

7507556444



# **CONSERVATION BY SIMULATION: AN INDIVIDUAL-BASED SPATIALLY EXPLICIT MODEL TO SIMULATE POPULATION DYNAMICS IN FRAGMENTED HABITAT**

**Thesis submitted in partial fulfilment for the degree of  
Doctor of Philosophy at the University of Leicester**

**Jolyon Alderman**

**April 2005**

UMI Number: U195630

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI U195630

Published by ProQuest LLC 2013. Copyright in the Dissertation held by the Author.  
Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against  
unauthorized copying under Title 17, United States Code.



ProQuest LLC  
789 East Eisenhower Parkway  
P.O. Box 1346  
Ann Arbor, MI 48106-1346

## ABSTRACT

### CONSERVATION BY SIMULATION: AN INDIVIDUAL-BASED SPATIALLY EXPLICIT MODEL TO SIMULATE POPULATION DYNAMICS IN FRAGMENTED HABITAT

Jolyon Alderman

This thesis describes PatchMapper, a model combining a population simulator based on individual behaviour, with a spatially explicit representation of a landscape. To investigate the robustness of the technique, representatives of three major taxa were modelled: the nuthatch (*Sitta europaea* L.), the white-footed mouse (*Peromyscus leucopus* Rafinesque) and the black hairstreak (*Satyrrium pruni* L.). For the nuthatch and white-footed mouse, the performance of PatchMapper was compared with published models of the same species, but using different approaches, including, for the nuthatch, a comparison against observed numbers in a real landscape. To investigate the behaviour of the model, a sensitivity analysis was also undertaken.

Written in Java, for portability, the model enables the user to select demographic and behavioural parameters via an interactive interface and includes a real-time (computer) display of the position of individuals during the simulation. Novel aspects of the model include perceptual range and field-of-view. Internally generated neutral landscapes can be used for modelling general cases, with imported digitised landscapes enabling specific study areas to be modelled. Habitat area and habitat quality dynamics can also be modelled. Dispersal flow diagrams can be generated, providing a visual explanation of the effects of landscape changes on inter-patch dispersal paths and populations in target patches.

Performance compared well with published models, predicting a feasible match with observed numbers of nuthatches in the real landscape. Revealing predictable and realistic responses, the sensitivity analysis revealed that the model coding was valid. The value of specific case studies was illustrated, along with the dangers of relying on intuition when evaluating the response of species to habitat fragmentation. The individual-based SEPM approach was found to be best suited to the modelling of univoltine territorial species (such as nuthatch), with a single dispersal phase between fledging and territorial establishment. When demonstrating the model, the visual outputs proved particularly effective. Providing a set of features not seen in published models and enabling modelling at both local and landscape scales, PatchMapper is offered as a prediction tool for those engaged in activities such as biodiversity conservation and habitat management.

Word count: 33,000

## ACKNOWLEDGMENTS

I hereby acknowledge the following contributors:

My supervisory team: Professor Phil Picton and Doctors Duncan McCollin and Robin Crockett of University College Northampton, for their guidance throughout.

Dr. Shelley Hinsley of the Centre for Ecology and Hydrology, Monks Wood, for guidance in drafting papers for publication.

Paul Malcolm of the Northamptonshire Forest District of Forest Enterprise, for supplying digitised landscapes of the Monks Wood area. Also, for a guided tour of the Forestry Commission's GIS: an example of how a computer system should be implemented.

Paul Burrows, for permission to use his photograph of a nuthatch, as part of my presentation to the International Association of Landscape Ecologists (UK chapter), 2004 annual conference.



# CONTENTS

<b>List of Figures and Tables .....</b>	<b>xi</b>
 <b>1. Introduction .....</b>	 <b>1</b>
1.1 Acknowledgement of the Decline in Biodiversity .....	1
1.2 Modelling: a Weapon in the Fight against the Decline in Biodiversity...	2
1.3 Aims and Objectives .....	4
1.4 Thesis Structure .....	5
 <b>2. Spatially Explicit Population Modelling .....</b>	 <b>6</b>
2.1 Introduction .....	6
2.2 Population Ecology Modelling .....	6
2.2.1 Introduction .....	6
2.2.2 Population Ecology Model Classifications .....	7
2.3 Landscape Modelling .....	8
2.3.1 Introduction .....	8
2.3.2 Modelling with Neutral Landscapes .....	9
2.3.3 Multiple Habitat Types .....	10
2.3.4 Landscape Dynamics .....	11
2.3.5 Landscape Transformation Algorithms .....	13
2.4 Species Modelling .....	15
2.4.1 Introduction .....	15
2.4.2 When is a Metapopulation not a Metapopulation? .....	15
2.4.3 The 'Levins' Model .....	17
2.4.4 Single vs. Multiple Species Modelling .....	18
2.4.5 Dispersal Rules .....	19
2.4.6 Dispersal Mortality .....	20
2.4.7 Perceptual Range .....	21

---

<b>2.5 Problems with Grid-Based SEPMs .....</b>	<b>22</b>
2.5.1 Introduction .....	22
2.5.2 Scale .....	24
<b>2.6 Features Commonly Included in Existing SEPMs .....</b>	<b>26</b>
2.6.1 Introduction .....	26
2.6.2 Common Characteristics and Uses .....	26
2.6.2.1 A Survey of Population Ecology Models .....	26
2.6.2.2 A Survey of SEPMs .....	27
2.6.2.3 Commonly Used Landscape Resolutions .....	28
2.6.2.4 Model Survey Summary .....	29
<b>2.7 Summary .....</b>	<b>29</b>
 <b>3. Model Framework .....</b>	 <b>31</b>
3.1 Introduction .....	31
3.2 Basic Principles .....	31
3.3 Model Structure .....	33
3.4 Overall Simulation Process .....	34
3.5 User Screens .....	36
3.6 Landscape Modelling .....	37
3.6.1 Introduction .....	37
3.6.2 Internally Generated Landscapes .....	38
3.6.3 Imported Landscapes .....	39
3.6.4 Modelling Habitat Quality .....	40
3.6.5 Modelling Landscape Dynamics .....	41
3.6.5.1 Internal Landscape Transformation Algorithm .....	41
3.6.5.2 Landscape Transformation by Controlled Importation .....	42
3.7 Species Modelling .....	44
3.7.1 Introduction .....	44
3.7.2 Modelling Immigration and Perceptual Range .....	46
3.7.3 Multi-Species Modelling .....	47

