at the time of range expansion are unknown, however the western population system is panmictic and therefore the pooled frequencies of all known western sites (Fuller *et al.* 1996, Wilson *et al.* 2002) were used to determine the putative genetic constitution of the population at Glenlea (haplotype A=0.64,

haplotype B=0.13, haplotype C=0.23). At the start of each simulation run, the population size at Glenlea was set to 100 and the number of individuals carrying each of the three haplotypes (A, B and C) was determined by the frequency of that haplotype.

Stochasticity is an intrinsic element of natural processes and so randomness was incorporated into the model both at the landscape level, by the choice of dispersal path between sites, and at the population level, via (1) the assignment of haplotypes to individuals during the population growth phase and (2) the selection of the genetic composition of individuals in dispersing propagules.

The simulations consisted of two discrete phases. The colonisation phase simulated movement through resource patches from Glenlea to each of the Eastern sites which were initially vacant. This occurred via one of the five dispersal paths between sites described in the preceding chapter. This simulation of the colonisation phase resulted in the establishment of populations with known haplotype frequencies in each of the Eastern sites. In the second (interaction) phase of the simulation, dispersing propagules were selected from populations at each of the colonised sites and moved through resource patches between each site pair in the Eastern system. In all patch to patch processes (that is population growth followed by the generation of a dispersal propagule), the genetic composition of individuals was chosen at random based on haplotype frequencies. One thousand simulations were performed, each of which comprised of a single colonisation phase followed by a single interaction phase. After each of these phases the population at each site was scaled to 100 individuals while maintaining the haplotype frequencies present at the site.

3.3 Results

3.3.1 Colonisation Phase

Some Eastern system sites were more isolated from Glenlea than others due to the spatial configuration of soil patches and forests within the region. Most sites had a high probability of colonisation during this phase (Table 3.1), although Claravale and Verniew were unlikely to be colonised from Glenlea. However, even at sites that

showed a high probability of colonisation, there was large variation in proportional immigration success. Verniew accepted an insignificant (0.1%) number of immigrants with Polworth accepting only a very small proportion (<1%). All other sites accepted a small to moderate proportion of immigrants (5% - 20%) with the exception of Currawong which accounted for over 40% of the total immigrants accepted into the eastern system. Proportional immigration success from Glenlea into the Eastern system indicates the isolation of many sites in the Eastern system from the Western system, with the most probable entry path being Glenlea to Currawong.

3.3.2 Geographical Distribution of Haplotypes After Colonisation

Allele distribution was strongly influenced by the distribution of soils and dense forests in the region. This was due to sampling effects along dispersal paths that resulted in small population sizes related to soil type or filtering effects due to dispersal through dense forests. Both of these 'bottleneck' effects acted to increase the probability of genetic differences between Glenlea and each of the Eastern system sites, due to variations in allele frequencies or exclusion of one or more alleles.

In over half of the colonisation events between Glenlea and the Eastern system sites at least one haplotype was excluded (Table 3.2). When bottlenecks occur, low frequency alleles are most likely to be lost due to sampling errors (Nei *et al.* 1975). This was indeed the case, with the B haplotype showing the highest probability (0.42) of exclusion (Table 3.2). Polworth was again notable since despite a very high probability of colonisation of this site (Table 3.1), the probabilities of exclusion of both the B and C haplotypes were far higher than for any other site (Table 3.2). Thus it is most likely that Polworth would be colonised exclusively by A haplotype individuals.

As well as the potential loss of alleles, variations in allele frequencies during the colonisation phase may have been sufficient to lead to differentiation of each of the newly founded Eastern system populations from Glenlea. To assess this possibility a

Table 3.1. The success of colonisation from Glenlea with site specific propagule characteristics and proportion of the total immigration pool accepted into a site over 1000 simulations.

Site	Successful colonisation events	Successes per path	Propagule size	Proportional immigration success
Bowann	793	195	701	
		191	754	
		209	830	
		198	1240	0.18
Claravale	410	193	78	
		217	780	0.05
Currawong	1000	199	131	
		194	371	
		206	2345	
		202	2354	
		199	3202	0.43
Glenalba	1000	194	206	
		195	254	
		213	586	
		217	903	
		181	1028	0.15
Polworth	1000	227	7	
		197	15	
		202	31	
		187	86	
		187	102	0.01
Thornlee	1000	203	7	
		209	204	
		220	464	
		192	898	
		176	2056	0.17
Verniew	223	223	39	0.002

goodness of fit test was used with the Glenlea frequencies of haplotypes A, B and C (scaled to a population of 100) as the extrinsic hypothesis. Regardless of site, an extremely high proportion of runs to recipient sites resulted in populations with haplotype frequencies different to Glenlea (mean = 90.8%) (Table 3.3).

Table 3.2. The number of exclusions of each haplotype (A, B or C) from propagules during colonisation of each site over 1000 simulation runs.

Site	**Successful runs**	**A absent**	**B absent**	**C absent**
Bowann	793	4	347	203
Claravale	410	1	196	110
Currawong	1000	8	265	140
Glenalba	1000	1	266	128
Polworth	1000	108	644	508
Thornlee	1000	68	320	204
Verniew	223	17	158	114
Total	5426	207	2196	1407

Newly founded Eastern system populations were therefore very unlikely to show similar allele frequencies to Glenlea (Table 3.3), even when those sites showed a high probability of colonisation and accepted a significant proportion of the immigrating pool (Table 3.1).

To assess the likelihood of population genetic similarities among newly founded populations within the Eastern system, a contingency table was constructed for each run of the model to determine if sites which were colonised during that run within the Eastern system were homogenous. If colonisation did not occur at a site on a particular run, that site was excluded from the analysis for that run. No simulation runs resulted in an homogenous Eastern population system (Table 3.4).

Table 3.3. The percentage of successful colonisation runs in which a newly founded population showed genetic differences to the Glenlea population.

Site	Successful runs	Percentage of runs [1]
Bowann	793	92.8 (736)
Claravale	410	95.1 (390)
Currawong	1000	84.1 (841)
Glenalba	1000	84.5 (845)
Polworth	1000	95.4 (954)
Thornlee	1000	85.1 (851)
Verniew	223	98.7 (220)

(1) Number of runs in parentheses

The results of the colonisation modelling show that colonisation of the Eastern system from Glenlea was most likely to result in a system where the A and C haplotypes had a high probability of being included in the founder populations at most sites, although the C haplotype showed a lower probability of inclusion at Polworth. Individuals carrying the B haplotype were the most likely to be omitted from founder populations. Furthermore, population genetic differences were likely between Glenlea and each of the newly established Eastern system populations, and among these populations. These results are consistent with the genetic data of Wilson *et al.*(2002).

Table 3.4. The number of colonisation runs in which a genetically heterogenous Eastern system was formed [1].

Simulation runs	*p* values
0	$p \geq 0.05$
1	$0.05 > p \geq 0.01$
1	$0.01 > p \geq 0.001$
812	$0.001 > p$

(1) 186 model runs were excluded due to low expected values

3.4 Interaction Phase

Within the Eastern system all sites showed a high probability of interaction (Table 3.5). Thus Verniew and Claravale, which were unlikely to be colonised from Glenlea (a western system population), were more likely to be colonised from other sites within the Eastern system. Although all sites showed a high probability of interaction, the proportion of total immigrants accepted varied widely among sites during this phase. Bowann, Glenalba, Thornlee and Claravale form a group which accepted a moderate to large proportion of the total pool of immigrants (Table 3.5). Currawong accepted relatively few immigrants over all simulation runs while Verniew and Polworth showed low and very low levels of interaction within the system, respectively. This suggests that these latter 2 sites are relatively isolated from all other Eastern system sites.

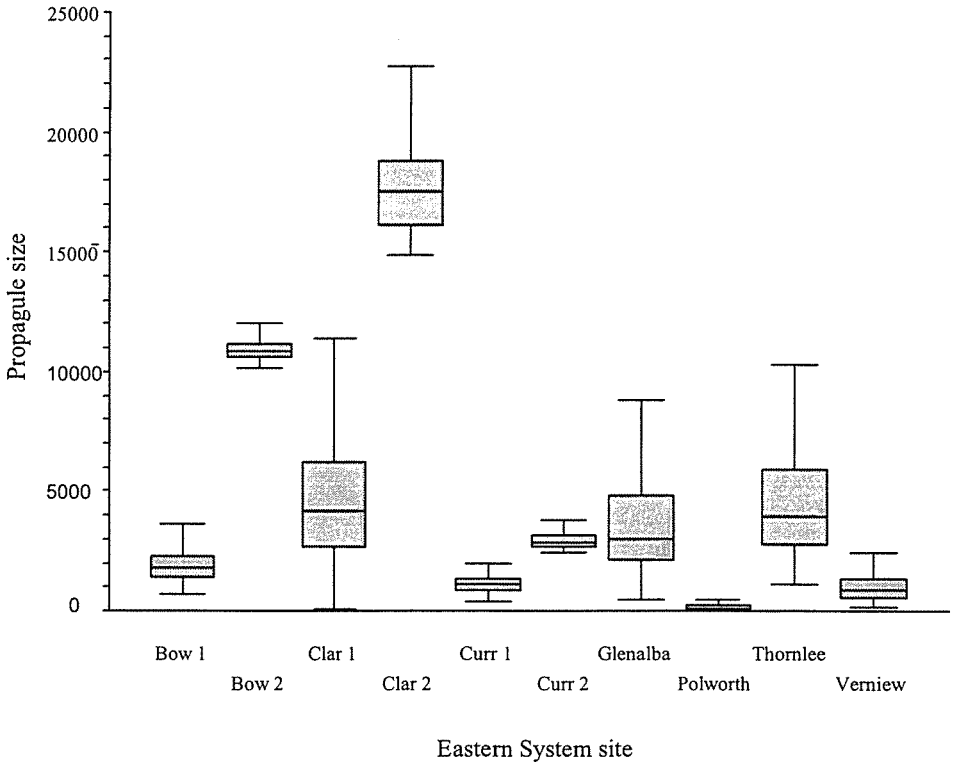
Table 3.5. Site specific characteristics of propagules proportion of the total immigration pool accepted at each site during the interaction phase within the Eastern system over 1000 simulation runs.

Site	**Number of successes**	**Median propagule size**	**Proportional immigration success**
Bowann	1000	1780	
		10864	0.13
Claravale	1000	4798	0.33
Currawong	1000	1076	
		2843.5	0.08
Glenalba	1000	2989.5	0.18
Polworth	984	109	0.01
Thornlee	1000	3914	0.23
Verniew	1000	898	0.05

The relative isolation of each of the Eastern system sites was further assessed by examining the range of propagule sizes accepted into the site (Figure 3.1). Most sites accepted a large range of propagule sizes, indicating relative isolation from some

sites and high connectivity with others. Even Currawong, which accepted a low proportion of the total immigrating pool, displayed a bimodal distribution in propagule sizes suggesting that this site showed moderate connectivity with at least one other site. Verniew showed less variation about a low median propagule size, indicating that this site showed low connectivity with other Eastern system sites. Polworth was again notable since it accepted propagules that were consistently very small (Figure 3.1).

Figure 3.1. Distribution of propagule sizes (medians and quartiles) accepted at Eastern system sites during the interaction phase. Note that where the distributions of propagule sizes were bimodal (Bowann, Claravale and Currawong), the distributions were split and box plots created for each component distribution (Bow1, Bow2; Cla1, Cla2; Cur1, Cur2).



3.4.1 Geographical Distribution of Haplotypes After Interaction

The A haplotype was excluded infrequently from propagules during the interaction phase and was only absent from sites which showed low to very low connectivity

with other sites within the Eastern system (Verniew and Polworth) (Table 3.6). Even at Verniew however, the A haplotype was only absent during a single simulation run and at Polworth was absent in less than 3% of the runs. In the long term therefore, the A haplotype was highly likely to be included in propagules arriving at all sites. Both the B and C haplotypes were excluded much more frequently than the A haplotype at all sites. However, at every site except Polworth the B haplotype was excluded more than twice as often as the C haplotype. At Polworth, there is a significant probability that both the B and C haplotypes would be absent from propagules that reach this site.

Table 3.6. The number of times each haplotype (A, B and C) was absent from a propagule during the interaction phase.

Site	**Successful runs**	**A absent**	**B absent**	**C absent**
Bowann	1000	0	169	60
Claravale	1000	0	220	75
Currawong	1000	0	192	72
Glenalba	1000	0	182	52
Polworth	984	27	455	275
Thornlee	1000	0	156	35
Verniew	1000	1	297	108
Total	6984	28	1671	677

Since the model is stochastic alleles, are unlikely to be completely excluded from all propagules which reached a site during all simulation runs. However, trends in the distribution of relative frequencies of alleles arriving at each site are indicative of the relative isolation of a site from the remainder of the system. The frequency histogram trends were very similar, both among haplotype distributions within each site and among sites (Figure 3.2). This similarity of pattern was particularly evident in the skew of the distributions. Skew is a useful measure for assessing the asymmetry of a distribution, and is generally considered significant if the ratio of the

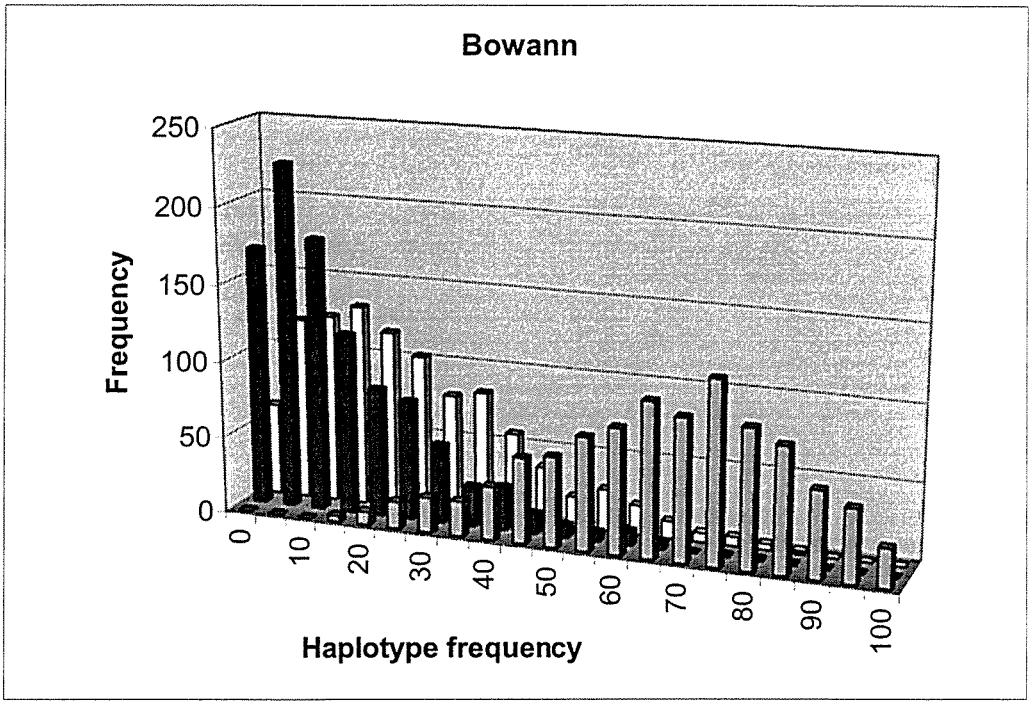
skewness statistic to the standard error of skewness (s.e.s) is ±2 (Tabachnik and Fidell 1996).

All haplotype frequency distributions were asymmetric (Table 3.7). The distributions of A haplotypes at all sites were significantly negatively skewed, showing a tendency towards high positive values. There is thus a significant tendency for propagules to contain a high proportion of A haplotype individuals. Both the B and C haplotypes were significantly positively skewed at all Eastern system sites (Table 3.7), indicating a trend towards low values. The absolute value of the skewness ratio of the C haplotype distributions at all sites was much greater than that of the A haplotype distributions. Most notable, however, was the very strong positive skew of the B haplotype distributions. Thus most propagules contained a very low proportion of B haplotype individuals. This was most evident at Verniew and Polworth, where the skewness ratios were the largest of any sites. The haplotype distributions at these sites were characterised by the very large number of propagules deficient in the B haplotype (Figures 3.2e and 3.2g). In the long term there is therefore a tendency for propagules originating within the Eastern system and arriving at other Eastern sites to carry a higher than expected proportion of A haplotype individuals, and relatively low proportions of C haplotype individuals. There was also a very strong trend towards propagules with a very low to zero proportion of B haplotype individuals.

Interacting propagules also tended to show characteristics that differed from the Glenlea population (Table 3.8). While the medians of the A haplotype distributions approximated the proportion of A haplotypes in the Glenlea population, (haplotype A=0.64, haplotype B=0.13, haplotype C=0.23) the medians of both B and C haplotypes were smaller. This was particularly evident at Polworth where the median of the B haplotype was substantially smaller than the proportion of B haplotypes at Glenlea. In fact, the proportion of the B haplotype at Glenlea more closely approximated the third quartile values rather than the median at all sites, indicating very large losses of the B haplotype within the system.

Figure 3.2. Histograms of frequencies of A▒, B■ and C□ haplotypes in propagules arriving at Eastern system sites during the interaction phase over 1000 simulation runs.