<b>3.8 Model Outputs .....</b>	<b>48</b>
3.8.1 Introduction .....	48
3.8.2 Real-Time (Computer) Display .....	48
3.8.3 Landscape Pattern Metrics and Population Demographics .....	49
3.8.4 Recording Patch Demographics .....	51
3.8.5 Recording Dispersal Flow Paths .....	53
<b>3.9 Summary .....</b>	<b>53</b>
 <b>4. Species Modelling .....</b>	 <b>55</b>
4.1 Introduction .....	55
4.2 Modelling the Nuthatch .....	55
4.2.1 Introduction .....	55
4.2.2 Lifecycle Stages and Parameters .....	57
4.2.3 Movement Rules .....	59
4.2.4 Inter-Patch Movement .....	60
4.2.4.1 Basic Principles .....	60
4.2.4.2 Correlated Random Walk .....	61
4.2.4.3 Dispersal Mortality .....	62
4.2.4.4 Perceptual Range .....	62
4.2.4.5 Field-of-View .....	64
4.2.5 Intra-Patch Movement .....	65
4.2.6 Landscape and Territory Modelling .....	66
4.3 Nuthatch Model Application and Performance Comparison .....	68
4.3.1 Introduction .....	68
4.3.2 The Study Area .....	69
4.3.3 Methods .....	71
4.3.3.1 Introduction .....	71
4.3.3.2 Model Comparison .....	72
4.3.3.3 Population Viability .....	73
4.3.4 Results .....	75
4.3.4.1 Model Comparison .....	75
4.3.4.2 Population Viability .....	77
4.3.5 Discussion .....	79

<b>4.4 Modelling the White-Footed Mouse .....</b>	<b>82</b>
4.4.1 Introduction .....	82
4.4.2 Lifecycle Stages and Parameters .....	84
4.4.3 Territory Modelling .....	86
4.4.4 Modelling Dispersal .....	87
4.4.4.1 Inter-Patch Dispersal .....	87
4.4.4.2 Intra-Patch Dispersal .....	88
4.4.5 A Comparison with two Published Models .....	89
4.4.5.1 Introduction .....	89
4.4.5.2 Landscape Modelling .....	91
4.4.5.3 Comparison Tests .....	94
4.4.5.4 Results .....	94
4.4.5.5 Model Comparison Results Discussion .....	95
<b>4.5 Modelling the Black Hairstreak .....</b>	<b>96</b>
4.5.1 Introduction .....	96
4.5.2 Lifecycle Stages and Parameters .....	97
4.5.2.1 Modelling the Lifecycle .....	97
4.5.2.2 Dispersal Modelling .....	100
4.5.2.3 Modelling Local-Scale Dispersal .....	100
4.5.2.4 Modelling Landscape-Scale Dispersal .....	101
4.5.3 Habitat Modelling .....	101
4.5.3.1 Habitat Management Schemes .....	101
4.5.3.2 Modelling Habitat Ageing and Management Schemes .....	102
4.5.3.3 Modelling Habitat at the Landscape Scale .....	102
4.5.4 Habitat Management Scheme Comparisons .....	103
4.5.4.1 Introduction .....	103
4.5.4.2 Habitat Management Schemes .....	103
4.5.4.3 Results .....	105
4.5.4.4 Habitat Management Schemes Discussion .....	106
<b>4.6 Chapter Summary .....</b>	<b>108</b>
 <b>5. Sensitivity Analyses and Discussion .....</b>	 <b>109</b>
<b>5.1 Introduction .....</b>	<b>109</b>
<b>5.2 Nuthatch Model Sensitivity Analyses .....</b>	<b>109</b>
5.2.1 Introduction .....	109
5.2.2 Demographic Sensitivity Analyses .....	110
5.2.3 Immigration Direction .....	112
5.2.4 Perceptual Range .....	113
5.2.4.1 Perceptual Range for the General Case .....	114
5.2.4.2 Perceptual Range for a Specific Case .....	115
5.2.5 Immigration and Perceptual Range .....	116
5.2.6 Field-of-View .....	116

<b>5.3 Nuthatch Model Sensitivity Analysis Results .....</b>	<b>117</b>
5.3.1 Demographic Sensitivity Analysis .....	117
5.3.2 Immigration Direction .....	122
5.3.3 Perceptual Range .....	124
5.3.3.1 Results for the General Case .....	124
5.3.3.2 Results for the Specific Case .....	125
5.3.3.3 Immigration and Perceptual Range .....	130
5.3.4 Field-of-View .....	131
<b>5.4 Nuthatch Model Sensitivity Analysis Discussion .....</b>	<b>134</b>
5.4.1 Demographic Sensitivity Analysis .....	134
5.4.2 Habitat Surveys .....	135
5.4.3 Immigration Direction and Field-of-View .....	138
5.4.4 Perceptual Range .....	139
5.4.4.1 The Case for Dispersal Flow Diagrams .....	140
5.4.4.2 Dispersal Flow Diagram Summary .....	146
<b>5.5 White-Footed Mouse Model Sensitivity Analysis .....</b>	<b>147</b>
5.5.1 Introduction .....	147
5.5.2 The Analyses .....	148
5.5.2.1 Demographic Sensitivity Analyses .....	148
5.5.2.2 Landscape Related Sensitivity Analyses .....	148
5.5.3 Results .....	149
5.5.3.1 Demographic Sensitivity Analyses .....	149
5.5.3.2 Landscape Related Sensitivity Analyses .....	153
5.5.4 White-Footed Mouse Model Sensitivity Analysis Discussion .....	156
<b>5.6 Black Hairstreak Model Sensitivity Analysis .....</b>	<b>157</b>
5.6.1 Introduction .....	157
5.6.2 Results .....	158
5.6.3 Black Hairstreak Model Sensitivity Analysis Discussion .....	162
<b>5.7 Chapter Summary .....</b>	<b>163</b>
 <b>6. Summary and Conclusions .....</b>	 <b>164</b>
6.1 Introduction .....	164
6.2 Summary and Discussions of the Main Findings .....	165
6.2.1 General Findings .....	165
6.2.2 Specific Findings from the Nuthatch Model .....	166
6.2.3 Species Modelling .....	170
6.2.4 The Visual Aspect .....	171
6.2.5 Potential Model Artefacts .....	171
6.3 Potential Applications .....	172

<b>6.4 Conclusions and Future Research Directions .....</b>	<b>173</b>
6.4.1 Conclusions .....	173
6.4.2 Future Research Directions .....	174
 <b>Appendices .....</b>	 <b>176</b>
<b>A Major Milestones .....</b>	<b>177</b>
<b>B Papers .....</b>	<b>179</b>
B.1 Simulating Population Viability .....	180
B.2 Modelling the effects of dispersal and landscape configuration .....	190
<b>C Survey Results .....</b>	<b>213</b>
C.1 Population Ecology Models .....	214
C.2 Published SEPMs .....	217
C.3 Commonly Used Landscape Resolutions .....	223
C.4 Tree Diameters .....	226
<b>D Multi-Species Modelling .....</b>	<b>227</b>
D.1 Introduction .....	227
D.2 The Example .....	227
<b>E Spatial Quantification .....</b>	<b>229</b>
E.1 Introduction .....	229
E.2 Spatial Quantification .....	229
E.3 Commonly Used Landscape Pattern Metrics .....	232
<b>F The Principles of Java .....</b>	<b>234</b>
<b>G Program Structure .....</b>	<b>236</b>
<b>G.1 Population Lattice Bit-Fields .....</b>	<b>237</b>
G.1.1 Introduction .....	237
G.1.2 The Nuthatch .....	237
G.1.3 The White-Footed Mouse .....	237
G.1.4 The Black Hairstreak .....	237
<b>G.2 Habitat and Quality File Formats .....</b>	<b>243</b>
G.2.1 Introduction .....	243
G.2.2 Habitat Landscape File Format .....	243
G.2.3 Quality Landscape File Format .....	244
<b>H Habitat and Quality Modelling .....</b>	<b>245</b>
H.1 Introduction .....	245
H.2 Methods .....	245
H.3 Results .....	246
H.4 Discussion .....	247

---

<b>I User Guide .....</b>	<b>248</b>
I.1 Introduction .....	248
I.2 Model Screen .....	248
I.2.1 Generate Sub-Screen .....	249
I.2.2 Species Sub-Screen .....	254
I.2.3 Results Sub-Screen .....	255
I.3 Generic Species Screen .....	257
I.4 <i>Sitta europaea</i> (nuthatch) Screen .....	261
I.5 <i>Peromyscus leucopus</i> (white-footed mouse) Screen .....	265
I.6 <i>Satyrium pruni</i> (black hairstreak) Screen .....	268
 <b>References .....</b>	 <b>272</b>

# LIST OF FIGURES AND TABLES

## Figures

2.1	The effects of extent on spatial pattern .....	25
3.1	A functional block diagram of PatchMapper .....	32
3.2	The coupled-lattice structure of PatchMapper .....	33
3.3	The overall simulation process .....	35
3.4	An example 'model' user-screen .....	37
3.5	An example of an internally generated neutral landscape .....	39
3.6	An example of an externally generated neutral landscape .....	40
3.7	Habitat and quality modelling with PatchMapper .....	41
3.8	Modelling increasing patch size .....	43
3.9	The population modelling sequence .....	45
3.10	The 'results' user-screen .....	51
3.11	An imported landscape showing the 'box' principles .....	52
4.1	The 'nuthatch' user-screen .....	56
4.2	The nuthatch lifecycle modelled by PatchMapper .....	59
4.3	Nuthatch dispersal paths .....	61
4.4	Inter-patch search coverage pattern .....	63
4.5	Intra-patch search coverage pattern .....	66
4.6	Main study area location .....	70
4.7	The main study area landscapes .....	72
4.8	The centralised study area landscapes .....	74
4.9	Mean predicted pairs as a function of immigration rate .....	76



4.10	Mean remaining population as a function of quality area .....	78
4.11	Mean remaining population as a function of additional habitat .....	79
4.12	The 'white-footed mouse' user-screen .....	83
4.13	The white-footed mouse lifecycle modelled by PatchMapper .....	84
4.14	The basic comparison model landscape .....	92
4.15	Comparison test habitat and quality landscapes .....	93
4.16	Population Ratios for the connectivity scenarios .....	95
4.17	The 'black hairstreak' user-screen .....	97
4.18	The major stages in the modelled black hairstreak lifecycle .....	98
4.19	The test blackthorn patch .....	104
4.20	The replacement strip shapes .....	105
4.21	Population ratios for the three management scenarios .....	106
5.1	A sample neutral landscape with 4% total habitat area .....	113
5.2	A sample neutral landscape with 10% total habitat area .....	114
5.3	The centralised and adjusted landscapes .....	115
5.4	Response to variations in territory size .....	118
5.5	Response to variations in breeding success probability .....	119
5.6	Response to variations in fledged young .....	120
5.7	Response to variations in winter survival rate .....	120
5.8	Response to variations in summer survival rate .....	121
5.9	Response to variations in matrix dispersal mortality .....	121
5.10	Response to variations in habitat dispersal mortality .....	122
5.11	The sensitivity of population size to immigration direction .....	123
5.12	Mean predicted pairs for the general case .....	124
5.13	Mean predicted pairs as a function of perceptual range .....	126