(a)



(b)

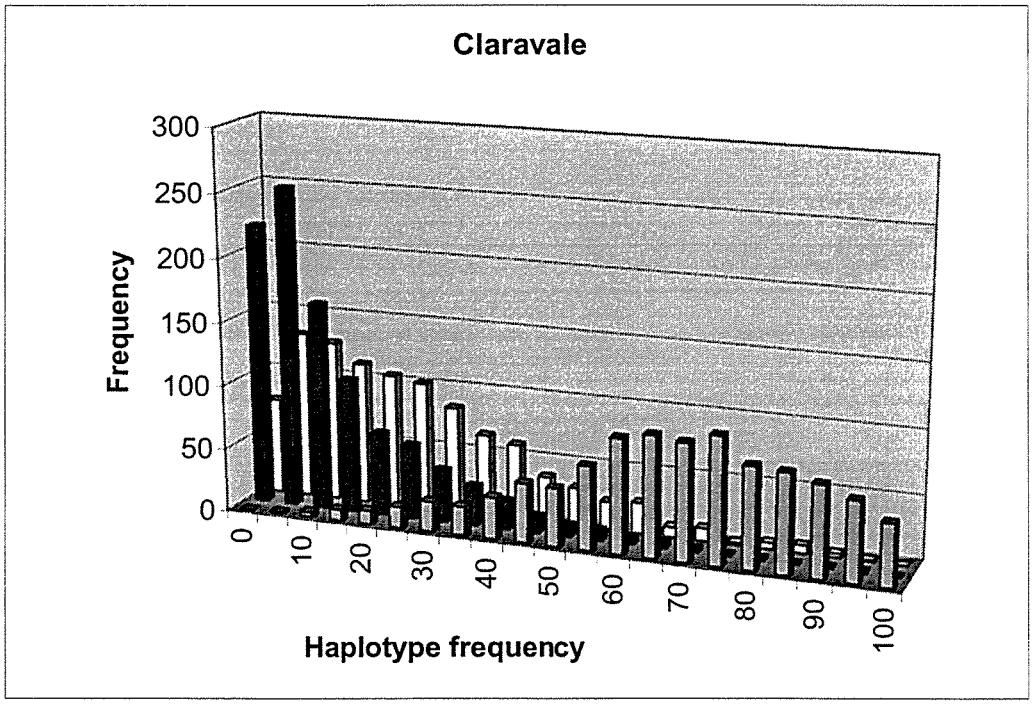
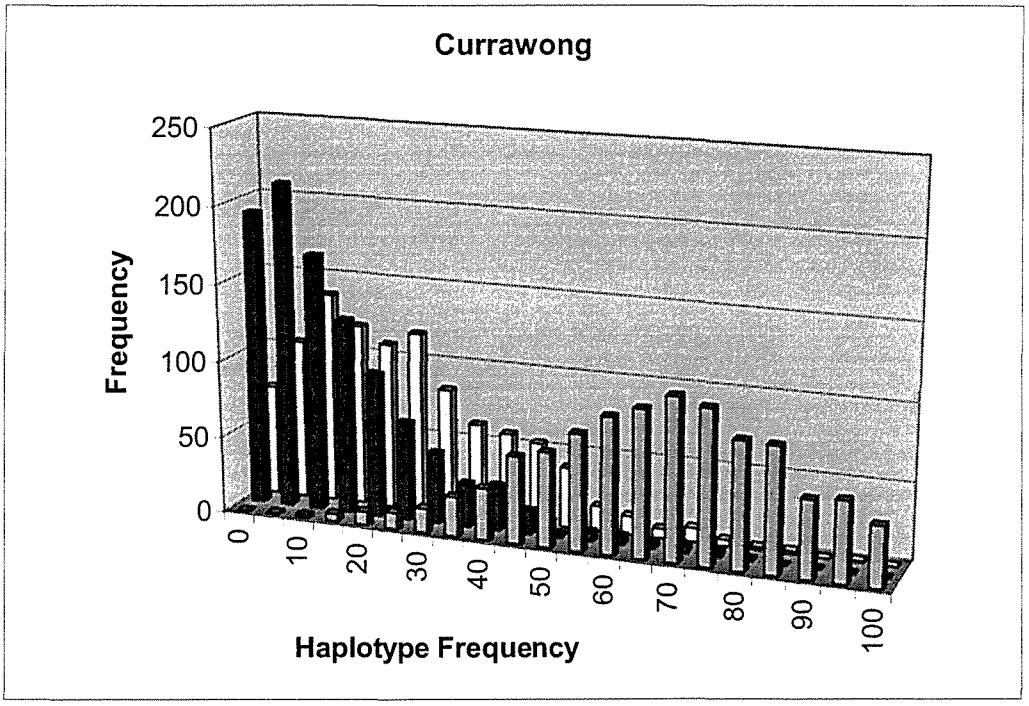


Figure 3.2 (c)


Currawong
Frequency
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype Frequency

(d)

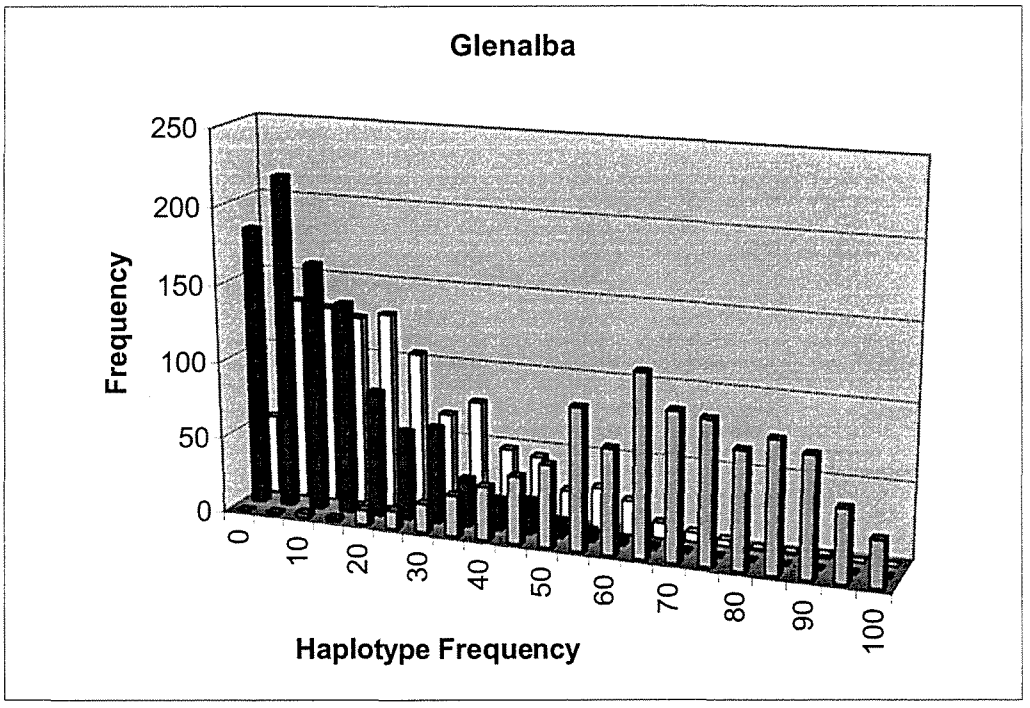
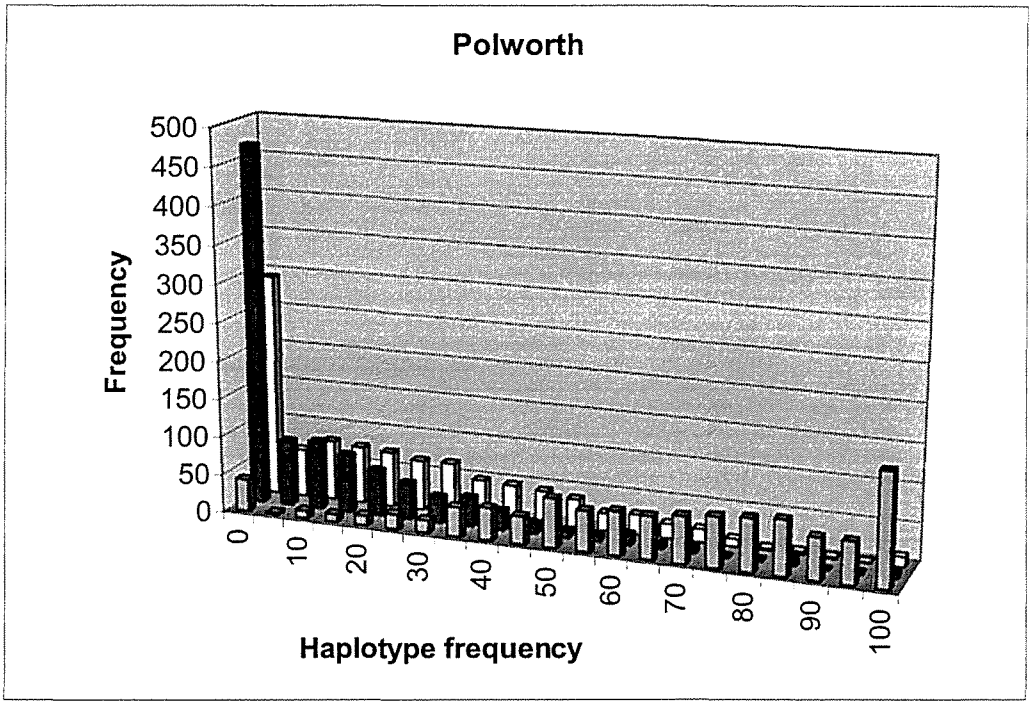

Glenalba
Frequency
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype Frequency

Figure 3.2 (e)


Polworth
Frequency
500
450
400
350
300
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype frequency

(f)

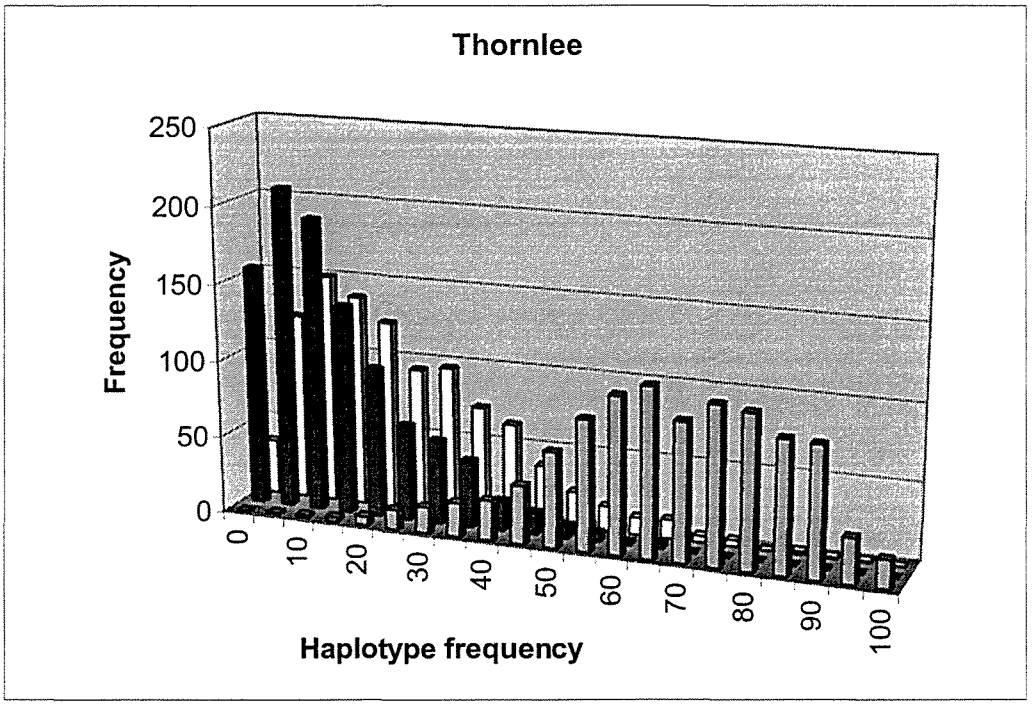

Thornlee
Frequency
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype frequency

Figure 3.2 (g)

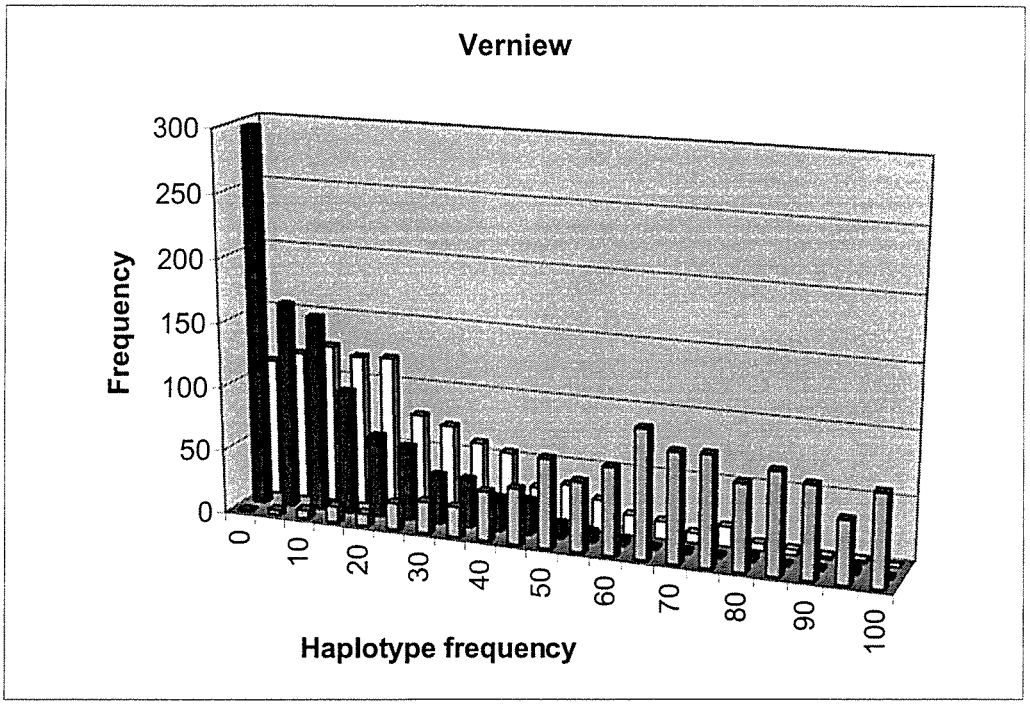


Table 3.7. Skewness ratios (skewness: standard error of skewness) for each of the distributions of frequencies of A, B and C haplotypes arriving at Eastern system sites during the interaction phase.

	Haplotype		
	A	**B**	**C**
Bowann	-5.35	20.62	11.88
Claravale	-6.34	24.30	13.56
Currawong	-4.83	22.42	11.50
Glenalba	-5.52	17.51	12.36
Polworth	-7.67	28.39	14.64
Thornlee	-6.32	16.60	12.89
Verniew	-6.16	25.04	14.32

Table 3.8. Medians, quartiles and ranges for the distributions of haplotype frequencies arriving at Eastern system sites during the interaction phase.

Site	Haplotype	Median	Quartile 1	Quartile 3	Range
Bowann	A	66	52.75	78	87
	B	8	2	19	82
	C	18	8	32	82
Claravale	A	67	53	82	96
	B	7	1	16	91
	C	18	7	32	95
Currawong	A	66	52	79	98
	B	8	2	18	78
	C	19	8	31	91
Glenalba	A	66	53	80	96
	B	8	2	18	70
	C	18	8	31	90
Polworth	A	69	48	87	100
	B	3	0	18	100
	C	16	0	35	100
Thornlee	A	66	54	79	98
	B	9	2	18	64
	C	18	9	30	91
Verniew	A	66	50	82	100
	B	7	0	19	100
	C	17	7	32	95

3.4.1.1. Variation in Dense Forest Patch Sizes

Dense forests are an important component of habitat heterogeneity in the Eastern rabbit population system (Chapter 2). It is likely that the distribution of dense forests has had important effects on the distribution of alleles within this system. The simulations above were conducted under the assumption that the distribution of dense forests in the Mitchell region have been relatively stable since the range expansion of the wild rabbit from the west (Stoddart and Parer 1988). Although it is difficult to assess the exact extent of any clearing of dense forest in this region, it is

possible that dense forest patches were larger at the time of range expansion. To account for this possibility, linear dispersal distances through dense forests were increased by 50%. All other parameter values were held constant and 1000 simulations were run to determine the distribution of alleles after interaction. Frequency distributions for A, B and C haplotypes (Figure 3.3) were very similar to those of the previous simulations (Figure 3.2). All sites again tended to receive propagules with a low proportion of C haplotype individuals and a very low proportion of B haplotype individuals. As in previous simulations, the haplotype frequency distributions at Polworth (Figure 3.3e) and Verniew (Figure 3.3e) were characterised by the very large number of propagules deficient in the B haplotype.

Figure 3.3. Histograms of frequencies of A■, B■ and C□ haplotypes in propagules arriving at Eastern system sites during the interaction phase when dispersal distances through dense forests were increased by 50% (1000 simulation runs).

(a)

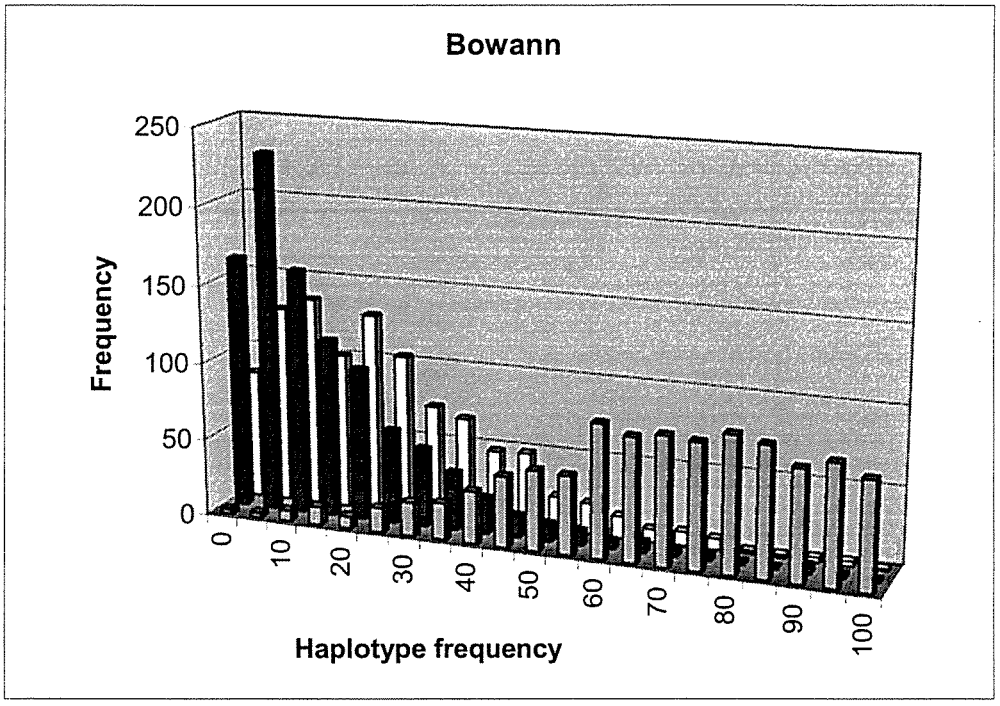
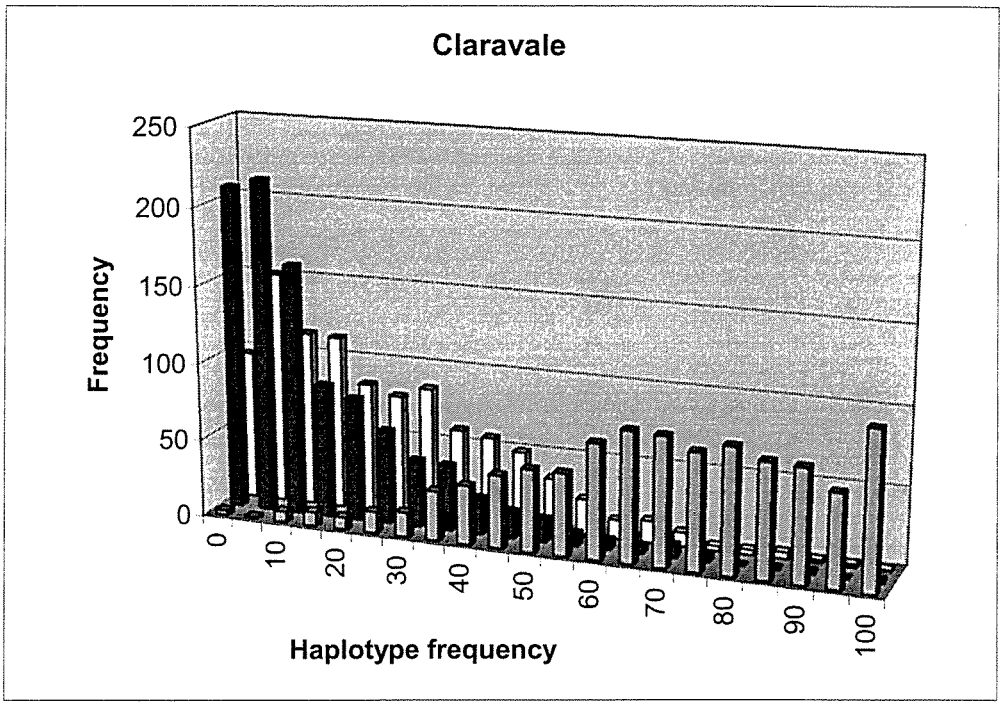


Figure 3.3 (b)


Claravale
Frequency
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype frequency

(c)

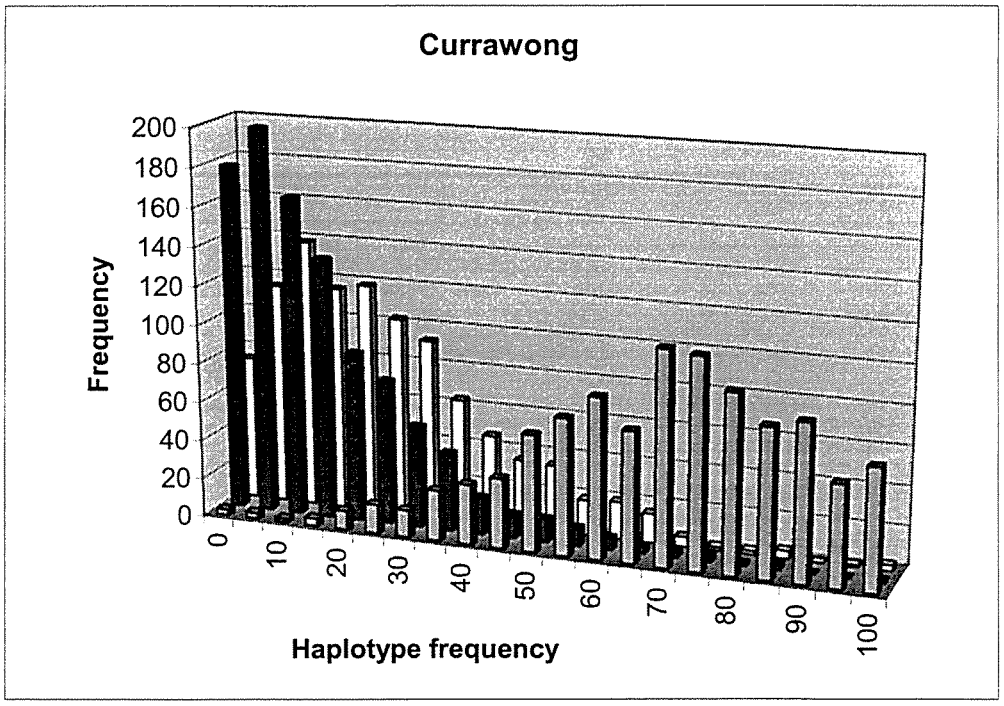
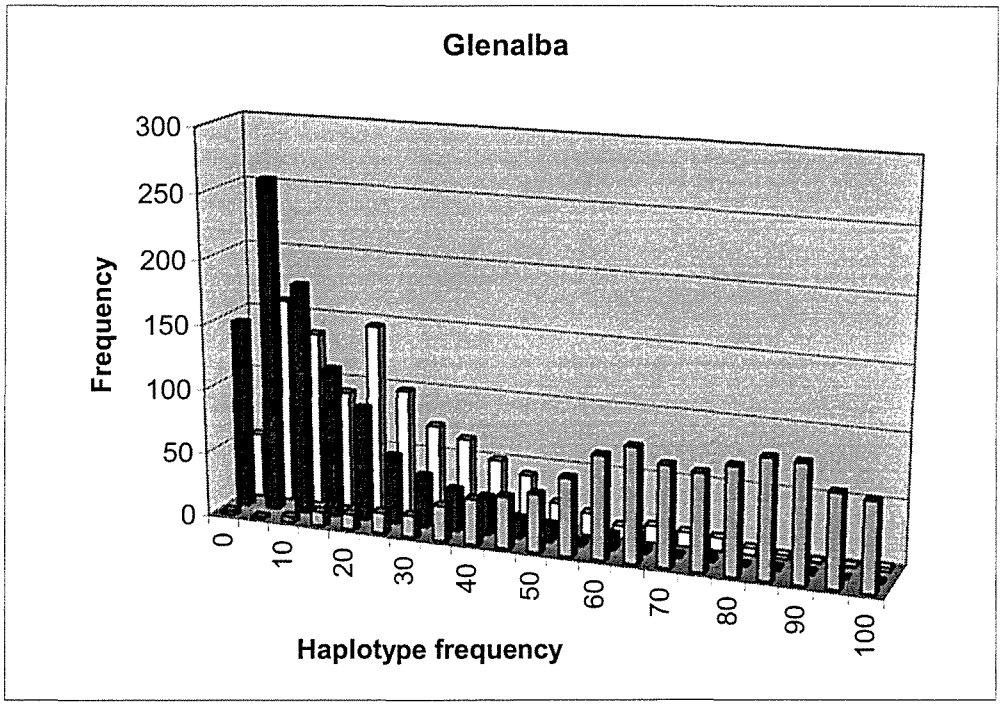

Currawong
Frequency
200
180
160
140
120
100
80
60
40
20
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype frequency

Figure 3.3 (d)


Glenalba
Frequency
300
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype frequency

(e)

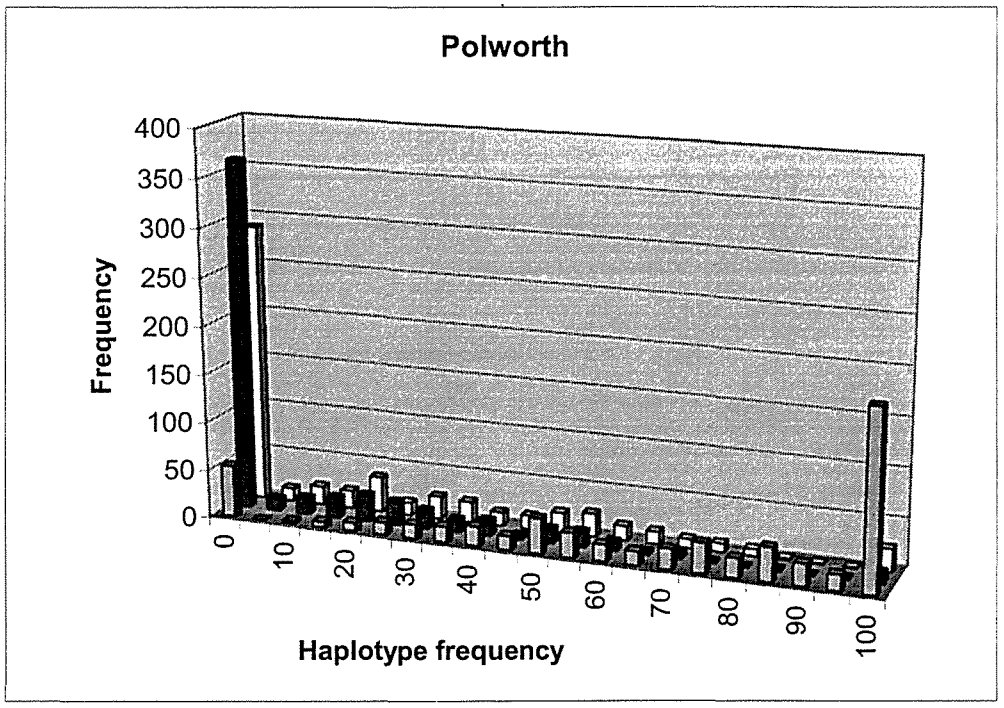
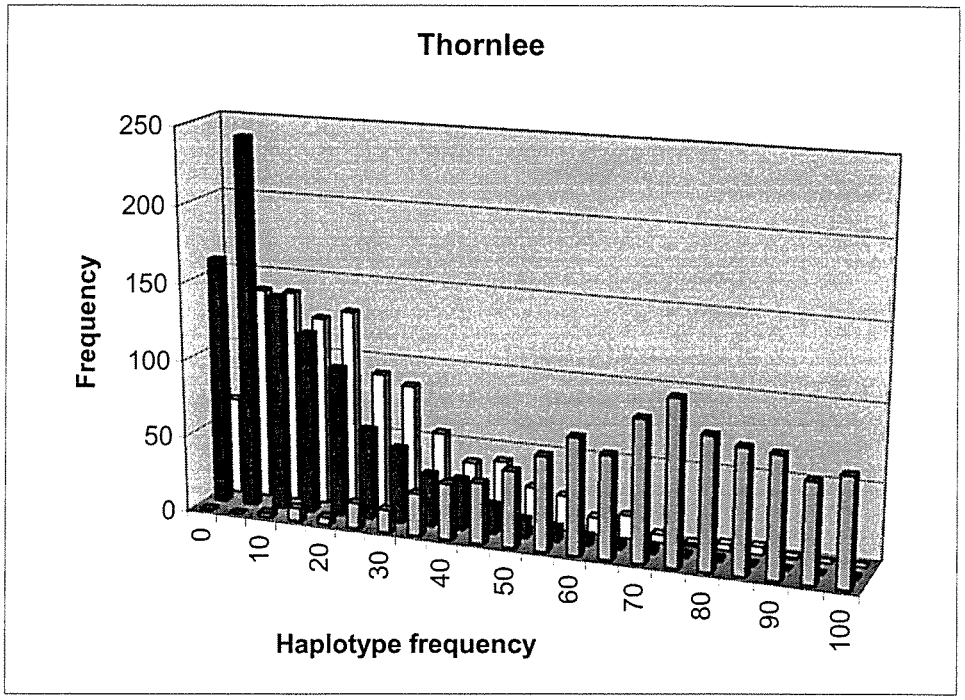
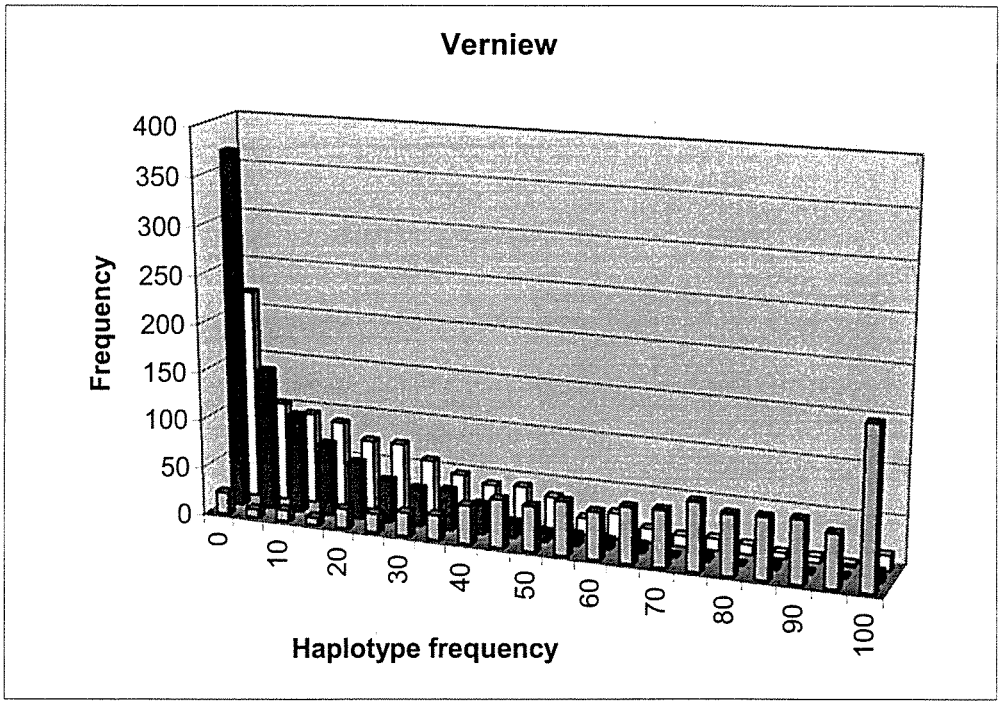

Polworth
Frequency
400
350
300
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype frequency

Figure 3.3 (f)


Thornlee
Frequency
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype frequency

(g)


Verniew
Frequency
400
350
300
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
90
100
Haplotype frequency

There is a strong similarity in pattern of haplotype frequency distributions between sets of simulation runs (Figures 3.2 and 3.3). Even when using larger dense forest patches, the effects of habitat heterogeneity on connectivity, and on the distribution of alleles in the region, are very similar. The current distribution of dense forests in the region can therefore be considered sufficient to assess habitat heterogeneity effects during range expansion of the wild rabbit into the Mitchell region.

3.5 Discussion

The results of the simulation model show that the spatial distribution of soil types and dense forests across the Mitchell region had substantial effects on the partitioning of immigrants within the system during both the initial range expansion from the west (colonisation phase) and during subsequent interactions among Eastern system sites. In extreme cases the reduction in colonisation potential was sufficient to make the possibility of colonisation from Glenlea unlikely (Verniew and Claravale). However even at the sites most highly connected to Glenlea, newly colonised populations showed significant differences in allele frequencies to those of the colonising source. Bottlenecks along dispersal paths were sufficient to induce significant differences in allele frequencies between Glenlea and newly colonised populations in most simulation runs.

In approximately half of the newly colonised populations individual alleles (particularly the B haplotype) were excluded entirely. This was not unexpected given that B was the lowest frequency haplotype at Glenlea and was thus most likely to be excluded following population bottlenecks (Nei *et al.* 1975). These results suggest that habitat heterogeneity among sites was sufficient to produce the relative isolation of the Eastern system as a whole from Glenlea, and hence from the entire Western population system. The results also show that habitat heterogeneity can explain the establishment of a population system that is highly genetically structured with populations that tended to be deficient in, or show a low frequency of, B haplotype individuals.

Although essentially isolated from the Western system, the results of the interaction phase suggests there is potential for high levels of connectivity among some sites within the Eastern system and relative isolation of others. Estimated propagule sizes among Eastern sites varied widely and indicated substantial habitat heterogeneity within the region. Four sites (Bowann, Currawong, Glenalba and Thornlee) clearly showed moderate to high levels of interaction with other sites within the system in terms of propagule size, and this was reflected in the similarity of the genetic constitution of propagules arriving at these sites during the interaction phase.

During the interaction phase propagules were often large to very large, and tended to consist of a high frequency of individuals carrying the A and a low frequency of individuals carrying the C haplotype. Propagules also tended to be deficient in B haplotype, or to show very low frequencies of this allele. The very strongly skewed B haplotype distributions also suggest the tendency for bottlenecks along dispersal paths (which resulted from habitat heterogeneity) to further reduce B haplotype frequencies within interacting propagules, or to remove the B haplotype entirely from propagules. Thus even when B haplotype individuals entered the Eastern system at low frequency during colonisation, stochastic events along dispersal paths among sites tended to decrease their frequency still further. In the long term, moderate to high levels of connectivity among populations at Bowann, Currawong, Glenalba and Thornlee are likely to lead to genetic similarities among these populations. Each of these populations is likely to consist of a high frequency of individuals carrying the A haplotype and a low frequency of individuals carrying the C haplotype. Individuals carrying B haplotype individuals may be in a low frequency or be absent entirely.

Claravale and Verniew were more likely to be colonised from within the Eastern system than from Glenlea. Claravale experienced the highest level of interaction of any of the Eastern system sites and so despite any initial genetic differences when newly founded, in the long term the Claravale population would tend to show similar haplotype frequencies to the highly connected subset of sites (Bowann, Currawong, Glenalba and Thornlee). In contrast, Verniew experienced low connectivity with the remainder of the Eastern system. Thus while Verniew was likely to be colonised from within the Eastern system, the genetic structure of the population is unlikely to be strongly influenced by interactions within the system through time, and any genetic differences with other Eastern system sites may persist.

Although the overall interaction of Currawong within the Eastern system was only slightly greater than that of Verniew, the distribution of propagule sizes arriving at the site was bimodal. Thus while Currawong experienced low interaction with most Eastern system sites, it probably experienced a moderate level of interaction with at least one other Eastern site. Currawong was unlikely to show significant interactions

with Verniew or Polworth since these sites experience low to very low interaction with all other sites within the system. Currawong was more thus most likely to show interactions with one or more of the remaining Eastern system sites (Bowann, Claravale, Glenalba or Thornlee). These populations formed a group that are highly connected, and so moderate levels of interaction between Currawong and one or more of these populations would also tend to lead to genetic similarity over the long term.

Polworth stands out as a site which was highly isolated both during the colonisation and interaction phases. Propagules arriving at Polworth were consistently very small and were often deficient in B and C haplotype individuals. The Polworth population was therefore likely to be fixed for the A haplotype, indicating the isolation of this site from other Eastern system sites.

3.5.1 Comparison of Model Output with Population Genetic Samples

The model presented in Chapter 2 provides strong support for the effect of habitat heterogeneity on the long term relative levels of interaction among sites in the Eastern system. Not only does the model of isolation by habitat heterogeneity explain the relative connectivity between sites (Chapter 2) but, as shown here, it is also able to explain the varied genetic structure of sites within the eastern system. By inducing bottlenecks along dispersal paths, habitat heterogeneity has had significant effects on both the colonisation and interaction phases that resulted in the current genetic structure of the system. Given that the habitat heterogeneity model can explain both relative connectivity and genetic structure to such a strong extent it suggests that habitat heterogeneity is a major determinant of connectivity within the system. The habitat heterogeneity model can thus confidently be used to make tentative predictions about the long term characteristics of the Eastern rabbit population system. These predictions can then be compared with real data describing the current population genetic structure of the Eastern system (Wilson *et al.* 2002) to assess the importance of habitat heterogeneity on dispersal processes between the Western and Eastern rabbit population systems, and among populations within the Eastern system. These predictions and comparisons are summarised in Table 3.8.

Table 3.9. Tentative predictions of genetic characteristics of the Eastern rabbit population system based on simulation results with comparisons to known state of the Eastern system based on population genetic data (Wilson *et al.* 2002).

Hierarchical level	**Attribute**	**Simulation Prediction**	**Real system**
Eastern vs Western system	Regional population genetic structure	Genetic differences between Glenlea and all Eastern system sites	Eastern system significantly genetically different from Western system
Eastern System	B haplotype frequencies	Low to zero frequency at all sites	Absent from all sites
Eastern System	within region population genetic structure	High probability of population genetic differences within system	Significant population genetic structuring
Within Eastern system	Genetic similarities among subsets of Eastern system sites	Genetic similarities among Bowann, Claravale, Currawong, Glenalba and Thornlee populations likely; this group likely to be different to Polworth and Verniew	Bowann, Claravale, Currawong, Glenalba and Thornlee form a panmictic subgroup. Polworth and Verniew show significant differences in allele frequencies to this group and each other.
Site	Genetic divergence	Polworth highly likely to show very low frequencies of B and C haplotypes or to be fixed for A haplotype	Fixed for A haplotype
Site	Genetic divergence	Verniew likely to have A and C haplotypes but genetic differences to all other sites	Verniew has A and C haplotypes but is genetically divergent from all other Eastern system sites

As Table 3.8 shows, the simulation model is a good predictor of a number of population genetic attributes of the Eastern system, from regional differences (Western versus Eastern system) to population genetic characteristics at specific sites. The heterogenous spatial distribution of resources and dense forests is thus highly predictive of the dispersal potential of rabbits both during colonisation of the Eastern system from the west and during later interactions among sites.

The simulation modelling in Chapters 2 and 3 was conducted using a dispersal parameter appropriate for female rabbits in the Mitchell region, and most ecological models to date have focussed exclusively on the female component of a population (Ranta *et al.*1999). However, several studies have shown that wild rabbit populations may exhibit male biased dispersal (Parer 1982, Webb *et al.* 1995, Kunkele and von Holst 1996) which may affect the relative isolation of local rabbit populations within the region. In order to further assess patterns of connectivity within the Eastern system, an additional simulation was conducted to account for both male and female rabbit dispersal, and will be discussed in the next chapter.