5.14	Mean number of successful external immigrants .....	128
5.15	Mean number of successful internal immigrants .....	129
5.16	Mean predicted pairs for the centralised landscape .....	130
5.17	Predicted mean pairs as a function of perceptual range and field-of-view .....	132
5.18	Sensitivity to variations in field-of-view and immigration direction .....	133
5.19	Ranked demographic parameters .....	134
5.20	The possibility of a higher nuthatch habitat quality category .....	135
5.21	Range of tree diameters .....	138
5.22	Dispersal flow diagrams for the centralised landscape .....	142
5.23	Centralised and adjusted landscape dispersal flow diagrams .....	146
5.24	Response to variations in breeding success probability .....	149
5.25	Response to variations in the number of young .....	150
5.26	Response to variations in nestling survival probability .....	151
5.27	Response to variations in juvenile survival probability .....	151
5.28	Response to variations in sub-adult survival probability .....	152
5.29	Response to variations in adult survival probability .....	152
5.30	Response to variations in winter survival probability .....	153
5.31	Response to variations in dispersal mortality .....	154
5.32	Response to variations in perceptual range .....	154
5.33	Response to variations in territory size .....	155
5.34	Response to variations in strip replacement cycles .....	158
5.35	Response to variations in strip widths .....	160
5.36	Response to variations in blackthorn age .....	161
5.37	Response to variations in dispersal probability .....	162
D.1	Modelling two generic species .....	228

E.1	A demonstration of misleading results .....	231
F.1	The principles of Java .....	235
H.1	Habitat and quality centralised landscapes .....	246
H.2	The effects of habitat and quality modelling .....	247
I.1	The generate sub-screen .....	249
I.2	The species sub-screen .....	254
I.3	The results sub-screen .....	255
I.4	The generic species' screen .....	257
I.5	The nuthatch screen .....	261
I.6	The white-footed mouse screen .....	265
I.7	The black hairstreak screen .....	268

## Tables

2.1	Four ecological categories with typical modelling applications .....	6
3.1	The landscape pattern metrics recorded by PatchMapper .....	49
3.2	The population demographic measures recorded by PatchMapper .....	50
4.1	Published sources of nuthatch demographics .....	58
4.2	Nuthatch habitat quality classification .....	70
4.3	Woodland and nuthatch breeding habitat areas .....	74
4.4	Analytical model predictions .....	76
4.5	Published sources of white-footed mouse demographics .....	85
4.6	White-footed mouse breeding period week numbers .....	86
4.7	White-footed mouse per-step dispersal mortality probabilities .....	89
4.8	The modelled black hairstreak demographic parameters .....	99

5.1	Default nuthatch deterministic parameters .....	110
5.2	The tested nuthatch parameters and their range of variation .....	111
5.3	A comparison of the centralised and neutral landscape characteristics ...	111
5.4	The tested white-footed mouse parameters and their range of variation ..	147
A.1	Major Milestones .....	177
C.1.1	A survey of population ecology model types .....	214
C.2.1	A survey of published SEPMS .....	217
C.3.1	A survey of commonly used landscape resolutions .....	223
C.4.1	A survey of tree diameters .....	226
E.1	A survey of commonly used metrics .....	233
G.1.1	Nuthatch population lattice: plane 0 (main cell) .....	238
G.1.2	Nuthatch population lattice: plane 0 (territory cell) .....	239
G.1.3	Nuthatch population lattice: plane 1 (territory cell) .....	239
G.1.4	White-footed mouse population lattice: plane 0 (main cell) .....	240
G.1.5	White-footed mouse population lattice: plane 0 (territory cell) .....	241
G.1.6	White-footed mouse population lattice: plane 1 (territory cell) .....	241
G.1.7	Black hairstreak population lattice: plane 0 .....	242
G.1.8	Black hairstreak population lattice: plane 1 .....	242
G.2.1	Habitat landscape file RGB codes .....	243
G.2.2	Quality landscape file RGB codes .....	244

# 1. INTRODUCTION

## 1.1 Acknowledgement of the Decline in Biodiversity

Species extinction rates have been increasing rapidly throughout the last 100 years or so, alarming environmentalists and other scientists. The list of endangered species grows ever longer and a period of extinction comparable to the five mass extinctions evident in the fossil record is rapidly becoming an alarming possibility (Valentine 1970; Niklas *et al.* 1983; Strong *et al.* 1984; Wilson 1985; Begon *et al.* 1996; Stiling 2002).

The term 'biodiversity' describes the variety of all life on earth, not just the number of species but also the variety of life at all scales, from ecosystems, communities, species and populations, to the genetic variation within species (Wilson 1994; Forman 1995; Begon *et al.* 1996). Local extinctions reduce local biodiversity, which if left unchecked can lead to the extinction of species at a regional and even global level (Wilson 1994). Concerns over the current extinction rate and the consequent reduction in biodiversity, led to the 1992 Earth Summit in Rio de Janeiro where signatories agreed to take steps to rehabilitate and restore degraded ecosystems and to promote the recovery of threatened species.

The decisions made at the summit filtered down to country level, leading in Britain to the development of the 1994 United Kingdom Biodiversity Action Plan (UKBAP) (HMSO 1994). Local steering groups were formed to implement habitat and species action plans, with the aim of recording the current level of biodiversity and to suggest and take steps to at least maintain, and hopefully enhance, species diversity (HMSO 1995). One organisation involved with the UKBAP is the Royal Society for the Protection of Birds who, as a lead partner, have taken responsibility for coordinating and encouraging actions and for reporting progress for 36 priority species (RSPB 2004). Another example is the British Entomological and Natural History Society, co-operating with Butterfly Conservation in their Threatened Moths Project and their assessment of the status of some UKBAP priority species (Parsons *et al.* 2000; Phillips 2000; Young 2001).