Chapter 4. Modelling Male and Female Rabbit Dispersal

4.1 Introduction

While theoretical models suggest that dispersal within a subdivided population system will affect characteristics such as system persistence (eg Murdoch *et al.* 1996, Rohani *et al.* 1996, Holyoak and Lawler 1996, Hill *et al.* 2002), in many species one sex tends to disperse more than the other. In most avian taxa which have been studied dispersal is mainly female biased, while male biased dispersal is more common in mammals (Greenwood 1980). A number of studies have established that dispersal in rabbits tends to be males biased both in Australia (Dunsmore 1974, Daley 1979, Parer 1982, Parer and Fullagar 1986) and in Europe (Kunkele and von Holst 1996, Webb *et al.* 1995). Male rabbits also tend to disperse further than female rabbits (Kunkele and von Holst 1996, Richardson *et al.* 2002).

An obvious corollary of a male bias in dispersal is that females tend to be philopatric. This difference in dispersal tendency between the sexes can impact on the dynamics of range expansions (Hengeveld 1989) and on the dynamics of a population system once it is established (Hanski and Gilpin 1991). Establishment of local populations during range expansion or after local extinction requires both sexes in dioecious species. The rate of spread of an invasion or the probability of re-establishment after extinction will therefore be limited primarily by the dispersal potential of the philopatric sex. Any sex based differences in dispersal capacity might therefore have an important influence on patterns of connectivity

As seen in the preceding chapters it seems likely that the spatial distribution of resources and of dense forests has the potential to influence relative connectivity among at least the female component of local rabbit populations within a population system in semi-arid Australia. However, a male bias in dispersal of wild rabbits may affect patterns of connectivity among local populations when the population is considered as a whole. A simulation study accounting for both male and female dispersal was therefore conducted to examine patterns of connectivity among local populations in the Eastern rabbit population system.

4.2 Model Application

To determine the effect of a male bias in dispersal, a simulation was run (habitat heterogeneity model, Appendix 1) using a combined male and female dispersal parameter which was estimated from the same sources of empirical data as per Chapter 2 (Daly 1979 and Table 3 in Parer 1982). Both Daly (1979) and Parer (1982) present numbers of male and female dispersers allowing the combined dispersal parameter for males and females to be calculated (0.37). In addition to a greater tendency to disperse, male rabbits can disperse twice as far as female rabbits (Kunkele and von Holst 1996, Richardson *et al.* 2002) which may influence their dispersal potential through dense forests. To account for this, the distance at which the logarithmic decrease function was applied in patches of dense forest was increased by 50%. Thus 100% of a propagule dispersed successfully through linear distances of dense forest of less than 2.25 km, 10% of a propagule moved through linear distances of 2.25 to 4.5 km, and 1% of a propagule was able to disperse greater than 4.5 km. All other parameters were identical to those used in Chapter 2.

4.3 AFLP Study

Since the dispersal parameter used in the current simulations was an estimate for males and females, it was necessary to validate simulation results with a genetic marker which is biparentally inherited. For this purpose, Amplified Fragment Length Polymorphism (AFLP) markers were screened on rabbit liver samples. Samples had been used previously for the estimation of mtDNA haplotype frequencies in the Eastern system (Wilson *et al.* 2002). The AFLP technique was performed according to the protocol of Ajmone-Marsan *et al.* (1997). Restriction digestion and ligation of adaptors were performed on a Selby dry block heater. Approximately 400ng of DNA was incubated with the *Taq*1 restriction enzyme for 1 hour at 65 ^{o}C. *Taq*1 (recognition sequence TCGA) was used as the dominant cutter with *Eco*R1 as the rare cutter.

After fragments were generated, specific adaptors were ligated to the sticky ends of the restriction site with DNA ligase. Ligation of adaptors occurred at 37 ^{o}C for 3 hours. The template DNA created by the digestion-ligation process was then diluted

10x with TE buffer for use in pre-selective amplification. Amplification procedures were undertaken on a programmable PTC-100 (MJ-Research Incorporated). Pre-selective polymerase chain reaction (PCR) was performed with *To*1 and *Eo*1 primers. The following temperature cycle profile was used: 1) 30 cycles of denaturing at 94 °C for 30 minutes, 2) annealing and extension for 1 hour at both 72 °C and 56 °C and 3) a final step of 10 minutes at 72 °C. The amplification reaction was diluted 10x with TE buffer.

The three most variable *Eco*R1/*Taq*1 primer combinations (E33-T49, E33-T50 and E42-T49) were chosen for selective PCR from preliminary analysis (results not shown). Fragments were radioactively marked with [^{33}P] -labelled ATP incorporated into the newly polymerised DNA as the base adenine. Selective amplification began with denaturing for 30 minutes, and annealing and extension at 61.5 °C for 30 minutes and 72 °C for 1 hour. The 61.5 °C step was reduced by 0.7 °C in temperature for every succeeding cycle until 56 °C was reached. 30 cycles of the above cycle profile were performed with 56 °C as the final annealing temperature. This was followed by a final step of 5 minutes at 72 °C. PCR products were then mixed with 7ul of gel loading dye and denatured for 3-5 minutes at 95 °C. To ensure that contamination did not influence any of the PCR results and that scoring of loci was consistent, a control was used each time.

Polyacrylamide gel electrophoresis (PAGE) was performed on a large gel rig produced by Life Technologies. Gels were pre-run for 1 hour and wells were cleaned of excess urea prior to sample loading. Reaction products were loaded on a 5% polyacrylamide gel and run for 2 hours and 45 minutes in TBE buffer (Tris, boric acid, EDTA). Gels were dried onto Whitman blotting paper and exposed to AGFA X-ray films for between 20-36 hours.

The AFLP procedure was performed twice on six initial samples using the same primer sets to test if the procedure was reproducible for this species. Samples produced reproducible banding patterns at scorable loci. Two individuals scored all gels independently and only clearly identifiable loci were used in the analysis. One

hundred and forty eight (148) putative loci were identified, of which 113 were polymorphic and retained for analysis. Pairwise F_{ST} was estimated using Arlequin (Schneider *et al.* 2000), and the mean of pairwise F_{ST} was calculated for each site as per Chapter 2 (Table 4.1).

Note that some samples originally used in the study of Wilson *et al.* (2002) were unavailable, which resulted in smaller sample sizes for some populations than the mtDNA study (Table 4.1). Only 3 samples were available from the Thornlee population. This population was therefore excluded from both the current simulation study and from the AFLP analysis. Additionally only one population was available on the soil patch at which the Glenlea population is located whereas in Chapter 2 the haplotype frequencies of 4 populations were combined for genetic analysis. To ensure that removal of the Thornlee population and use of a single Glenlea population did not significantly impact on the simulation results the simulation was rerun using identical parameters to those used in Chapter 2 (i.e. using a female dispersal parameter) but excluding Thornlee from both the simulation and genetic analysis and using haplotype frequencies for the Glenlea population for genetic analysis. All regression analyses were conducted as per Chapter 2.

4.4 Results

Relative connectivity indices for a scenario of female dispersal in the Eastern system (excluding the Thornlee population) are shown in Table 4.2. A marginal improvement in the fit of the model output to population genetic data under this scenario was evident (Figure 4.1) as compared with the fit of the model to genetic data in Chapter 2 (Figure 2.3; r^2=0.84). It is therefore unlikely that the exclusion of the Thornlee population and calculation of population genetic statistics (F_{ST}) based on a single Glenlea population would significantly impact on the model when dispersal from the whole population is considered.

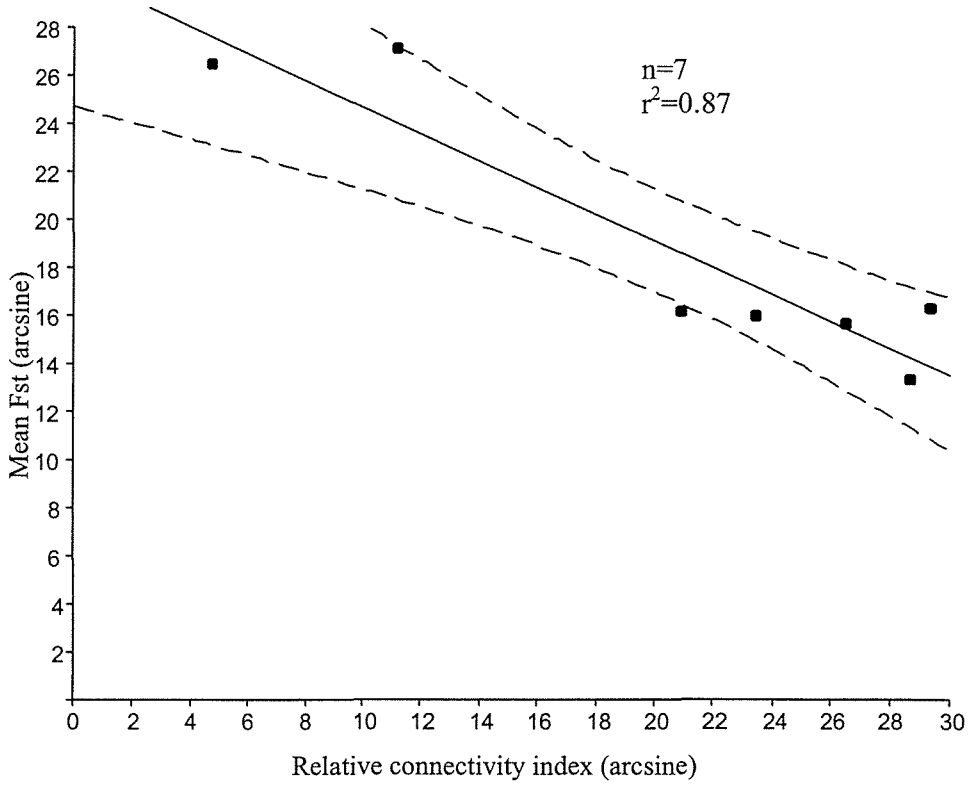
Table 4.1. Mean of pairwise F_{ST} estimates (with sample size in parentheses) and standard errors of the mean (s.e.m) for mtDNA and AFLP's for seven sites within the Mitchell region.

	mtDNA		**AFLP**	
Site	**F_{ST}**	**s.e.m**	**F_{ST}**	**s.e.m**
Bowann	0.05371 (33)	0.031	0.0592 (25)	0.006
Claravale	0.07865 (31)	0.04	0.06194 (17)	0.007
Currawong	0.07604 (31)	0.042	0.06813 (28)	0.008
Glenalba	0.0734 (30)	0.041	0.07946 (27)	0.011
Glenlea	0.07754 (42)	0.027	0.0528 (23)	0.008
Polworth	0.1988 (30)	0.057	0.07236 (14)	0.009
Verniew	0.20752 (34)	0.059	0.08927 (25)	0.008

Table 4.2. Model output matrix under scenario 1 (female dispersal; excluding Thornlee): Number of successful colonisers and relative connectivity indices for seven sites within the Mitchell region.

		Bowann	Claravale	Currawong	Glenalba	Glenlea	Polworth	Verniew	**System to site index**
	Bowann	0	12955	1402	4087	4446	42	57	0.182
	Claravale	24136	0	3096	10006	960	162	894	0.311
Contribution	Currawong	1069	931	0	4193	9109	8	614	0.126
from site	Glenalba	6676	6073	8278	0	3391	392	2666	0.218
to system	Glenlea	2982	276	9126	1689	0	50	0	0.112
	Polworth	130	133	24	638	139	0	0	0.008
	Verniew	182	899	2018	2188	0	0	0	0.042
Site to system index		0.279	0.169	0.19	0.181	0.143	0.005	0.034	
Mean relative connectivity index		0.231	0.24	0.158	0.199	0.128	0.007	0.038	

Figure 4.1. Relative long term connectivity indices (female dispersal) versus population genetic data for seven sites within the Mitchell region, with 95% pointwise confidence intervals (---).

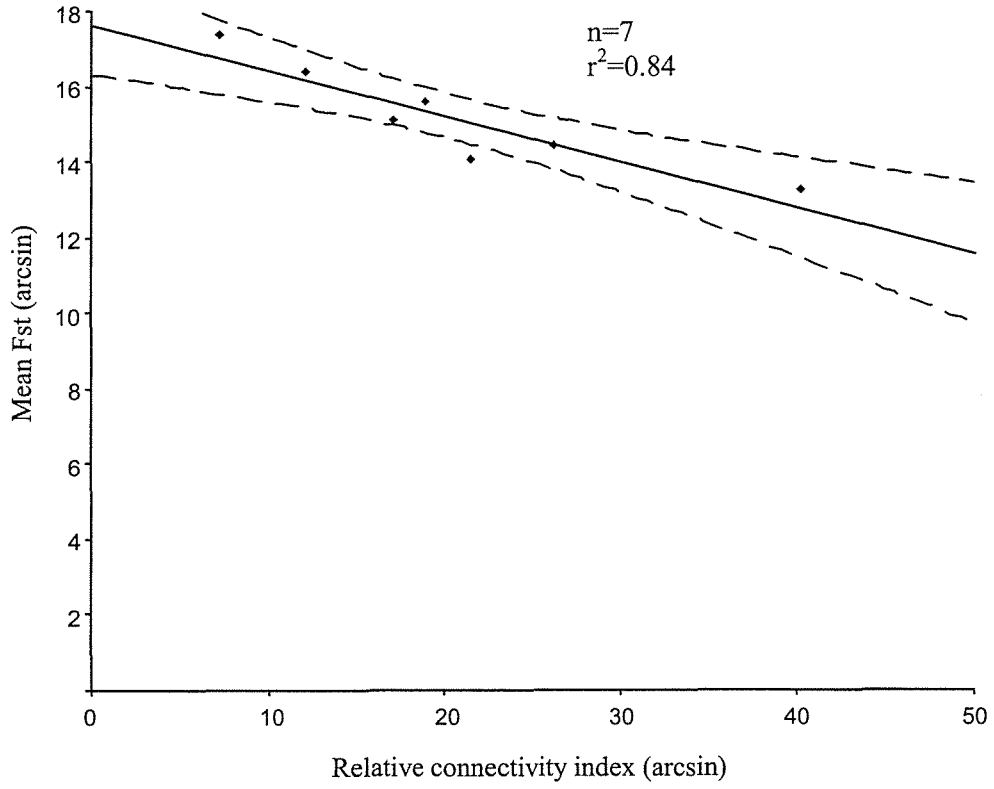


When combined male and female dispersal was considered (scenario 2), there was again a broad range of connectivity indices (Table 4.3), although the pattern of connectivity within the system changed considerably when compared with female only dispersal (Table 4.2). The connectivity index for Polworth was substantially higher than with female only dispersal. While Verniew remained isolated, Currawong was more isolated when combined male and female dispersal was modelled than for females. Glenlea showed a low probability of interactions with other sites for females (Table 4.2), but here was highly connected to the Eastern system (Table 4.3). Once again, connectivity indices account for a large proportion of the variation in population genetic data (Figure 4.2).

Table 4.3. Model output matrix under scenario 2 (combined male and female dispersal, excluding Thornlee): Number of successful colonisers and relative connectivity indices for seven sites within the Mitchell region.

		Bowann	Claravale	Currawong	Glenalba	Glenlea	Polworth	Verniew	**System to site index**
	Bowann	0	161959	17415	170994	2634693	5891	6317	0.153
	Claravale	304612	0	20522	352572	4414948	432910	3779	0.281
Contribution	Currawong	11486	6309	0	157584	1424963	3630	1696	0.082
from site	Glenalba	273689	213757	309872	0	28814	8024	92527	0.047
to system	Glenlea	1689037	1357193	1426013	14618	0	731353	69699	0.269
	Polworth	10697	436567	11475	12809	2385745	0	55670	0.148
	Verniew	15550	3791	5515	88645	224840	54875	0	0.020
Site to system index		0.117	0.111	0.091	0.041	0.57	0.063	0.012	
Mean relative connectivity index		0.135	0.196	0.086	0.044	0.417	0.106	0.016	

Figure 4.2. Relative long term connectivity indices (scenario 2: combined male and female dispersal) versus population genetic data for seven sites within the Mitchell region, with 95% pointwise confidence intervals (---).



4.5 Discussion

In order to better understand the dynamics of regional population systems in which habitat heterogeneity can isolate local populations, it is useful to examine any differences in dispersal potential between males and females within the system. When considering a recently introduced species such as the wild rabbit, such differences are likely to have had impacts on the colonisation dynamics of the species and to affect the current behaviour of the system. This is particularly likely in systems in which extinctions and recolonisations are important, such as in regions which are influenced by environmental stochastic effects or in which epizootics (eg Rabbit Haemorrhagic Disease, RHD) can lead to occasional high mortality levels within local populations.

It is informative to examine differences in connectivity indices between female-only dispersal (scenario 1), and combined male and female dispersal (scenario 2). As both simulations account for females dispersal characteristics, any differences between the female only simulation and the combined male and female simulation can be attributed to the dispersal of males. Polworth is highly isolated for females, but these results show that the site has a substantially higher level of interaction with the system for males. This suggests that the probability of recolonisation of this site would be low after an extinction event (for instance, due to drought or control measures). Even if males were to successfully reach the Polworth site after an extinction, establishment of a breeding population (and thus recolonisation) could only occur after females had also successfully dispersed to Polworth from other sites. This is unlikely given the very low level of female interaction between Polworth and other Eastern system sites.

Population extinctions may also result from the spread of diseases (Hess 1996). The capacity to differentiate between male and female interaction potential is particularly useful when considering diseases that are spread by individual contact. While the interaction of Polworth with the remainder of the system is still low for males, it is far higher than for females. Thus transmission of the disease to the Polworth site would depend largely on relatively high male dispersal, while recolonisation of the site would be constrained due to the lower dispersal potential of females.

Differences in connectivity indices for males and females are evident not only within the Eastern system, but also between Glenlea (a Western system site) and the Eastern system. Connectivity indices suggest that interactions between the two systems are low for females (Glenlea connectivity index = 0.128; Table 4.1). However, the current modelling suggests a very high male interaction potential between the two systems (Glenlea connectivity index = 0.42; Table 4.3). These differences in dispersal potential between males and females are once again likely to impact on the dynamics of the Eastern system, both in the recolonisation of the Eastern system if a broad scale event brought about a regional extinction (due to limited recolonisation potential from the west because of low connectivity for females), and the transmission of diseases (high potential for disease transmission from the west due to high probability of male interaction between Glenlea and the Eastern system).

In contrast to Polworth and Glenlea, the isolation of Verniew from the remainder of the system is relatively unchanged regardless of the whether female-only dispersal or combined male and female dispersal is considered. Verniew is highly isolated for both males and females and so is unlikely to be recolonised after an extinction event. Further, the isolation of this site makes it unlikely that a disease would be transmitted to the Verniew population, either from the west or from other sites within the Eastern system.

The habitat heterogeneity model accounts well not only for connectivity levels among females within the Eastern system (Chapters 2 and 3) but, as shown here, also provides an very strong explanation for connectivity levels within the whole Eastern population system when appropriate sex specific dispersal characteristics are used. It is thus highly likely that the spatial distribution of soils and dense forests within the Mitchell region affects both females and males in the Eastern population system, but affects them in different ways. This has led to distinct patterns of connectivity for males and females. As this chapter has shown, it is essential to determine any differences between male and female connectivity patterns in order to fully understand dynamics within regional systems. The capacity for the habitat heterogeneity model to explain such a large proportion of the genetic structure in the Eastern system, for both males and females, confirms the utility of model as an aid to understanding the processes which shape regional population systems.

Chapter 5. General Discussion

Understanding the factors which influence the dynamics of populations is of significant interest from both theoretical and management perspectives. While local populations will be affected by internal dynamics processes, they may also interact within a population system (Andrewartha and Birch 1954, den Boer 1968, Levins 1970, Pulliam 1988, Hengeveld 1989). Where this occurs, it is necessary to examine population systems at a scale broader than that of local populations in order to understand important system attributes.

Dispersal from extant local populations has the potential to bring about the colonisation of previously uninhabited territory during range expansion, influencing the initial spatial distribution and genetic characteristics of newly established local populations. In established systems, high levels of connectivity will tend to homogenise demographic and genetic differences among populations that might otherwise differentiate due to local environmental conditions and/or genetic drift (Slatkin 1985). In addition, high connectivity levels have the potential to alter system function. This may occur due to the mitigation of local or broad scale extinction processes (Brown and Kodric-Brown 1977, Pulliam 1988), the recolonisation of vacant patches after extinctions (Levins 1969) or by increasing the transmission rate of diseases (Mollison 1977, Hess 1996). In contrast, local populations which exhibit low levels of long term interaction are likely to show genetic structuring, and processes buffering extinction are less likely. Connectivity levels therefore have the potential to affect the persistence and functioning of regional systems (Harrison and Hastings 1996, Hanski and Simberloff 1997).

Models of population distribution based on different connectivity patterns, such as source-sink or metapopulation models, are useful tools to aid in understanding the dynamics of real population systems. To be of maximum benefit however, a model must capture the major processes underlying the population system in question. In contrast to population genetic models, most ecological models to date have not considered the potential for interactions in a spatially extended system where interactions occur at a scale beyond that of a single dispersal event. In some such systems, the spatial distribution of resources which affect key demographic

processes (such as population growth) and of landscape elements which impede the dispersal potential of individuals are likely to play a role in determining the long term mean level of interaction among local populations (Chapter 2).

While the model of habitat heterogeneity introduced in Chapter 2 can be seen as a tentative and relatively simple first step in describing such systems, the model could easily be extended to incorporate other features. For example, in the Eastern rabbit population system local population extinctions are likely to be correlated due to broad scale stochastic effects (periods of drought), and therefore will be relatively independent of local population size. In other systems (eg metapopulations) local population size may well be important in determining extinction risk, and thus the potential to provide colonisers for adjacent patches along a dispersal path. If patch area provides an adequate indicator of population size, an appropriately scaled index of patch area could be included in the model for each patch along a dispersal path. While assigning indices to patch areas in a way that realistically reflects extinction risk may not be a simple process, such parameters are frequently estimated (for instance by using Population Viability Analysis). In addition to adding factors, it may be reasonable to alter the form of particular variables. For example, in systems in which density dependent processes have been shown to be important it would be a simple modification to change the growth function used here to one that is bounded by the carrying capacity for each patch type.

Models provide a convenient means for summarising important dynamics processes but should be applied judiciously. Even when examining the same species in different regions, different processes may impact on population system dynamics. The model of habitat heterogeneity provides a very good fit to population genetic data (as described by the current level of genetic differentiation) in the Eastern rabbit population system, and it is apparent that the spatial distribution of soils and dense forests have been important in shaping the characteristics of the system (Chapter 2). The Western rabbit population system (Fuller 1996) is genetically panmictic, covers a vast region of arid western Queensland and is contiguous with the Eastern system. When the model of habitat heterogeneity was applied to the six populations in the Western system (Appendix 3), predicted long term mean connectivity indices based on soil type show a poor fit to population genetic data provided by Fuller *et al*

(1997)(r^2= 0.22, p=0.36) suggesting that connectivity among local populations is not affected by habitat heterogeneity in this panmictic system. This is to be expected, since in the Western system there are a few, very large soil patches in the region (heterogeneity in soil type is low) and there are no dense forests. Interactions among local populations in the Western system therefore are unlikely to be impeded by habitat heterogeneity. In this population system, dynamics are more likely to be related to high rates of local extinction in the highly unstable arid environment followed by relatively unimpeded recolonisation, as evidenced by high levels of gene flow (Fuller 1996, 1997).

In systems where habitat heterogeneity influences long term interactions among established local populations, it may have also influenced the probability of colonisation of sites during a range expansion and thus the initial genetic characteristics of newly established local populations (Chapter 3). The spatial distribution of resources and viscous landscape elements within a region has the potential to affect the characteristics of propagules which seed local populations, and thus the characteristics of the local populations arising from those propagules (Chapter 3). When the factors which impede the probability of interaction among local populations persist through time such population differences are also likely to persist (Slatkin 1985).

Notable population genetic characteristics of the Eastern rabbit population system include the absence of the B haplotype which is present in all Western system populations, fixation of the A haplotype at Polworth, and genetic similarities among other Eastern populations (Bowann, Claravale, Currawong, Glenalba and Thornlee) with substantial population genetic divergence of the Verniew population. Each of these features is consistent with a process whereby habitat heterogeneity:

1) leads to a range of colonisation probabilities from a colonising source;
2) has the potential to substantial reduce the size of propagules along dispersal paths to sites that are colonised, thereby inducing bottlenecks; and
3) leads to a range of interaction probabilities among local populations in the long term, allowing for levels of gene flow sufficient to reduce initial

population genetic differences among some populations and maintain differences with others.

The model is therefore able to determine the influence of habitat heterogeneity both during establishment of the system and during subsequent interactions among established populations.

The spatial distribution of resources and viscous landscape elements within a region may influence the dispersal capacity of males and females differently. Different patterns of connectivity might therefore be exhibited between the male and female components of the system (Chapter 4). Such differences are likely to influence the dynamics of regional systems, particularly in those systems where natural or deliberate extinctions of local populations occur. For instance, female rabbits are primarily responsible for the construction of warrens, which are central to the establishment of successful populations (Myers *et al.* 1994). It is thus essential to assess the dispersal potential of female rabbits when considering the likelihood of recolonisation of a site after a local population extinction. Sites which have low levels of female interaction with other populations will consequently have a low probability of recolonisation. However, the higher male interaction probabilities to some sites within the Eastern system (Chapter 4) is also noteworthy, since the transmission rate of diseases which require individual contact are strongly influenced by patterns of dispersal (Hess 1996, Grenfell and Harwood 1997, Fulford *et al.* 2002). The difference between male and female dispersal potential to a site such as Polworth suggests that the probability of male mediated transmission of a disease to Polworth would be far higher than the probability of recolonisation of the site, due to lower female interaction probabilities.

In this study, the effects of sex biased dispersal on connectivity among local rabbit populations was assessed and showed that, in this system, habitat heterogeneity affects the dispersal of males and females differently. Connectivity indices were validated using both maternal (Chapter 2) and bi-parental (Chapter 4) genetic markers and explained a large proportion of the variation in both data sets. This strongly suggests that the habitat heterogeneity model has accounted for the major

ecological processes which affect both male and female dispersal among rabbit populations in this system.

5.1 Management Implications

Factors which influence dispersal probabilities have the potential to influence the sites which are colonised initially during a range expansion, and ongoing connectivity levels have the potential to affect population system dynamics due to recolonisation and rescue effects. Connectivity levels will also affect the pattern of spread of diseases (Mollison 1977, Hess 1996), which may pose threats to endangered species (Hess 1996) or act as valuable tools for the management of pest species (eg RHDV). Identifying factors which cause variations in long term connectivity among populations is therefore a prerequisite for the effective management of regional systems.

Population genetic data have the potential to be highly informative regarding long term levels of interaction among populations. With these data, management units (Moritz 1994) can be defined to allow conservation or control efforts to be implemented at an appropriate level of scale. However, population genetic data do not provide an understanding of the factors which promote or inhibit interaction levels. In order to be useful, population genetic data need to be interpreted with reference to appropriate models which most closely reflect the system in question. Traditionally, island models (Wright 1931, Slatkin 1985) and stepping stone models (Kimura and Crow 1964) (which may incorporate geographic barriers) have been used for reference. For example, if population system dynamics can be explained adequately using a one dimensional stepping stone model the geographic distance between demes should explain much of the variability in population genetic data (eg Chenoweth *et al.* 1998).

In systems where habitat heterogeneity influences the probability of interactions among local populations, it is species' specific factors which influence interaction probabilities that should provide guidelines for management efforts. As this study has shown, habitat factors can be identified by regional habitat heterogeneity models.

To be useful for management, a model must be able to identify critical factors that can then be manipulated as appropriate for conservation or control. Also, if it can be demonstrated that a model adequately incorporates the major factors and processes influencing the population system, as in this study, the model can be used to give some general predictions of the effects of such manipulations, or of other control strategies such as the deliberate introduction of diseases. These points are best illustrated with reference to the Eastern rabbit population system.

Rabbit control strategies can be categorised as local (intended to affect one or a few populations eg warren ripping or poisoning in the case of the wild rabbit) or broad scale (intended to affect many populations, such as myxomatosis or RHDV). The use of epizootics as broad scale measures to control pest populations has had significant short term successes in Australia, and so has been the subject of intense scientific scrutiny (Fenner and Fantini 1999, Cooke 2002). Disease outbreaks may be difficult to predict since the pattern of spread of a disease may be influenced by a number of variables such as transmission vectors and environmental factors such as rainfall and temperature (Smyth *et al.* 1997). If contact among individuals is an important means of disease transmission, however, then the level of connectivity among populations will influence the regional spread of the disease. Indeed, the importance of incorporating rates of local population interaction in epidemiological models has been recognised for some time (eg Barlow 1993, 1994, Grenfell and Harwood 1997, Fulford *et al.* 2002).

On the basis of the spatial distribution of resources (soils) and dense forests in the Eastern system, a planned release of a disease would be most effective if implemented at a site (or sites) that showed high connectivity with other sites (eg Bowann or Claravale). For instance, the introduction of RHDV into one or both of these local rabbit populations during an appropriate climatic period is likely to provide an efficient component of a control strategy since the disease should spread rapidly to highly connected sites (Hess 1996). However the disease is unlikely to spread rapidly to sites with low connectivity such as Verniew, where localised release of the virus or other effective local control methods should be implemented.

Diseases such as RHD increase the mortality rate within local populations, and are released with the aim of lowering the regional density of the target pest species. Increasing mortality in pest populations has a long history, although the deliberate introduction of diseases is a relatively recent strategy. It has been suggested, however, that it is ethically preferable and more acceptable to the general public to reduce the density of pest populations by lowering their fertility via methods such as immunocontraception (Barlow 1994, McCallum 1996). Immunocontraception involves delivering specific antigens into a recipient animal, with the aim of invoking an immune response and rendering the animal infertile (Barlow 2000). Baits and genetically tailored viruses are typically considered as potential delivery mechanisms. While practical problems exist, and relatively little research into the population responses of imposed sterility on target species has been conducted (although see Saunders *et al.* 2002), immunocontraception ha been promoted as a possible means for effective control of pest species.

Several theoretical models have been developed to examine aspects of immunocontraception using viruses as delivery agents, such as the persistence of the virus in a population and potential reductions in host density (Barlow 1994, Hood *et al.* 2000). Most models to date have been non-spatial (although see Sato *et al.* 1994). If the viral vector used to carry antigens requires individual contact for transmission, for instance a sexually transmitted disease, the connectivity among local populations within a region will impact on patterns of disease spread. Furthermore, it may be important to consider any differences in the dispersal potential of males and females of the target species, since this may affect transmission rates and the potential for population recovery after control (Ji *et al.* 2001). Connectivity between Glenlea and the Eastern system was far higher when combined male and female dispersal was modelled (Table 4.3) than under a female dispersal scenario (Table 4.2). If a viral vector were to spread from the west to the Eastern system, greater connectivity would lead higher disease transmission rates than if dispersal potential between the sexes was equal. As noted above, this is particularly interesting since while disease transmission rates would be largely determined by the more vagile sex (males), population recovery (recolonisation, rescue effects and rates of population increase) would be constrained since they would be governed by more sessile females.

When control measures are successful, local population densities or even regional densities of a pest species may be markedly reduced in the short term. It has been estimated that rabbit population densities reduced by up to 90% after introduction of myxomatosis in Australia (Fenner and Fantini 1999), although densities have increased subsequently due to attenuation in the virulence of the myxoma virus and increased resistance of wild rabbits (Myer *et al.* 1994, Saint *et al.* 2001). Rabbit Haemorrhagic Disease has shown a more limited, patchy success with densities of wild rabbits in some regions reduced substantially after deliberate introductions or natural spread of the disease (Bowen and Read 1998, Mutze *et al.* 1998). If the success of control measures varies regionally, the dispersal of colonising propagules from less affected regions into highly affected regions may provide a mechanism for the re-establishment of pest populations. Although some remnant populations are likely to remain within the highly affected region, this process should generally emulate a range expansion. If so, and if resource or landscape factors affect long term connectivity levels within the region, a habitat heterogeneity model would be useful for identifying those local populations which exhibit high levels of connectivity with potential source populations. This knowledge could assist in establishing efficient monitoring programmes or allow for the early effective implementation of control measures.

Although historically wild rabbits have been a major pest in the Mitchell region, rabbit population densities in the region currently are very low (pers. obs.). This contrasts with the Western system where deliberate release of the virus has had little ongoing effect (Department of Natural Resources 2001). If RHDV provides poor rabbit control in the Western system the possibility exists that a Western system population such as Glenlea could potentially act as a source for the reintroduction of wild rabbits into the Eastern system. Monitoring re-introductions of wild rabbits into the Eastern system would ideally be conducted at a site such as Currawong which showed high potential for colonisation from Glenlea (Chapter 3). Conversely, establishing a monitoring site at Verniew is unlikely to be informative. Colonisation of this site is likely to occur from within the Eastern system rather than from Glenlea, with rabbits required to be established at several sites within the Eastern system before colonisation of Verniew occurred.

Control strategies have been traditionally based on the manipulation of critical population processes such as mortality. However when local populations interact within a system, targeting intrapopulation processes in isolation is unlikely to result in effective control. Since dispersal is a key process in regional systems, identifying factors which affect dispersal and have the potential to be manipulated should provide an important component of management strategies. Two factors significantly influence isolation within the Eastern system namely the spatial distribution of resources and of dense forests, and the spatial distribution of dense forests has the potential to be manipulated. Planting tracts of forest of sufficient dimensions would reduce connectivity among local rabbit populations, reduce the potential for recolonisation and rescue effects and so increase the probability of success of localised control strategies. Certainly this study shows that the retention of existing tracts of dense forest is an important component of a long term control strategy.

In conclusion, this study has shown the value of a habitat heterogeneity model to test the hypotheses that the heterogeneous distribution of resources and other habitat factors can affect long term connectivity levels among local populations within a regional system. It is important to note that the validity of the assumptions underlying any model can only be assessed with reference to data which reflect the same processes the model describes, and are independent of its construction. As shown here, population genetic data are extremely useful for assessing female (Chapter 2) and male (Chapter 4) levels of interaction among local populations and so provide an excellent means of validation of the model, but do not explain the factors which cause these interaction levels.

The habitat heterogeneity model explained well the pattern of long term connectivity among local rabbit populations within the Mitchell region which has led to the isolation of Verniew and much higher interaction probabilities at sites such as Bowann and Claravale (Chapter 2). The model accounted for most of the variation in the genetic data over a wide range of population parameters (Chapter 2). Confirmation of the rigour of the model was further provided by a more detailed explanation of the genetic characteristics of the Eastern system when the well known

west to east range expansion of the rabbit was modelled (Chapter 3). Not only did the model account for specific genetic characteristics of populations within the Eastern system (for example, high probability of fixation of the A haplotype at Polworth and genetic similarities among a highly connected subset of Eastern system sites), it also showed a high probability of the loss of the B haplotype when the wild rabbit colonised the Mitchell region. All of these characteristics are consistent with the genetic data (Wilson *et al.* 2002). The model therefore gave insight into the past and long term processes which have led to the formation and maintenance of the highly structured Eastern rabbit population system.

Differences in the dispersal characteristics of males and females have the potential to influence connectivity patterns among local populations (Chapter 4). The habitat heterogeneity model showed that Polworth, a highly isolated site for females, is much more accessible to males. In contrast, Verniew is highly isolated for both males and females within the Eastern system. Thus, not only did the model account for female patterns of connectivity within the system but demonstrated that habitat heterogeneity influences male and female patterns of connectivity differently. Once again variation in the appropriate genetic data set was explained well by the model.

The habitat heterogeneity model presented in this study explains not only the factors which have led to the establishment of a distinct Eastern rabbit population system when range expansion is considered, but accounts for over 80% of the variation in genetic data when female and combined male and female dispersal was modelled. The explanation of such a large proportion of the variability in two genetic data sets provides very good evidence that the model is robust and has captured the major processes influencing interactions among local rabbit populations in this system. The habitat heterogeneity model therefore provides a powerful approach to understanding the processes underlying regional dynamics, which highlights its utility as a tool to aid in the management of regional systems.

Recognition that habitat heterogeneity has the potential to influence connectivity levels among local populations in some systems will allow for more efficient and cost effective management programmes to be developed. In the Eastern rabbit population system, identification of relative long term connectivity levels among

sites, for both males and females, should allow for the implementation of appropriate localised control measures at isolated sites and broad scale measures (such as the introduction of RHDV) at more highly connected sites, particularly those sites which show high potential for male interaction and low potential for female interaction.

Connectivity patterns among local populations within a system influence regional dynamics in many ways: the transmission of diseases (Hess 1996), rescue effects which may buffer populations from adverse influences (Brown and Kodric-Brown, 1977) and the potential for recolonisation after extinctions. The determination of connectivity levels is therefore important for management of species, either of pest population or populations which are endangered. For example, although the wild rabbit is a pest species in Australia, the spread of RHDV through its natural range in Spain has caused drastic declines in abundance in many regions, prompting calls for conservation measures to be implemented (Villafuerte *et al.* 1995). The suggestions for population control outlined in this study could be easily adapted in a conservation context, for example to increase connectivity among local populations if appropriate.

Appendix 1: Habitat Heterogeneity Simulation Model

The habitat heterogeneity model simulates site to site dispersal interactions among any number of sites within a population system, with a series of growth and dispersal steps among patches between sites. Growth in each patch is determined by a resource index based on the quality of major resources in the patch. Dispersal can be impeded by habitat factors (eg dense forests), where the size of dispersing propagule is determined by the use of an appropriate dispersal resistance function.

A1.1 Input files

The habitat heterogeneity model requires a number of input files.

1. **Inputs.txt**: Specifies the location of resource files, and includes important data for running the model such as the number of sites to simulate, population growth and dispersal parameters and the number of paths between sites.

2. **Popfile.txt**: Contains the number of sites to test, the number of haplotypes within the system, site names and known haplotype frequencies at the site. This file can be used for the input of haplotype frequencies, and is not used in this version of the Habitat Heterogeneity Simulation Model.

3. **Resource files**: Files which contain a matrix of resource indices. There is a separate file for each resource between each pair of sites. For instance, 1_2.soi contains the soil resource indices for all patches which are intersected by the 5 linear dispersal paths between Bowann and Claravale. Vegetation is ignored (indexed as 1) in all patches which do not contain dense forests. Vegetation resource indices (eg 7_6.veg) were adapted to account for the linear distance a dispersal path travels through dense forest patches when they are encountered (according to the appropriate dispersal resistance function) and to remove growth and dispersal processes from dense forest patches.

A1.2 Output Files

The habitat heterogeneity model outputs a file for each site to site interaction, containing the number of dispersers which reach a site from one other site (eg 1_2.001 records the number of individuals that reach Claravale as a result of dispersal from Bowann). The number of dispersers which have arrived along each dispersal path is recorded in the file separately. Site to site interactions can thus be evaluated separately, or can be combined into a matrix to assess interactions within the system.