## 1.2 Modelling: a Weapon in the Fight Against the Decline in Biodiversity

Studies into biodiversity conservation can be carried out using observations and field experiments. These approaches are difficult if long timescales are involved and are effectively impractical if the effects of large-scale landscape transformations and comparisons of the outcomes resulting from various habitat-management and land-use schemes are to be investigated (Jeffers 1982). One practical approach is to compare and analyse the results of a set of simulations by using a model that predicts individual patch and landscape population sizes by simulating the dispersal of individuals within a representation of the landscape (Wennergren et al. 1995). The availability of such a model would aid groups involved with implementation of the UKBAP to meet the overall aims of the 1992 Earth Summit, in rehabilitating and restoring degraded ecosystems and promoting the recovery of threatened species.

Cellular automata are grid-based mathematical models in which each cell in the grid is a single identical, but independently-behaving, entity which assumes one of a set of possible discrete states in accordance with a set of deterministic or stochastic (using random sampling from probability distributions) rules applied at time intervals (Wolfram 1984; Childress *et al.* 1996; Dunkerley 1997). The state of each cell is based on the state of neighbouring cells. Each cell is simple, but acting together they become capable of complex behaviour (Green 1994). Cellular automata, along with fuzzy logic and neural networks, are subsets of a class of mathematical models called 'polyautomata', which are often applied to modelling the non-linear behaviour of natural systems (Smith 1976; Wolfram 1984). Landscapes are dynamic systems which are difficult to model by traditional methods such as differential equations, but cellular automata ideally lend themselves to the modelling of landscapes and sets of individual organisms inhabiting those landscapes (Hogeweg 1988; Milne 1988; Green 1989; Baudry and Tatoni 1993; Green 1994; Forman 1995; Patten and Jørgensen 1995; Gustafson 1998).

Cellular automata are useful for both specific case studies and investigating general principles. Example uses include investigations into the plausible mechanisms of water partitioning in spatially unstructured plant communities (Dunkerley 1997) and the survival of lateral spreading clonal plants, such as herbaceous perennials, when subjected to different regimes of spatially localised disturbances (Inghe 1989). Other examples uses include the simulation of fire spread (Green *et al.* 1990), starfish outbreaks (Hogeweg and Hesper 1990), the spread of disease in feral pigs (Pech *et al.* 1992) and forest dynamics (Green 1989).

One class of model, often grid-based and encompassing the principles of the cellular automaton, is the spatially explicit population model (SEPM). This type of model combines a population simulator, with an explicit representation of a landscape, often obtained from a geographical information system (GIS). The landscape typically comprises habitat information, superimposed on a grid, allowing the inclusion of habitat patches that are spatially distributed in a realistic manner (Dunning *et al.* 1995; Ruckelshaus *et al.* 1996). The population inhabits the grid with the spatial distribution of the habitat affecting species persistence and coexistence. The two components are inter-linked to form a single model. Ruckelshaus *et al.* (1996) stated that SEPMs 'are individual-based and can therefore represent realistic behaviour', but this is not completely correct as many SEPMs are population-based, such as those used by Palmer (1992) and Travis and Dytham (1998). Nevertheless, such a model should enable the spatial distribution of landscape elements and individuals to be specified and the effect of habitat loss and fragmentation on population dynamics to be studied (Dunning *et al.* 1995; Turner *et al.* 1995).

The results can be presented in a graphical manner and used as a guide for land-use managers (Dunning *et al.* 1995; Ruckelshaus *et al.* 1996; Frank and Wissel 1998), but more is needed for a mathematical analysis (Durrett and Levin 1994). For this reason a SEPM should also produce a set of numerical measures to enable post-simulation analysis (Turner *et al.* 1995).

This thesis is concerned ultimately with the development of an individual-based SEPM.

### 1.3 Aims and Objectives

The overall aim of this thesis was to develop, test and apply an individual-based SEPM to the analysis of population viability in fragmented habitat.

Within this context, the specific objectives were:

- 1) To review the areas of population ecology modelling relevant to this thesis.
- 2) To develop an easy-to-use individual-based SEPM, which provides a real-time (computer) visual display and models:
  - a) Digitised real and neutral landscapes
  - b) Representatives of different taxonomic groups
  - c) Landscape dynamics
  - d) Multiple habitat types
- 3) To validate the model against published models and studies.
- 4) To consider the implications of the results for wider application within the fields of landscape ecology and biodiversity conservation.

The research took the form of computer-based spatial and temporal modelling, using artificial and real landscapes of regional interest, in order to establish links between ecological processes and habitat fragmentation. The model included a population simulator to study the effects of different landscape structures on species persistence and survival. It is envisaged that the resultant model will be of assistance to organisations involved in conservation and land-use planning, such as the various local steering groups involved with the UKBAP. The ultimate aim is to help bring about an increase, or at least to halt the decline, in biodiversity.



## 1.4 Thesis Structure

Chapter two starts the thesis with a review of the literature covering relevant areas of spatially explicit population modelling. Chapter three describes the framework of the model and its overall construction and Chapter four details the modelling of three different taxa: a resident territorial bird, the nuthatch (*Sitta europaea* L.), the white-footed mouse (*Peromyscus leucopus* Rafinesque) and the black hairstreak butterfly (*Satyrrium pruni* L.). This chapter also includes performance comparisons against published models and studies. A sensitivity analysis of the modelled taxa is presented in Chapter five. Chapter six reviews the results and the main findings of the research and also discusses some potential applications and possible future research directions. The major milestones passed during the work undertaken for this thesis, including two published papers, are listed in Appendix A. The papers themselves are reproduced in Appendix B. A user guide is presented in Appendix I, which is placed last in the appendices for ease of use.

## 2. SPATIALLY EXPLICIT POPULATION MODELLING

### 2.1 Introduction

This chapter presents a review of the elements of spatially explicit population modelling which led to the development of the model and the features included therein. The model structure, comparison tests and sensitivity analyses are described in subsequent chapters.