A1.3 Simulation Model Code

Comments have been made in bold to clarify sections of the QBasic code. Programmers comments follow an apostrophe and are ignored by the programme.

```
' ------------------------------------------------------------
' Habitat Heterogeneity Simulation Model
'  ------------------------------------------------------------

CLS  'clear screen

'INPUT "Enter input file:", infile$ '--- add for user input of filename
infile$ = "inputs.txt" ' --- automatic select inputs.txt

' ------------------------------------------------------------
' read in input data
' ------------------------------------------------------------

f = FREEFILE
OPEN infile$ FOR INPUT AS #f
LINE INPUT #f, buf$
INPUT #f, d         'dispersal constant
' ------------------------------------------------------------
' read in population file
' ------------------------------------------------------------
g = FREEFILE
OPEN popfile$ FOR INPUT AS #g
LINE INPUT #g, buf$
INPUT #g, nosites    'number of sites
INPUT #g, nohaplos   'number of haplotypes
LINE INPUT #g, buf$
DIM sitename$(nosites)
DIM initfreq(nosites, nohaplos)
```

```
FOR a = 1 TO nosites
 INPUT #g, sitename$(a) 'input sitenames
 FOR b = 1 TO nohaplos
  INPUT #g, initfreq(a, b)  'input initial frequencies
 NEXT b
NEXT a
CLOSE #g
LINE INPUT #f, buf$
INPUT #f, nopaths     'number of paths between sites
LINE INPUT #f, buf$
INPUT #f, pathtodo
LINE INPUT #f, buf$
INPUT #f, datapath$     'output path
datapath$ = RTRIM$(datapath$)
IF RIGHT$(datapath$, 1) <> "\" THEN
 datapath$ = datapath$ + "\"
 END IF
LINE INPUT #f, buf$
INPUT #f, outext$     'output filename
LINE INPUT #f, buf$
INPUT #f, nostest     'number of sites to test
IF nostest > nosites THEN
 PRINT "ERROR: You are trying to test more sites than appear in the population file
"; popfile$
 END
END IF
REDIM stest(nostest)
LINE INPUT #f, buf$
FOR a = 1 TO nostest
 INPUT #f, stest(a)   'array of sites to test
NEXT a
LINE INPUT #f, buf$
INPUT #f, reverse     'is reverse on/off
LINE INPUT #f, buf$
INPUT #f, pntpatch    'print patch details
LINE INPUT #f, buf$
LINE INPUT #f, buf$
INPUT #f, popinc       ' Growth factor
LINE INPUT #f, buf$
INPUT #f, seed      ' Initial population size seed

CLOSE #f


PRINT "Habitat Heterogeneity Model "
PRINT "Initialisation - " + infile$
PRINT "Population     - " + popfile$

PRINT "From -     To -     Iteration -"
```

```
' ---------------------------------------------------------
' work out which to sites to test
' ---------------------------------------------------------

FOR s1a = 1 TO nostest - 1
 FOR s2a = s1a + 1 TO nostest
  FOR rev = 0 TO reverse
   IF rev = 0 THEN
    s1 = s1a
    s2 = s2a
   ELSE
    s1 = s2a
    s2 = s1a
   END IF

   filen$ = LTRIM$(STR$(stest(s1))) + "_" + LTRIM$(STR$(stest(s2)))

   IF pntpatch = 1 THEN
    h = FREEFILE
    OPEN datapath$ + filen$ + ".pop" FOR OUTPUT AS #h
   END IF
   i = FREEFILE
   OPEN datapath$ + filen$ + "." + outext$ FOR OUTPUT AS #i

   '---------------------------------------------------------
   ' determine how many rows of data are in the soil file
   '---------------------------------------------------------
   o = FREEFILE
   OPEN datapath$ + filen$ + ".soi" FOR INPUT AS #o
   cnt = 0
   DO WHILE NOT EOF(o)
    LINE INPUT #o, l$
    IF LTRIM$(l$) <> "" THEN cnt = cnt + 1
   LOOP
   CLOSE #o

   ' ---------------------------------------------------------
   ' read in soil data
   ' ---------------------------------------------------------
   g = FREEFILE
   OPEN datapath$ + filen$ + ".soi" FOR INPUT AS #g
   REDIM soi(cnt, nopaths)
   FOR a = 1 TO cnt
    FOR b = 1 TO nopaths
     INPUT #g, soi(a, b)
    NEXT b
   NEXT a
```

Ensures all site to site interactions are simulated

Arrays to store resource indices

```
CLOSE #g

' ---------------------------------------------------------
' read in veg data
' ---------------------------------------------------------
g = FREEFILE
OPEN datapath$ + filen$ + ".veg" FOR INPUT AS #g
REDIM veg(cnt, nopaths)
FOR a = 1 TO cnt
 FOR b = 1 TO nopaths
  INPUT #g, veg(a, b)
 NEXT b
NEXT a
CLOSE #g


' ---------------------------------------------------------
' read in v1 data
```

A dummy variable which could be used to add additional resource indices for a region if required

```
' ---------------------------------------------------------
g = FREEFILE
OPEN datapath$ + filen$ + ".v1" FOR INPUT AS #g
REDIM v1(cnt, nopaths)
FOR a = 1 TO cnt
 FOR b = 1 TO nopaths
  INPUT #g, v1(a, b)
 NEXT b
NEXT a
CLOSE #g

' ---------------------------------------------------------
' calculate no of patches in each path
```

Necessary since different paths between any two sites may consist of different numbers of habitat patches

```
' ---------------------------------------------------------
REDIM nopatch(nopaths)
FOR a = 1 TO nopaths
 b = 1
 DO
  IF b = cnt THEN
   b = cnt + 1
   EXIT DO
```

```
 END IF
 b = b + 1
 LOOP WHILE soi(b, a) <> 0
 nopatch(a) = b - 1
NEXT a

' ---------------------------------------------------------
' calculate combination matrix
' ---------------------------------------------------------
REDIM COMB(cnt, nopaths)
FOR a = 1 TO cnt
 FOR b = 1 TO nopaths
  COMB(a, b) = soi(a, b) * veg(a, b)
 NEXT b
NEXT a

' ---------------------------------------------------------
' perform single iteration along all paths from x to y
' ---------------------------------------------------------
pathtodo = nopaths
FOR path = 1 TO pathtodo


 LOCATE 7, 8      'print in same place every run
 PRINT LTRIM$(STR$(s1))
 LOCATE 7, 17
 PRINT LTRIM$(STR$(s2))
 LOCATE 7, 33
 PRINT LTRIM$(STR$(path)) + "   " 'print current status

 ' ---------------------------------------------------------
 ' calculate initial patch population
 ' ---------------------------------------------------------

 ppop = INT(popinc * COMB(1, path) * seed)  'Growth

 pop = ppop

 ' ---------------------------------------------------------
 ' calculate dispersal from patch 1
 ' ---------------------------------------------------------
   disp = INT(pop * d)
   p = 1 'patch is 1
```

The resource index for each patch crossed by a dispersal path, incorporating the dispersal resistance function when appropriate

```
  ' ------------------------------------------------------
  'Repeat for remaining patches.
 '------------------------------------------------------
  ' go along all patches from site x to y
  ' ------------------------------------------------------
  FOR p = 2 TO nopatch(path)
    ppop = INT(popinc * COMB(p, path) * disp)
    pop = ppop

   IF pntpatch = 1 THEN

    PRINT #h, filen$ + "," + LTRIM$(STR$(it)) + "," + LTRIM$(STR$(path)) + ","
    + LTRIM$(STR$(p));
    PRINT #h, "," + LTRIM$(STR$(disp))
   END IF

   ' ------------------------------------------------------
   ' print number of dispersers to output file

   ' ------------------------------------------------------
   IF p = nopatch(path) THEN
    PRINT #i, LTRIM$(STR$(path));
    PRINT #i, "," + LTRIM$(STR$(disp))
   END IF

   ' ------------------------------------------------------
   ' calculate dispersers
   ' ------------------------------------------------------
   disp = INT(pop * d)

  NEXT p   ' patch loop
 NEXT path   ' path loop

 IF pntpatch = 1 THEN
  CLOSE #h
 END IF
 CLOSE #i

 NEXT rev  'do reverse
NEXT s2a ' loop to sites
NEXT s1a ' loop from sites
CLOSE
```

Prints details of dispersal into each patch along a site to site dispersal path if required

Prints the number of dispersers into a site when the final patch is encountered

Appendix 2. Range Expansion Model

The basic form of the Range Expansion model is the same as the Habitat Heterogeneity model, but here sites within the population system are colonised from one or more sources, after which these populations potentially interact. During both colonisation and interaction phases, growth and dispersal is affected by the spatial distribution of resources and other habitat factors. In this model however, the haplotype frequencies at the colonising site(s) are included as a model input, and haplotypes are randomly selected during growth and dispersal processes. In this study each iteration of the model consisted of a single colonisation phase (dispersal from the colonising site to each of the remaining sites in the system) and a single interaction phase (interactions among colonised sites), although the model allows for multiple interactions among sites for each colonisation phase. The dispersal path taken during both colonisation and interaction phases is randomly selected.

A2.1 Input Files

Input files are identical to those used in the Habitat Heterogeneity simulation model, except:

(a) the number of colonisations (iterations) to perform is specified in inputs.txt;
(b) the frequencies of each haplotype at the colonising site are input via the population file (popfile.txt). Haplotype frequencies for each haplotype for all other sites are input as 0;
(c) Multiple iterations among sites can be performed for each colonisation phase; and
(d) The size of colonised sites before interaction may be set to a different size than that of the colonising source (in this study, sizes were always set to 100).

A2.2 Output Files

The programme generates two sets of output files: 1) the number of individuals of each haplotype entering a site from all other sites, and the sum of those individuals; and 2) the proportion of the total number of individuals entering the site which carry

each haplotype. These are printed to the files during colonisation and the successive interaction among sites, for all iterations of the model.

A2.3 Simulation Model Code

Comments have been made in bold to clarify sections of the QBasic code.

Programmers comments follow an apostrophe

```
' ------------------------------------------------------------
' Range Expansion Model
' evaluates effect of  habitat heterogeneity on connectivity
' during range expansion 29/8/2001
' ------------------------------------------------------------
CLS  'clear screen
RANDOMIZE TIMER 'randomise by clock

'INPUT "Enter input file:", infile$ '--- add for user input of filename
infile$ = "ipeast.txt" ' --- automatic select inputs.txt

' ------------------------------------------------------------
' read in input data
' ------------------------------------------------------------

f = FREEFILE
OPEN infile$ FOR INPUT AS #f

LINE INPUT #f, buf$
INPUT #f, d          'dispersal constant
LINE INPUT #f, buf$
INPUT #f, popfile$   'population filename

' ------------------------------------------------------------
' read in population file
' ------------------------------------------------------------
g = FREEFILE
OPEN popfile$ FOR INPUT AS #g
LINE INPUT #g, buf$
INPUT #g, nosites    'number of sites
INPUT #g, nohaplos   'number of haplotypes
LINE INPUT #g, buf$
DIM sitename$(nosites)
DIM glefreq(nosites, nohaplos)
DIM initfreq(nosites, nohaplos)
FOR a = 1 TO nosites
 INPUT #g, sitename$(a) 'input sitenames
 FOR b = 1 TO nohaplos
  INPUT #g, glefreq(a, b)  'input initial frequencies
 NEXT b
NEXT a
```

```
CLOSE #g
' ------------------------------------------------------------
' finished reading population file
' ------------------------------------------------------------
LINE INPUT #f, buf$
INPUT #f, glenit   ' colonisation iterator
LINE INPUT #f, buf$
INPUT #f, sysit   'Number of system interactions
LINE INPUT #f, buf$
INPUT #f, nopaths     'number of paths between sites
LINE INPUT #f, buf$
INPUT #f, pathtodo    'path to use 0=random
LINE INPUT #f, buf$
INPUT #f, datapath$     'output path
datapath$ = RTRIM$(datapath$)
IF RIGHT$(datapath$, 1) <> "\" THEN
 datapath$ = datapath$ + "\"
END IF
LINE INPUT #f, buf$
INPUT #f, outext$     'output filename
LINE INPUT #f, buf$
INPUT #f, outext1$
LINE INPUT #f, buf$
INPUT #f, nostest     'number of sites to test
IF nostest > nosites THEN
 PRINT "ERROR: You are trying to test more sites than appear in the population file
"; popfile$
 END
END IF
REDIM stest(nostest)
LINE INPUT #f, buf$
FOR a = 1 TO nostest
 INPUT #f, stest(a)   'array of sites to test
NEXT a
LINE INPUT #f, buf$
INPUT #f, colsite     ' site number of the colonising site
LINE INPUT #f, buf$
INPUT #f, reverse     'is reverse on/off
LINE INPUT #f, buf$
INPUT #f, pntpatch    'print patch details
LINE INPUT #f, buf$
INPUT #f, popinc      ' Growth factor
LINE INPUT #f, buf$
INPUT #f, glepop      ' Initial population seed for colonising source
LINE INPUT #f, buf$
INPUT #f, syspop     'site population size for each iteration


CLOSE #f
```

```
PRINT "Range expansion Model 29/8/2001"
PRINT "Initialisation - " + infile$
PRINT "Population    - " + popfile$
PRINT "From -    To -    Glenit -    Sysit - "

    filen3$ = "num"
    l = FREEFILE
    OPEN datapath$ + filen3$ + "." + "num" FOR OUTPUT AS #l

FOR glen = 1 TO glenit   'Number of introductions from Glenlea

initpath = 0

   filen1$ = "glen" + LTRIM$(STR$(glen))
    j = FREEFILE
    OPEN datapath$ + filen1$ + "." + outext1$ FOR OUTPUT AS #j

    filen2$ = "sys" + LTRIM$(STR$(glen))
    k = FREEFILE
    OPEN datapath$ + filen2$ + "." + outext1$ FOR OUTPUT AS #k


    filen3$ = "disp" + LTRIM$(STR$(glen))
    l = FREEFILE
    OPEN datapath$ + filen3$ + "." + outext1$ FOR OUTPUT AS #l

 REDIM systor(nosites, nohaplos) ' storage for each  eastern system cycle

r = 1

FOR sys = 1 TO sysit 'System cycle loop
```

Uses colonisation site frequencies during colonisation phase, otherwise uses frequencies at sites based on colonised populations

```
 IF sys = 1 THEN
 methpop = glepop       'Glenlea seed for 1st iteration
  FOR a = 1 TO nosites
   FOR b = 1 TO nohaplos
    initfreq(a, b) = glefreq(a, b)
   NEXT b
  NEXT a

  ELSEIF sys <> 1 THEN
```

```
    FOR a = 1 TO nosites  'reiterates frequencies for each subsequent run
    FOR b = 1 TO nohaplos
     initfreq(a, b) = systor(a, b)
     NEXT b
     NEXT a
     methpop = syspop
' ------------------------------------------------------------
' work out which to sites to test
' ------------------------------------------------------------
FOR s1 = 1 TO nostest  'to sites loop


  REDIM hapstor(nosites, nohaplos)' stores numbers of each haplotype into a site

 FOR s2 = 1 TO nostest    'from sites loop

IF s2 = s1 THEN
 s2 = s2 + 1
  IF s2 > nosites THEN EXIT FOR 'exits s2 loop
   END IF
   filen$ = LTRIM$(STR$(stest(s2))) + "_" + LTRIM$(STR$(stest(s1)))

   IF pntpatch = 1 THEN
    h = FREEFILE
    OPEN datapath$ + filen$ + ".pop" + LTRIM$(STR$(sys)) FOR OUTPUT AS #h
   END IF
   i = FREEFILE
   OPEN datapath$ + filen$ + "." + outext$ FOR OUTPUT AS #i

   '-------------------------------------------------------
   ' determine how many rows of data are in the soil file
   '-------------------------------------------------------
   o = FREEFILE
   OPEN datapath$ + filen$ + ".soi" FOR INPUT AS #o
   cnt = 0
   DO WHILE NOT EOF(o)
    LINE INPUT #o, l$
    IF LTRIM$(l$) <> "" THEN cnt = cnt + 1
   LOOP
   CLOSE #o

   ' ------------------------------------------------------------
   ' read in soil data
   ' ------------------------------------------------------------
   g = FREEFILE
   OPEN datapath$ + filen$ + ".soi" FOR INPUT AS #g
   REDIM soi(cnt, nopaths)
   FOR a = 1 TO cnt
    FOR b = 1 TO nopaths
     INPUT #g, soi(a, b)
```

```
 NEXT b
NEXT a
CLOSE #g

' ---------------------------------------------------------
' read in veg data
' ---------------------------------------------------------
g = FREEFILE
OPEN datapath$ + filen$ + ".veg" FOR INPUT AS #g
REDIM veg(cnt, nopaths)
FOR a = 1 TO cnt
 FOR b = 1 TO nopaths
  INPUT #g, veg(a, b)
 NEXT b
NEXT a
CLOSE #g

' ---------------------------------------------------------
' calculate no of patches in each path
' ---------------------------------------------------------
REDIM nopatch(nopaths)
FOR a = 1 TO nopaths
 b = 1
 DO
  IF b = cnt THEN
   b = cnt + 1
   EXIT DO
  END IF
  b = b + 1
 LOOP WHILE soi(b, a) <> 0
 nopatch(a) = b - 1
NEXT a

' ---------------------------------------------------------
' calculate combination matrix
' ---------------------------------------------------------
REDIM COMB(cnt, nopaths)
FOR a = 1 TO cnt
 FOR b = 1 TO nopaths
  COMB(a, b) = soi(a, b) * veg(a, b)
  NEXT b
NEXT a

' ---------------------------------------------------------
' perform x iterations of site x to y
' ---------------------------------------------------------
 LOCATE 7, 8      'print in same place every run
 PRINT LTRIM$(STR$(s2))
 LOCATE 7, 17
 PRINT LTRIM$(STR$(s1))
```

```
   LOCATE 7, 33
   PRINT LTRIM$(STR$(glen))
   LOCATE 7, 46
   PRINT LTRIM$(STR$(sys)) + "   "'print current status


   REDIM hapfreq(nohaplos)

   IF pathtodo = 0 THEN
    path = INT((RND * nopaths) + 1)' select path at random
   ELSE
    path = pathtodo'use path specified in input.txt
   END IF

IF sys = 1 THEN initpath = path

   ' ------------------------------------------------------------
   ' set up initial population based on patch attributes
   ' ------------------------------------------------------------

   ' ------------------------------------------------------------
   ' calculate patch pop
   ' ------------------------------------------------------------
IF sys = 1 THEN

    ppop = INT(popinc * COMB(1, path) * methpop)

   pop = 0

   FOR a = 1 TO nohaplos
    hapfreq(a) = INT(initfreq(stest(s2), a) * ppop)
    pop = pop + hapfreq(a)
   NEXT a

ELSEIF sys <> 1 THEN

 pop = 0
 ppop = INT(popinc * COMB(1, path) * methpop)

 FOR a = 1 TO nohaplos
  hapfreq(a) = distor(s2, a) 'find haplotype freq's in first patch from prev run
 NEXT a
```

If population size is greater or smaller than that based on resources and growth factor (eg due to rounding errors), stochastic increase or decrease

```
FOR a = 1 TO nohaplos  determine size of population
 pop = pop + hapfreq(a)
NEXT a

IF ppop > pop THEN
    IF pop > 0 THEN
     REDIM toadd(nohaplos) 'array for new individuals
     FOR ww = 1 TO nohaplos
      toadd(ww) = 0
     NEXT ww
     FOR a = 1 TO ppop - pop
      rnum = INT((RND * pop) + 1)
      tot = 0
      FOR c = 1 TO nohaplos
       tot = hapfreq(c) + tot
       IF rnum <= tot THEN
        toadd(c) = toadd(c) + 1
        EXIT FOR
       END IF
      NEXT c
     NEXT a
     '-------------------------------------
     ' add new individuals to population
     '-------------------------------------
     pop = 0
     FOR ww = 1 TO nohaplos
      hapfreq(ww) = hapfreq(ww) + toadd(ww)
      pop = pop + hapfreq(ww)
     NEXT ww
    END IF
  END IF

IF pop > ppop THEN
    IF pop > 0 THEN

     FOR a = 1 TO pop - ppop
      rnum = INT((RND * pop) + 1)
      tot = 0
      FOR c = 1 TO nohaplos
       tot = hapfreq(c) + tot
```

```
      IF rnum <= tot THEN
       hapfreq(c) = hapfreq(c) - 1
       pop = pop - 1
       EXIT FOR
      END IF
     NEXT c
    NEXT a
   END IF
 END IF
END IF

 ' ---------------------------------------------------------
 ' calculate dispersal from patch 1
 ' ---------------------------------------------------------
  disp = INT(pop * d)
  p = 1 'patch is 1
 '---------------------------------------------------------
 ' prepare hapfreq of the dispersers into next patch
 '---------------------------------------------------------
  fillto = disp     ' fill to disp
  nodisper = 0
```

Random selection of dispersers from patch population 1

```
 '---------------------------------------------------------
 ' randomly select dispersers from initial population
 '---------------------------------------------------------
 REDIM dishfreq(nohaplos)
 REDIM sthfreq(nohaplos)

 FOR a = 1 TO disp
  rnum = INT((RND * pop) + 1)
  tot = 0
  FOR c = 1 TO nohaplos
   tot = hapfreq(c) + tot
   IF rnum <= tot THEN
    hapfreq(c) = hapfreq(c) - 1
    dishfreq(c) = dishfreq(c) + 1
    pop = pop - 1
    EXIT FOR
   END IF
  NEXT c
  '------------------------------
  ' disperse all individuals
  '------------------------------
  IF a = fillto THEN
   REDIM sthfreq(nohaplos)
   FOR b = 1 TO nohaplos
    sthfreq(b) = dishfreq(b)
    dishfreq(b) = 0
```

```
    NEXT b
   END IF
  NEXT a

  FOR a = 1 TO nohaplos
   hapfreq(a) = sthfreq(a)
   sthfreq(a) = 0
  NEXT a


  ' ---------------------------------------------------------
  ' end of dispersal section
  ' ---------------------------------------------------------

  ' ---------------------------------------------------------
  ' go along all patches from site x to y
  ' ---------------------------------------------------------
  FOR p = 2 TO nopatch(path)


   ' ---------------------------------------------------------
   ' calculate patch population
   ' ---------------------------------------------------------
    ppop = INT(popinc * COMB(p, path) * disp)
```

Put dispersers into site

```
   '-------------------------------------------------
   ' increase incoming to the patch pop
   '-------------------------------------------------

   pop = 0
   FOR a = 1 TO nohaplos
    pop = pop + hapfreq(a)
   NEXT a

' If last patch, calc no of each haplotype entering

 IF p = nopatch(path) THEN
  REDIM hapin(nohaplos)
  FOR a = 1 TO nohaplos
   hapin(a) = 0
  NEXT a
  FOR b = 1 TO nohaplos
   hapin(b) = hapfreq(b)
  NEXT b

 END IF
```

Stochastic population growth

```
IF ppop > pop THEN

IF pop > 0 THEN
 REDIM toadd(nohaplos) 'array for new individuals
 FOR ww = 1 TO nohaplos
  toadd(ww) = 0
 NEXT ww
 FOR a = 1 TO ppop - pop
  rnum = INT((RND * pop) + 1)
  tot = 0
  FOR c = 1 TO nohaplos
   tot = hapfreq(c) + tot
   IF rnum <= tot THEN
    toadd(c) = toadd(c) + 1
    EXIT FOR
   END IF
  NEXT c
 NEXT a
'-------------------------------------
' add new individuals to population
'-------------------------------------
 pop = 0
 FOR ww = 1 TO nohaplos
  hapfreq(ww) = hapfreq(ww) + toadd(ww)
  pop = pop + hapfreq(ww)
 NEXT ww
END IF
ELSEIF ppop < pop THEN

 IF pop > 0 THEN
  FOR a = 1 TO pop - ppop
   rnum = INT((RND * pop) + 1)
   tot = 0
   FOR c = 1 TO nohaplos
    tot = hapfreq(c) + tot
    IF rnum <= tot THEN
     hapfreq(c) = hapfreq(c) - 1
     pop = pop - 1
     EXIT FOR
    END IF
   NEXT c
  NEXT a
 END IF
END IF

     End stochastic population growth
' ------------------------------------------------------------
```

```
' print patch haplotype frequencies if required
' ------------------------------------------------------------
IF pntpatch = 1 THEN
PRINT #h, LTRIM$(STR$(glen)) + "," + LTRIM$(STR$(sys)) + "," +
LTRIM$(STR$(path)) + "," + LTRIM$(STR$(p));
FOR a = 1 TO nohaplos
 PRINT #h, "," + LTRIM$(STR$(hapfreq(a)));
NEXT a
PRINT #h, "," + LTRIM$(STR$(disp))
END IF
' ------------------------------------------------------------
' print haplotype frequencies to output file
' ------------------------------------------------------------

IF p = nopatch(path) THEN
```

Print output for last patch

```
FOR a = 1 TO nohaplos
 hapstor(s2, a) = hapstor(s2, a) + hapin(a)
NEXT a

PRINT #i, LTRIM$(STR$(it));
FOR a = 1 TO nohaplos
 PRINT #i, "," + LTRIM$(STR$(hapin(a)));
NEXT a
PRINT #i, "," + LTRIM$(STR$(disp))
END IF
```

Calculate size of dispersing propagule

```
' ------------------------------------------------------------
' calculate size of dispersing propagule
' ------------------------------------------------------------

disp = INT(pop * d)


IF p <> nopatch(path) THEN 'perform dispersal if not in the last patch


FOR a = 1 TO nohaplos 'reset dispersing haplotypes
 dishfreq(a) = 0
NEXT a
```

Stochastic selection of dispersers

```
FOR a = 1 TO disp
 rnum = INT((RND * pop) + 1)
 tot = 0
 FOR c = 1 TO nohaplos
```

```
      tot = hapfreq(c) + tot
      IF rnum <= tot THEN
       hapfreq(c) = hapfreq(c) - 1
       dishfreq(c) = dishfreq(c) + 1
       pop = pop - 1
       EXIT FOR
      END IF
     NEXT c


      '---------------------------
      ' disperse all individuals
      '----------------------------
      REDIM sthfreq1(nohaplos)
      FOR b = 1 TO nohaplos
       sthfreq(b) = dishfreq(b)
       dishfreq(b) = 0
      NEXT b
     END IF
    NEXT a

    FOR a = 1 TO nohaplos
     hapfreq(a) = sthfreq(a)
     sthfreq(a) = 0
    NEXT a


   ' ------------------------------------------------------------
   ' end of dispersal section
   ' ------------------------------------------------------------


  IF pntpatch = 1 THEN
   CLOSE #h
  END IF
  CLOSE #i

NEXT s2   'loop from sites
```

Calculate numbers and frequencies of individuals that have entered the site from all other sites

```
REDIM temp(nohaplos) 'temp array for frequency  calculation
FOR a = 1 TO nohaplos
 temp(a) = 0
NEXT a
```

```
 FOR a = 1 TO nohaplos
  FOR b = 1 TO nosites
   temp(a) = temp(a) + hapstor(b, a)
  NEXT b
  NEXT a

  IF s1 = colsite THEN ' prevents further interaction from colonising source
     FOR a = 1 TO nohaplos
       temp(a) = 0
   NEXT a
  END IF

  FOR b = 1 TO nohaplos
  distor(s1, b) = temp(b)
  NEXT b

   sum = 0
   x = 0


   FOR a = 1 TO nohaplos 'total number into s1 site
     sum = sum + temp(a)
   NEXT a

IF sum = 0 THEN sum = sum + 1


FOR a = 1 TO nohaplos 'calc frequency of haplotypes
     x = temp(a) / sum
     systor(s1, a) = x
     x = 0
     NEXT a


    PRINT #l, LTRIM$(STR$(glen)) + "," + LTRIM$(STR$(sys)) + "," +
LTRIM$(STR$(path)) + "," + LTRIM$(STR$(s1));
     FOR b = 1 TO nohaplos
     PRINT #l, "," + LTRIM$(STR$(temp(b)));
      NEXT b
     PRINT #l, ""

  NEXT s1 ' loop to sites

   r = r + 1 'Glenlea loop counter
```

Print output files

```
 FOR a = 1 TO nosites
    PRINT #k, LTRIM$(STR$(glen)) + "," + LTRIM$(STR$(path)) + ",";
LTRIM$(STR$(sys)) + "," + LTRIM$(STR$(a));
```

```
  FOR b = 1 TO nohaplos
   PRINT #k, "," + LTRIM$(STR$(systor(a, b)));
  NEXT b
  PRINT #k, ""
  NEXT a

NEXT sys                                                    Interaction loop

  FOR a = 1 TO nostest
    PRINT #j, LTRIM$(STR$(a)) + "," + LTRIM$(STR$(initpath)); 'print site
number
    FOR b = 1 TO nohaplos
    IF b < nohaplos THEN
      PRINT #j, "," + LTRIM$(STR$(systor(a, b)));
       ELSE
     PRINT #j, "," + LTRIM$(STR$(systor(a, b)))
     END IF
   NEXT b
   PRINT ""
   NEXT a


  CLOSE #j
 CLOSE #k
 CLOSE #l
 NEXT glen
  CLOSE #q
CLOSE
```

Appendix 3: Model Application to the Western Rabbit Population System

The habitat heterogeneity model (Appendix 2) was applied to wild rabbit populations in the arid western region using soil classifications (good, intermediate and poor) and soil quality indices (1, 0.61 and 0.31 respectively) as per Chapter 2. Soil patches in the western region were defined using Western Arid Region Land Use Series (WARLUS) parts 1 and 3 (CSIRO). Growth and dispersal indices were also identical to those used in Chapter 2 (7.88 and 0.29 respectively). There were no dense forests in this region.

Six local patch populations in the region were selected to coincide with populations sampled by Fuller (1995, 1996, 1997) (Thurloo, Molesworth, Jiggerboo, Nappa Merrie, Bundoona and Eyre Creek), and dispersal paths between pairs of populations were defined as per Chapter 2. The simulation program was seeded with 100 individuals at each of the selected sites, and relative connectivity indices were calculated (Table A3.1).

Local populations sampled by Fuller (1995) which occurred on the same soil patch were combined for genetic analysis as per Chapter 2 (Thurloo 1, Thurloo 2 and Thurloo Bore; Molesworth and Orient; Jiggerboo and Watts). The mean of pairwise F_{ST} was calculated for each soil patch population (Table A3.2) and regressed against relative connectivity indices as per Chapter 2. Very little of the variation in population genetic data was accounted for by relative connectivity indices (r^2=0.22, p= 0.36).

Table A3.1 Model output matrix: Number of successful colonisers and relative connectivity indices for six sites within the arid Western region.

		Bundoona	Eyre Creek	Jiggerboo	Molesworth	Nappa Merrie	Thurloo	**System to site index**
	Bundoona	0	15500	4805	15500	4805	15500	0.109
	Eyre Creek	15500	0	15500	50000	15500	15500	0.218
Contribution	Jiggerboo	15500	15500	0	15500	15500	15500	0.151
from site	Molesworth	15500	15500	15500	0	15500	15500	0.151
to system	Nappa Merrie	15500	15500	15500	15500	0	15500	0.151
	Thurloo	50000	15500	15500	15500	15500	0	0.218
Site to system index		0.218	0.151	0.130	0.218	0.130	0.151	
Mean relative connectivity index		0.164	0.185	0.141	0.185	0.141	0.185	

Table A3.2 Mean of pairwise F_{ST} estimates and standard errors of the mean (s.e.m) for six sites within the western population system.

Site	**F_{ST}**	**s.e.m**
Bundoona	0.0137	0.017
Eyre Creek	0.0059	0.009
Jiggerboo	0.0137	0.015
Molesworth	0.0573	0.014
Nappa Merrie	0.009	0.008
Thurloo	0.0275	0.016

References

Aars, J., and R. A. Ims. 2000. Population dynamic and genetic consequences of spatial density- dependent dispersal in patchy populations. American Naturalist **155**:252-265.

Adler, F.R., and B. Nuernberger. 1994. Persistence in Patchy Irregular Landscapes. Theoretical Population Biology **45**:41-75.

Ajmone-Marsan, P., A. Valentini, M. Cassandro, G. Vecchiotti-Antaldi, G. Bertoni, and M. Kuiper. 1997. AFLP (TM) markers for DNA fingerprinting in cattle. Animal Genetics **28**:418-426.

Andrewartha, H. G., and L. C. Birch. 1954. The Distribution and Abundance of Animals. University of Chicago Press, Chicago.

Banks, S. C., L. F. Skerratt, and A. C. Taylor. 2002. Female dispersal and relatedness structure in common wombats (*Vombatus ursinus*). Journal of Zoology **256**:389-399.

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

Barlow, N. D. 1994. Predicting the effect of a novel vertebrate biocontrol agent - a model for viral-vectored immunocontraception of New-Zealand possums. Journal of Applied Ecology **31**:454-462.

Barlow, N. D. 2000. The ecological challenge of immunocontraception: editor's introduction. Journal of Applied Ecology **37**:897-902.

Birky, C. W., T. Maruyama, and P. Fuerst. 1983. An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. Genetics **103**:513-527.

Boughton, D. A. 1999. Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. Ecology **80**:2727-2739.

Bowen, Z., and J. Read. 1998. Population and demographic patterns of rabbits (*Oryctolagus cuniculus*) at Roxby Downs in arid South Australia and the influence of rabbit haemorrhagic disease. Wildlife Research **25**:655-662.

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

Brandt, C. A. 1992. Social factors in immigration and emigration. *in* N. C. Stenseth and W. Z. Lidicker, editors. Animal dispersal: small mammals as a model. Chapman and Hall., London.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology **58**:445 – 449.

Caughley, G. 1994. Directions in Conservation Biology. Journal of Animal Ecology **63**:215-244.

Caughley, G., D. Grice, R. Barker, and B. Brown. 1988. The Edge of the Range. Journal of Animal Ecology **57**:771-785.

Chenoweth, S. F., J. M. Hughes, C. P. Keenan, and S. Lavery. 1998. Concordance between dispersal and mitochondrial gene flow: isolation by distance in a tropical teleost, *Lates calcarifer* (Australian barramundi). Heredity **80**:187-197.

Clarke, A. L., B. E. Saether, and E. Roskaft. 1997. Sex biases in avian dispersal: A reappraisal. Oikos **79**:429-438.

Cole, L. C. 1957. Sketches of general and comparative demography. Cold Springs Harbour Symposium, Quantitative Biology **22**:1-15.

Cooke, B. 1977. Factors limiting the distribution of the wild rabbit in Australia. Proceedings of the Ecological Society Australia **10**:113 - 120.

Cooke, B. D. 1974. Food and other resources of the wild rabbit *Oryctolagus cuniculus* (L.). PhD Thesis. University of Adelaide.

Cooke, B. D. 2002. Rabbit haemorrhagic disease: field epidemiology and the management of wild rabbit populations. Revue Scientifique Et Technique De L Office International Des Epizooties **21**:347-358.

Cowan, D. P., and P. J. Garson. 1985. Variations in the social structure of rabbit populations: causes and demographic consequences. Pages 537 – 555 *in* R. M. Sibley and R. H. Smith, editors. Ecological Consequences of Adaptive Behaviour. Blackwell Scientific Publications, Oxford.

Daly, J. C. 1979. The ecological genetics of the European wild rabbit (*Oryctolagus cuniculus* (L.)) in Australia. PhD Thesis. Australian National University.

Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology **48**:333-360.

den Boer, P. J. 1968. Spreading of risk and stabilisation of animal numbers. Acta Biotheoretica **18**:165-194.

den Boer, P. J. 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). Oecologia **4**:1-28.

Department of Natural Resources. 2001. Annual report on weed and pest animal research. Department of Natural Resources, Queensland.

Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology & Evolution **11**:326-330.

Doebeli, M. 1995. Dispersal and Dynamics. Theoretical Population Biology **47**:82-106.

Doebeli, M. 1996. Quantitative genetics and population dynamics. Evolution **50**:532-546.

Doebeli, M. 1997. Genetic variation and the persistence of predator-prey interactions in the Nicholson-Bailey model. Journal of Theoretical Biology **188**:109-120.

Dunsmore, J. D. 1974. The rabbit in subalpine south-eastern Australia. I. Population structure and productivity. Australian Wildlife Research **1**:1 – 16.

Earn, D. J. D., P. Rohani, and B. T. Grenfell. 1998. Persistence, chaos and synchrony in ecology and epidemiology. Proceedings of the Royal Society of London Series B-Biological Sciences **265**:7-10.

Efford, M. 1998. Demographic consequences of sex-biased dispersal in a population of brushtail possums. Journal of Animal Ecology **67**:503-517.

Elton, C. S. 1927. Animal Ecology. Sidgwick & Jackson, London.

Erlich, P. R., and L. C. Birch. 1967. The "balance of nature" and "population control". American Naturalist **101**:97-107.

Fenner, F., and B. Fantini. 1999. Biological Control of Vertebrate Pests: The History of Myxomatosis, An Experiment in Evolution. CABI Publishing, Wallingford.

Ferreras, P. 2001. Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. Biological Conservation **100**:125-136.

Fisher, R. A. 1937. The wave of advance of advantageous genes. Annual Eugenics **7**:355-369.

Fleishman, E., C. Ray, P. Sjogren-Gulve, C. L. Boggs, and D. D. Murphy. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology **16**:706-716.

Fulford, G. R., M. G. Roberts, and J. A. P. Heesterbeek. 2002. The metapopulation dynamics of an infectious disease: Tuberculosis in possums. Theoretical Population Biology **61**:15-29.

Fuller, S. J. 1995. Patterns of differentiation in rabbit populations in arid Eastern Australia. PhD Thesis. Queensland University of Technology, Brisbane.

Fuller, S. J., P. B. Mather, and J. C. Wilson. 1996. Limited genetic differentiation among wild *Oryctolagus cuniculus* L. (rabbit) populations in arid eastern Australia. Heredity **77**:138-145.

Fuller, S. J., J. C. Wilson, and P. B. Mather. 1997. Patterns of differentiation among wild rabbit populations *Oryctolagus cuniculus* L. in arid and semiarid ecosystems of north-eastern Australia. Molecular Ecology **6**:145-153.

Gaines, M. S., and L. R. McClenaghan Jr. 1980. Dispersal in small mammals. Annual review of ecology and systematics **11**:163-196.

Gallowway, R. W., R. H. Gunn, and E. A. Fitzpatrick. 1974. Lands of the Balonne-Maranoa Area. Land Research Series No.34, Queensland. CSIRO, Melbourne.

Gaona, P., P. Ferreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). Ecological Monographs **68**:349-370.

Gause, G. F. 1935. Experimental demonstration of Volterra's periodic oscillation in the numbers of animals. Journal of Experimental Biology **12**:44-48.

Gilpin, M. 1991. The Genetic Effective Size of a Metapopulation. Biological Journal of the Linnean Society **42**:165-175.

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

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour **28**:1140-1162.

Grenfell, B., and J. Harwood. 1997. (Meta)population dynamics of infectious diseases. Trends in Ecology & Evolution **12**:395-399.