### 2.2 Population Ecology Modelling

#### 2.2.1 Introduction

The field of ecology can be divided into four inter-related categories, each providing possible subject areas for modelling (Table 2.1). The population ecology category, which includes metapopulation ecology, has been suggested as the area benefiting most from mathematical modelling (Gillman and Hails 1997). Population ecology modelling forms the subject area of this thesis.

Ecological categories	Typical modelling applications
Physiological	Foraging, digestion rates, rates of translocation and transpiration
Population	Biological control, harvesting regimes, spread of invasive species
Community	Community stability and diversity, coexistence
Ecosystem	Nutrient cycling, effects of global climate change

**Table 2.1:** Four ecological categories with typical modelling applications, adapted from Gillman and Hails (1997).

### 2.2.2 Population Ecology Model Classifications

Population ecology models can be divided into five classifications: analytical, deterministic single-population, stochastic single-population (SSP), metapopulation and SEPMs (Beissinger and Westphal 1998). SSP models are considered the most popular means of implementing a population viability analysis, using Monte-Carlo methods to sample probability distributions developed from the demographic characteristics of the modelled organism (Beissinger and Westphal 1998). Such models utilise the stage-based matrix principle and require at minimum, information about the mortality, fecundity, dispersal behaviour and habitat requirements of the organism being studied (Dunning *et al.* 1995). These data are required for each life stage, are difficult to collect and are not known for many species (Hokit *et al.* 2001). The elements of the SSP model are a best match to, but do not completely meet, the requirements of this project. The best match is the last category given by Beissinger and Westphal (1998), the SEPM (Section 1.2).

One particular advantage of SEPMs is the possibility of constructing them to produce a visual, real-time (computer) output, which is a potentially important factor in aiding the acceptance of computer models (Turner *et al.* 1995; Railsback 2001). Despite this advantage, only one individual-based SEPM, called 'J-walk', that purported to produce a real-time (computer) display, was found in the literature (Gardner and Gustafson 2004). The authors stated that individual and cumulative dispersal paths could also be generated, but the utility of the visual outputs was not discussed and no examples were given.

The next two sections in this chapter discuss the elements of landscape and species modelling relevant to this thesis.

## 2.3 Landscape Modelling

### 2.3.1 Introduction

Landscapes are frequently modelled as two-dimensional grids, or lattices, of square cells. To determine any commonality between the resolutions of modelled landscapes, a survey of published papers employing modelling with raster maps was undertaken. The survey revealed that most studies digitising real landscapes used square-celled lattices, with resolutions from  $100 \times 100$  to  $200 \times 200$ . A small number of models used hexagonal-celled lattices. The survey also revealed widely differing scales, from individual plant diameter to region-wide. The results of the survey are presented in Appendix C.3 and are further discussed in Section 2.6.2.3.

Lattices can be modelled using arrays, which are index-addressable storage structures available with most programming languages. Extending the concept to multi-dimensional arrays allows the inclusion of additional layers in the model, representing for example, multiple species, climate and anthropogenic features. A set of rules can then be constructed to govern inter- and intra- layer cell interaction, creating a coupled-lattice structure.

For a model to be suitable for general use and to enable landscape structure to directly influence population viability and distribution, realistic landscapes should be able to be created by the user or to be imported from an external source, such as a satellite or a GIS. In this manner, the spatial structure and temporal characteristics of habitat patches can be included in the population modelling process. Such models are an ideal tool for assisting ecologists to examine the connections between landscape patterns and species viability (Dunning *et al.* 1995; Turner *et al.* 1995; Ruckelshaus *et al.* 1996).

If artificial landscapes are to be generated, then their method of generation needs to be considered. Other issues of relevance to this thesis include the modelling of multiple habitat types, landscape dynamics and landscape transformation algorithms. These matters are discussed in the following sub-sections.

### 2.3.2 Modelling with Neutral Landscapes

Neutral landscapes are artificial landscapes generated with analytical algorithms, without reference to ecological processes and they are useful for obtaining general results, but not for modelling specific case studies (With 1997). Some studies using neutral landscapes have suggested that there is a threshold of approximately 20% habitat cover above which the spatial arrangement of habitat patches has no effect on population survival (Andren 1994; Fahrig 1997; Fahrig 1998). Countering this view, With and King (2001), who modelled four species types in a set of neutral landscapes with varying habitat cover, found that different habitat cover thresholds could be identified for the survival of each species and caution against the automatic use of this '20% rule' for conservation purposes. Further example uses of neutral landscape-based models include investigating the response of landscape metrics to changes in heterogeneity (Gustafson 1998), examining the relationships between landcover proportion and landscape pattern metrics (Gustafson and Parker 1992) and differentiating patterns that are the results of simple random processes from patterns that arise from more complex ecological processes (Keitt 2000).

Many (published) spatially explicit models use grid-based neutral landscapes, or percolation maps (Section 2.6.2.2), which are generated by randomly assigning each cell as habitat, with probability  $p$ , and matrix, with probability  $1-p$  (With 1997; Keitt 2000). The analysis of these models is based on percolation theory, which deals with the number and properties of clusters present on a (usually) square lattice (Stauffer and Aharony 1994). Such models tend to produce statistics that only loosely match real landscapes. Patch density, for example, (typically) greatly exceeds that of a real landscape (Saura and Martinez-Millan 2000).

Fractal algorithms are often used to generate realistic neutral landscapes (Palmer 1992), one such being the mid-point displacement method of Saupe (1988). One example of its use is given by Keitt (1997), who investigated the importance of spatial heterogeneity on the stability of an individual-based food web model. The applicability of fractals to landscape ecology is a matter of some debate. It has been argued ecological patterns are not fractals and that fractal algorithms generate landscapes that do not have scaling properties similar

to those observed in nature (Simberloff *et al.* 1987). These arguments are countered by Palmer (1992), who ascribes such claims to a faulty definition of fractals as self-similar objects, but goes on to say that fractal geometry should only be accepted when its utility for simulating the irregular patterns observed in nature is recognised. Nevertheless, some authors have found that fractal analysis is a useful technique for quantifying landscape properties (Milne 1988; Nikora *et al.* 1999). Realistic landscapes have been modelled using fractals, with one example being Watts and Griffiths (2004), who used fractal-based neutral landscapes to investigate structural connectivity in Welsh woodlands.

Clumping or clustering algorithms other than those employing fractal methods have also been employed to generate realistic landscapes, again with some success. Saura and Martinez-Millan (2000) for example, describe a modified random clusters (MRC) algorithm, which generates neutral landscape with selectable land-cover extent and types. This algorithm enables a wide range of spatial patterns to be generated, in which both the degree of fragmentation and the level of habitat abundance can be independently controlled. In their tests, the authors found that the number of patches, edge length and patch cohesion indices for landscapes generated by the MRC algorithm closely matched those found in real landscapes in nine counties of Georgia (USA), in Costa Rica and in old-growth forests in the Pacific Northwest of USA. As such, the MRC algorithm is claimed (by the authors) to be able to generate more realistic landscapes than previous landscape-generating models.

### 2.3.3 Multiple Habitat Types

The inclusion of multiple habitat-types in SEPM landscapes is useful in that it allows for a more realistic modelling of target and non-target habitat within a landscape, rather than a binary view of habitat and matrix (Baudry *et al.* 2003). Nevertheless, most published grid-based SEPMs that model dispersal between habitat patches were found to use only two landscape elements: habitat and non-habitat, e.g. Liu (1993), Venier and Fahrig (1996), Fahrig (1997), Keitt (1997), Fahrig (1998), With and King (1999) and King and With (2002). Two (of the few) published grid-based SEPMs that modelled dispersal between

habitat patches using more than one habitat type were Bender *et al.* (2003), who modelled matrix, habitat and territories within habitat; and Tischendorf *et al.* (2003), who modelled matrix, hospitable matrix and habitat. Both these studies evaluated isolation metrics, rather than population viability and dispersal flow. Two further examples of multi-habitat type modelling include Rushton *et al.* (1997) and Lurz *et al.* (2003), who modelled the spread and impact of grey (*Sciurus carolinensis* Gmelin) on red (*S. vulgaris* L.) squirrels in Norfolk and Cumbria, UK. In addition to the matrix, these models included habitat types used by each squirrel species and were concerned with inter-species competition.

### 2.3.4 Landscape Dynamics

Most studies of landscape dynamics concern animal or vegetation dynamics, a representative sample being insect population dynamics (Hassell *et al.* 1991), landscape vegetation modelling (Roberts 1996), population dynamics of red and grey squirrels (Rushton *et al.* 1997), invasion dynamics of *Pinus* species (Rouget *et al.* 2000) and butterfly population dynamics (Bergman and Kindvall 2004). Studies of patch and landscape dynamics are rare and this is an area noted as being short on study (Baskent 1999), although practical difficulties in data collection have been suggested as a probable reason for this (Bergman and Kindvall 2004).

One major difficulty encountered when considering landscape dynamics is the time taken for most landscapes to recover from habitat disturbances. Some events are cataclysmic, such as the Mount Saint Helens eruption in Washington State USA, in which large areas of land are changed in an extremely short period of time (Forman 1995), but the recovery of such affected areas often takes decades. Likewise, any changes in a forest management system will take typically 10 to 20 years for the results to be known, as will many other land-use changes. In agricultural landscapes, as pointed out by Swetnam *et al.* (2001), farms implement rotations over 3 to 10 years. Such scenarios present real practical problems with the collection and availability of suitable data, along with the comparison of such data without excessive (statistical) transformation (Li and Archer 1997; Gustafson 1998).

Few long-term studies concerning landscape transformation over time have been carried out. Those identified covered approximately 40 years in Ontario, Canada (Moss and Davis 1994); studies over 48 years in central Ohio, USA (Simpson *et al.* 1994); 138 years in Holland (Hulshoff 1995); 43 years in Texas, USA (Li and Archer, 1997) and 33 years in south-west Niger (Wu *et al.* 2000). Other examples include a study in Saxony, eastern Germany over 77 years (Herzog *et al.* 2001) and Baudry *et al.* (2003), who covered seven years of crop succession in western France.

One field in which there is at least recognition of the importance of patch and landscape dynamics is that of forestry management. Forest edge and interior dynamics have been shown to be related not only to initial forest cover, but also to the type of deforestation, suggesting that these patterns should be taken into account when modelling forest dynamics (Zipperer 1993). Baskent (1999) focussed on changes in forest landscape dynamics as a result of different harvesting patterns and initial landscape structure and determined that an understanding of the spatial dynamics of a forested landscape would be a significant step towards the implementation of a landscape management design process. Despite this recognition, very few attempts have yet been made to study forest landscape dynamics (or indeed the dynamics of other land-use types). One notable exception was the combination of a metapopulation model with a dynamic habitat model to investigate the effect of landscape dynamics on a butterfly (*Lopinga achine* Scopoli) metapopulation in southern Sweden (Bergman and Kindvall 2004). In this case, the authors found it essential to include both landscape dynamics and stochastic population modelling when carrying out their population viability analysis.



### 2.3.5 Landscape Transformation Algorithms

To enable the dynamic effects of habitat removal or addition to be studied, the ideal case would be able to change both the landscape and the rate at which it changes during each simulation run. Despite this requirement, the evidence suggests that many models do not have this facility (Appendix C.1). When landscape dynamics are modelled, it is often by asserting changes in the landscape before each run, rather than during each run. The results of the individual simulations are then often linked to create output graphs. Griffiths and Williams (2000), for example, modelled the effects of habitat fragmentation on amphibians by increasing the numbers of ponds. At each step they divided the same number of newts between all the ponds. This is not the same as creating a new pond and investigating when and/or if it became colonised. Further details of dynamic landscape coverage by published SEPMs are given in Appendix C.2.