Hall, L. S., and K. Myers. 1978. Variations in the microclimate in rabbit warrens in semi-arid New South Wales. Australian Journal of Ecology **3**:187-194.

Halley, J. M., and Y. Iwasa. 1998. Extinction rate of a population under both demographic and environmental stochasticity. Theoretical Population Biology **53**:1-15.

Hanski, I. 1990. Density dependence, regulation and variability in animal populations. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **330**:141-150.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Pages 17-38 *in* M. Gilpin and I. Hanksi, editors. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Hanski, I. 1994. Spatial scale, patchiness and population dynamics on land. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **343**:19-25.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics – brief history and conceptual domain. Biological Journal of the Linnean Society **42**:3-16.

Hanski, I., and M. Gyllenberg. 1993. 2 General metapopulation models and the core-satellite species hypothesis. American Naturalist **142**:17-41.

Hanski, I., and D. Zhang. 1993. Migration, metapopulation dynamics and fugitive co-existence. Journal of Theoretical Biology **163**:491-504.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5 – 26 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego CA.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Pages 89-103 *in* M. Gilpin and I. Hanksi, editors. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

Harrison, S. 1991. Local extinction in a metapopulation context - an empirical-evaluation. Biological Journal of the Linnean Society **42**:73-88.

Harrison, S., and A. Hastings. 1996. Genetic and evolutionary consequences of metapopulation structure. Trends in Ecology and Evolution **11**:180-183.

Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the Bay Checkerspot Butterfly, Euphydryas- *Editha bayensis* - evidence for a metapopulation model. American Naturalist **132**:360-382.

Harrison, S., and J. F. Quinn. 1989. Correlated environments and the persistence of metapopulations. Oikos **56**:293-298.

Hastings, A. 1982. Dynamics of a single species in a spatially varying environment - the stabilizing role of high dispersal rates. Journal of Mathematical Biology **16**:49-55.

Hastings, A. 1991. Structured models of metapopulation dynamics. Biological Journal of the Linnean Society **42**:57-71.

Hastings, A., and S. Harrison. 1994. Metapopulation dynamics and genetics. Annual Review of Ecology and Systematics **25**:167-188.

Hedrick, P. W. 1986. Genetic polymorphism in heterogeneous environments: a decade later. Annual Review of Ecology and Systematics **17**:535-566.

Hedrick, P. W., and M. Gilpin. 1997. Genetic effective size of a metapopulation. Pages 166-181 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation Biology. Ecology, Genetics, and Evolution. Academic Press, San Diego.

Hengeveld, R. 1989. Dynamics of Biological Invasions. Chapman and Hall, New York.

Hess, G. R. 1996. Linking extinction to connectivity and habitat destruction in metapopulation models. American Naturalist **148**:226-236.

Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society **58**:247-276.

Hill, J. K., C. D. Thomas, and O. T. Lewis. 1996. Effects of habitat size and isolation on dispersal by *Hesperia comma* butterflies: Implications for metapopulation structure. Journal of Animal Ecology **65**:725-735.

Hill, M. F., A. Hastings, and L. W. Botsford. 2002. The effects of small dispersal rates on extinction times in structured metapopulation models. American Naturalist **160**:389-402.

Hof, J., and C. H. Flather. 1996. Accounting for connectivity and spatial correlation in the optimal placement of wildlife habitat. Ecological Modelling **88**:143-155.

Holyoak, M., and S. P. Lawler. 1996. The role of dispersal in predator-prey metapopulation dynamics. Journal of Animal Ecology **65**:640-652.

Hone, J. 1999. On rate of increase (r): patterns of variation in Australian mammals and the implications for wildlife management. Journal of Applied Ecology **36**:709-718.

Hood, G. M., P. Chesson, and R. P. Pech. 2000. Biological control using sterilizing viruses: host suppression and competition between viruses in nonspatial models. Journal of Applied Ecology **37**:914-925.

Huffaker, C. B. 1958. Experimental studies of predation: Dispersal factors and predator-prey oscillations. Hilgardia **27**:343-383.

Ibrahim, K. M., R. A. Nichols, and G. M. Hewitt. 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. Heredity **77**:282-291.

Ims, R. A., and H. P. Andreassen. 1999. Effects of experimental habitat fragmentation and connectivity on root vole demography. Journal of Animal Ecology **68**:839-852.

Ims, R. A., and N. G. Yoccoz. 1997. Studying transfer processes in metapopulations: emigration, migration and colonisation. Pages 247-265 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego.

Ji, W., S. D. Sarre, N. Aitken, R. K. S. Hankin, and M. N. Clout. 2001. Sex-biased dispersal and a density-independent mating system in the Australian brushtail possum, as revealed by minisatellite DNA profiling. Molecular Ecology **10**:1527-1537.

Johnson, C. N. 1986. Sex-Biased Philopatry and Dispersal in Mammals. Oecologia **69**:626-627.

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

Keyghobadi, N., J. Roland, and C. Strobeck. 1999. Influence of landscape on the population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). Molecular Ecology **8**:1481-1495.

Kimura, M., and W. H. Weiss. 1964. The stepping stone model of genetic structure and the decrease of genetic correlation with distance. Genetics **49**:561-576.

Kozakiewicz, M. 1993. Habitat isolation and ecological barriers - the effect on small mammal populations and communities. Acta Theriologica **38**:1-30.

Krohne, D. T., and A. B. Burgin. 1987. Relative success of residents and immigrants in *Peromyscus leucopus*. Holartic Ecology **10**:196-200.

Kunkele, J., and D. vonHolst. 1996. Natal dispersal in the European wild rabbit. Animal Behaviour **51**:1047-1059.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist **142**:911-927.

Lawton, J. H., G. Daily, and I. Newton. 1994. Population-dynamic principles. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **344**:61-68.

Le Corre, V., and A. Kremer. 1998. Cumulative effects of founding events during colonisation on genetic diversity and differentiation in an island and stepping-stone model. Journal of Evolutionary Biology **11**:495-512.

Lemel, J., S. Belichon, J. Clobert, and M. E. Hochberg. 1997. The evolution of dispersal in a two-patch system: some consequences of differences between migrants and residents. Evolutionary Ecology **11**:613-629.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237-240

Levins, R. 1970. Extinctions. Pages 77 – 107 *in* M. Gerstenhaber, editor. Some Mathematical Problems in Biology. American Mathematical Society, Providence.

Lidicker, W. Z. 1975. The role of dispersal in the demography of small mammals. Pages 103 – 128 *in* K. Petrusewicz, F. B. Golley, and L. Ryszkowski, editors. Small mammals: productivity and dynamics of populations. Cambridge University Press, Cambridge.

Lidicker, W. Z., and N. C. Stenseth. 1992. To disperse or not to disperse: who does it and why? Pages 21-36 *in* N. C. Stenseth and W. Z. Lidicker, editors. Animal dispersal: small mammals as a model. Chapman and Hall, London.

Lindstrom, J., and H. Kokko. 1998. Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. Proceedings of the Royal Society of London Series B-Biological Sciences **265**:483-488.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Mariette, S., V. Le Corre, F. Austerlitz, and A. Kremer. 2002. Sampling within the genome for measuring within-population diversity: trade-offs between markers. Molecular Ecology **11**:1145-1156.

Massot, M., J. Clobert, J. Lecomte, and R. Barbault. 1994. Incumbent advantage in common lizards and their colonising ability. Journal of Animal Ecology **63**:431-440.

May, R. M. 1986. The Croonian Lecture, 1985 - When 2 and 2 do not make 4 - nonlinear phenomena in ecology. Proceedings of the Royal Society of London Series B-Biological Sciences **228**:241-266.

McCallum, H. 1996. Immunocontraception for wildlife population control. Trends in Ecology & Evolution **11**:491-493.

Mollison, D. 1977. Spatial contact models for ecological and epidemic spread. Journal of the Royal Statistical Society Series B- Methodological **39**:283-326.

Moritz, C. 1994. Applications of mitochondrial DNA analysis in conservation: a critical review. Molecular Ecology **3**:401-411.

Mueller, U. G., and L. L. Wolfenbarger. 1999. AFLP genotyping and fingerprinting. Trends in Ecology & Evolution **14**:389-394.

Murdoch, W. W. 1994. Population Regulation in Theory and Practice - the Robert-H- Macarthur-Award-Lecture Presented August 1991 in San-Antonio, Texas, USA. Ecology **75**:271-287.

Murdoch, W. W., S. L. Swarbrick, R. F. Luck, S. Walde, and D. S. Yu. 1996. Refuge dynamics and metapopulation dynamics: an experimental test. The American Naturalist **147**:424-444.

Mutze, G., B. Cooke, and P. Alexander. 1998. The initial impact of rabbit hemorrhagic disease on European rabbit populations in South Australia. Journal of Wildlife Diseases **34**:221-227.

Myers, K. 1958. Further observations on the use of field enclosures for the study of the wild rabbit *Oryctolagus cuniculus* (L.). CSIRO Wildlife Research **3**:40-49.

Myers, K. 1970. The rabbit in Australia. Pages 478 – 506 *in* P. J. d. Boer and G. R. Gradwell, editors. Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations. Centre for Agricultural Publishing and Documentation, Wageningen.

Myers, K., and W. E. Poole. 1963. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. V. Population dynamics. CSIRO Wildlife Research **9**:138 –143.

Myers, K., and B. S. Parker. 1965. A study of the biology of the wild rabbit in climatically different regions of eastern Australia. I. Patterns of distribution. CSIRO Wildlife Research **10**:1 – 32.

Myers, K., and B. S. Parker. 1975a. Effect of severe drought on rabbit numbers and distribution in a refuge area in semi-arid north-western New South Wales. Australian Wildlife Research **2**:103-120.

Myers, K., and P. B. S. 1975b. A study of the biology of the wild rabbit in climatically different regions of eastern Australia. VI. Changes in numbers and distribution related to climate and land systems in semi-arid North-Western New South Wales. Australian Wildlife Research **2**:11-32.

Myers, K., I. Parer, D. Wood, and B. D. Cooke. 1994. The rabbit in Australia. Pages 108 – 157 *in* H. V. Thompson and C. M. King, editors. The European Rabbit: the history and biology of a successful coloniser. Oxford University Press, New York.

Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution **29**:1-10.

Neigel, J. E. 1997. A comparison of alternative strategies for estimating gene flow from genetic markers. Annual Review of Ecology and Systematics **28**:105-128.

Nicholson, A. J. 1933. The balance of animal populations. Journal of Animal Ecology **2**:133-178.

Palmqvist, E., and P. Lundberg. 1998. Population extinctions in correlated environments. Oikos **83**:359-367.

Parer, I. 1982. Dispersal of the wild rabbit *Oryctolagus cuniculus*, at Urana in New South Wales. Australian Wildlife Research **9**:427–441.

Parer, I. 1987. Factors influencing the distribution and abundance of rabbits (*Oryctolagus cuniculus*) in Queensland. Proceedings of the Royal Society of Queensland **98**:73-82.

Parker, B. S., L. S. Hall, K. Myers, and P. J. Fullagar. 1976. The distribution of rabbit warrens at Mitchell, Queensland, in relation to soil and vegetation characteristics. Australian Wildlife Research **3**:129 – 148.

Parer, I., and J. A. Libke. 1985. Distribution of rabbit (*Oryctolagus cuniculus*) warrens in relation to soil type. Australian Wildlife Research:387 – 405.

Parer, I., and P. J. Fullagar. 1986. Biology of rabbits, *Oryctolagus cuniculus*, in subtropical Queensland. Australian Wildlife Research **13**:545-557.

Peltonen, A., and I. Hanski. 1991. Patterns of island occupancy explained by colonisation and extinction rates in shrews. Ecology **72**:1698-1708.

Petit, E., F. Balloux, and L. Excoffier. 2002. Mammalian population genetics: why not Y? Trends in Ecology & Evolution **17**:28-33.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist **132**:757-785.

Prugnolle, F., and T. de Meeus. 2002. Inferring sex-biased dispersal from population genetic tools: a review. Heredity **88**:161-165.

Pulliam, H. R. 1988. Sources, Sinks, and Population Regulation. American Naturalist **132**:652-661.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat Selection - a landscape perspective on population-dynamics. American Naturalist **137**:S50-S66.

Pulliam, H. R., J. B. Dunning, and J. G. Liu. 1992. Population-dynamics in complex landscapes - a case-study. Ecological Applications **2**:165-177.

Pusey, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology and Evolution **2**:295-299.

Ranta, E., V. Kaitala, and J. Lindstrom. 1999. Sex in space: population dynamic consequences. Proceedings of the Royal Society of London Series B-Biological Sciences **266**:1155-1160.

Ratcliffe, F. N. 1959. The rabbit in Australia. Pages 545-564 *in* Biogeography and Ecology in Australia: Monographica Biologica **8**. A. Keast, R. L. Crocker and C. S. Christian, editors. Junk, The Hague.

Richardson, B. J., R. A.Hayes, S. H.Wheeler and M. R. Yardin. 2002. Social structures, genetic structures and dispersal strategies in Australian rabbit (*Oryctolagus cuniculus*) populations. Behavioral Ecology and Sociobiology **51**:113-121.

Rogers, P. M., C. P. Arthur, and R. C. Soriguer. 1994. The rabbit in continental Europe. Pages 22 – 63 *in* H. V. Thompson and C. M. King, editors. The European Rabbit: the history and biology of a successful coloniser. Oxford University Press, New York.

Rohani, P., R. M. May, and M. P. Hassell. 1996. Metapopulations and equilibrium stability: the effects of spatial structure. Journal of Theoretical Biology **181**:97-109.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: Effects of landscape and population size. Ecology **81**:1642-1653.

Rural Lands Protection Board. 1987. Rabbits and their control in Queensland. Queensland Government, Queensland.

Ruxton, G. D. 1995. Population models with sexual reproduction show a reduced propensity to exhibit chaos. Journal of Theoretical Biology **175**:595-601.

Saint, K. M., N. French, and P. Kerr. 2001. Genetic variation in Australian isolates of myxoma virus: an evolutionary and epidemiological study. Archives of Virology **146**:1105-1123.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32**:305-332.

Sato, K., H. Matsuda, and A. Sasaki. 1994. Pathogen invasion and host extinction in lattice structured populations. Journal of Mathematical Biology **32**:251-268.

Saunders, G., J. McIlroy, M. Berghout, B. Kay, E. Gifford, R. Perry, and R. Van De Ven. 2002. The effects of induced sterility on the territorial behaviour and survival of foxes. Journal of Applied Ecology **39**:56-66.

Schmitt, T., and A. Seitz. 2002. Influence of habitat fragmentation on the genetic structure of *Polyommatus coridon* (Lepidoptera : Lycaenidae): implications for conservation. Biological Conservation **107**:291-297.

Schneider, S., D. Roessli, and L. Excoffier. 2000. Arlequin 2.0. A software for population genetic data analysis. Genetics and Biometry Laboratory, University of Geneva, Switzerland.

Schoener, T. W. 1991. Extinction and the nature of the metapopulation: a case system. Acta Oecologica **12**:53-75.

Skellam, T. G. 1951. Random dispersal in theoretical populations. Biometrika **38**:196 - 218.

Slatkin, M. 1985. Gene flow in natural populations. Annual Review of Ecology and Systematics **16**:393-430.

Slatkin, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution **47**:264-279.

Slatkin, M. 1994. Gene flow and population structure. Pages 3-17 *in* L. A. Real, editor. Ecological Genetics. Princeton Univ. Press, Princeton, NJ.

Smyth, R. E., B. D. Cooke, and A. E. Newsome. 1997. The spread of rabbit calicivirus in relation to environmental factors. Resource Futures and Vertebrate Pests Programs. CSIRO Wildlife and Ecology, Canberra.

Soriguer, R. C., and P. M. Rogers. 1981. The European wild rabbit in Mediterranean Spain. Pages 600–613 *in* K. Myers and C. D. McInnes, editors. Proceedings of the World Lagomorph Conference 1979. University of Guelph, Ontario.

Stacey, P. B., V. A. Johnson, and M. L. Taper. 1997. Migration within metapopulations: the impact upon local populations. Pages 267 – 291 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego CA.

Stenseth, N. C. 1981. The importance of population dynamics in heterogenous landscapes: management of vertebrate pests and some other animals. Agro-Ecosystems **7**:187-211.

Stodart, E., and I. Parer. 1988. Colonisation of Australia by the rabbit. CSIRO, Australia.

Surridge, A. K., K. M. Ibrahim, D. J. Bell, N. J. Webb, C. Rico, and G. M. Hewitt. 1999. Fine-scale genetic structuring in a natural population of European wild rabbits (*Oryctolagus cuniculus*). Molecular Ecology **8**:299-307.

Tabachnik, B. G., and L. S. Fidell. 1996. Using multivariate statistics, 3rd edition. HarperCollins, New York.

Thomas, C. D., M. C. Singer, and D. A. Boughton. 1996. Catastrophic extinction of population sources in a butterfly metapopulation. American Naturalist **148**:957-975.

Thomas, C.D., and W.E. Kunin. 1999. The spatial structure of populations. Journal of Animal Ecology **68**: 647-657.

Trout, R. C., and G. C. Smith. 1995. The reproductive productivity of the wild rabbit (*Oryctolagus cuniculus*) in southern England on sites with different soils. Journal of Zoology **237**:411-422.

van den Bosch, F., J. C. Zadoks, and J. A. J. Metz. 1988. Focus expansion in plant disease. II. Realistic parameter-sparse models. Phytopathology **78**:59-64.

Villafuerte, R., C. Calvete, J. C. Blanco, and J. Lucientes. 1995. Incidence of viral hemorrhagic disease in wild rabbit populations in Spain. Mammalia **59**:651-659.

Webb, N. J., K. M. Ibrahim, D. J. Bell, and G. M. Hewitt. 1995. Natal dispersal and genetic structure in a population of the European wild rabbit (*Oryctolagus cuniculus*). Molecular Ecology **4**:239-247.

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

Williams, C. K., I. Parer, B. J. Coman, J. Burley, and M. L. Braysher. 1995. Managing Vertebrate Pests: Rabbits. Bureau of Resource Sciences/CSIRO Division of Wildlife and Ecology. Australian Government Publishing Service, Canberra.

Wilson, G., N. Dexter, P. O'Brien, and M. Bomford. 1992. European wild rabbit (*Oryctolagus cuniculus*). Pages 8-13 *in* Pest Animals in Australia. Bureau of Rural Resources. Kangaroo Press, Australia.

Wilson, J. C., S. J. Fuller, and P. B. Mather. 2002. Formation and maintenance of discrete wild rabbit (*Oryctolagus cuniculus*) population systems in arid Australia: Habitat heterogeneity and management implications. Austral Ecology **27**:183-191.

Wolff, J. O. 1994. More on juvenile dispersal in mammals. Oikos **71**:349-352.

Wolff, J. O., and J. H. Plissner. 1998. Sex biases in avian natal dispersal: an extension of the mammalian model. Oikos **83**:327-330.

Wood, D. H. 1980. Demography of a rabbit population in an arid region of New-South-Wales Australia. Journal of Animal Ecology **49**:55-79.

Wright, S. 1931. Evolution in mendelian populations. Genetics **16**:97-159.

Wright, S. 1943. Isolation by distance. Genetics **28**:114-138.

Wright, S. 1951. The genetical structure of populations. Annals of Eugenics **15**:323-354.

Wu, J. G., J. L. Vankat, and Y. Barlas. 1993. Effects of patch connectivity and arrangement on animal metapopulation dynamics - a simulation study. Ecological Modelling **65**:221-254.