If the landscape changes during the run, individuals inhabiting the parts that change will be subjected to additional pressures not experienced in the unchanged habitat. The model may allow many effects to take place, such as allowing individuals to suffer reduced birth rates or migrate to suitable habitat. The reaction of individuals living in habitat patches which are isolated or reduced in size by the transformation can also be observed, as can the relative effects on these events caused by various rates of landscape change. The majority of existing models ignore these effects (Section 2.6.2).

If landscape transformations are to be modelled, then the algorithm must be realistic, even though the transformation may be site-specific and difficult to parametrise. A landscape transformation algorithm could produce reasonably regular changes, as with some forestry management schemes, but could also produce irregular changes, as with desertification resulting from overgrazing (Zipperer 1993; Forman 1995). An algorithm may be determined from a series of accurate historical maps, using the later ones to test the predictability of the algorithm. This method relies on the availability and accuracy of such maps and does not mean that the algorithm will necessarily hold true for the future. No papers were found that carried out a study with the aim of parametrising a SEPM in this manner, although several studies have been undertaken to investigate land-use changes.

One example analysed how urbanisation had transformed the desert landscape in the central Arizona – Phoenix region of the United States of America (Jenerette and Wu 2001). This model used a Markov-cellular automaton with rules created from empirical evidence and a genetic algorithm. The aim was to increase understanding of land-use change in the region, rather than to parametise a SEPM, but although it is very much site-specific there seems to be no reason why the algorithm could not be used for this purpose. Another example used combined dynamic landscape and stochastic population models to examine the effects of landscape changes on the butterfly *Lopinga achine* (Bergman and Kindvall 2004).

Possible reasons why realistic landscape transformation algorithms have not been generally included as part of SEPMs include difficulties in obtaining the necessary data and the specific nature of the results limiting their generality. Nevertheless, with habitat fragmentation being an important element of modern landscapes (Forman 1995), if the dynamics of changing habitat spatial structure and its effects on resident populations are to be analysed, then a method of including variable rate landscape transformation during a simulation run is required.

## 2.4 Species Modelling

### 2.4.1 Introduction

When considering the development of a species simulator, several issues need to be considered. Areas of relevance to this thesis include the definition of a metapopulation, single vs. multiple species modelling, dispersal rules, dispersal mortality and perceptual range. These matters are discussed in the following sub-sections.

### 2.4.2 When is a Metapopulation not a Metapopulation?

One of the main contributions to the field of conservation biology was the publication of the dynamic theory of island biogeography by MacArthur and Wilson (1963, 1967), the impact of which is described by Hanski (1999) and Hubbell (2001). Island biogeography theory largely overshadowed the concept of metapopulation ecology, which was introduced and developed by Levins (1969), around the same time.

Since the mid 1980s, metapopulation ecology has seen a surge of interest. At the same time there has been a decline in the popularity of the island biogeography theory (Hanski 1999). One possible reason behind this decline is that the island theory relates to patterns on oceanic islands spread over large spatial scales. Oceanic islands are not a common experience for most landscape ecologists, whereas the metapopulation theory relates to the more familiar fragmented habitat on a landscape scale (Hanski 1999). A further reason may be that the island theory assumes a permanent mainland species source that is sufficient to prevent 'global' extinction, whereas there is no such refuge in Levins's model, in which 'global' extinction is possible (Hanski 1999). The surge of interest in metapopulation theory has resulted in the metapopulation concept now being widely used in conservation biology. Examples include modelling the population dynamics of great crested newts (*Triturus cristatus* Laurenti) (Griffiths and Williams 2000), the biogeography of moths in a fragmented landscape (Ricketts *et al.* 2001) and the population viability analysis of the butterfly *Lopinga achine*, in a dynamic landscape (Bergman and Kindvall 2004).

The key characteristics of a metapopulation system are a landscape consisting of more or less isolated habitat patches, some of which are colonised by subpopulations (Levins 1969). Individuals are able to disperse to colonise empty patches with the subpopulations themselves being subjected to stochastic extinctions (Dytham 1995; Frank and Wissel 1998; Moilanen and Hanski 1998). These characteristics form three of the four conditions that have to be fulfilled by a classical metapopulation (Elmhagen and Angerbjorn (2001). The fourth characteristic is that asynchronous subpopulation dynamics are essential for reducing the risk of simultaneous subpopulation extinction (Hanski *et al.* 1995). The result is an assemblage of dynamic subpopulations, the key elements of which can be summed up as habitat patches, isolation, stochasticity, dispersal, colonisation and extinction. As long as subpopulation extinctions do not exceed habitat patch colonisations over the long term, the metapopulation remains viable (Hanski 1999; Weisser 2000).

When is a metapopulation not a metapopulation? Even though the term is in common usage, the exact definition of what constitutes a metapopulation is a matter of some debate. Consider a single species inhabiting a landscape consisting of homogenous habitat. Under the definition of a metapopulation given by Hanski *et al.* (1995) and Elmhagen and Angerbjorn (2001), a metapopulation cannot exist, but a population does. As the habitat fragments, habitat patches are formed and become increasingly isolated. At some point the definition will be met and a metapopulation will form, but at what point? As the fragmentation continues, the patches will become too isolated for individuals to successfully travel between them, dispersal is no longer possible and although the landscape may well contain sub-populations, under the definition, a metapopulation no longer exists. The question again arises: at what point does this occur?

Thomas and Kunin (1999) discussed this matter and suggested that time and effort has been wasted in attempting to categorise particular systems. The authors viewed the various labels given to populations and groups of populations (such as source-sink, metapopulations and single patchy populations) as points on a continuous plane, rather than as separate categories. Other studies also recognise the problem. Marsh and Trenham (2000) in considering a ponds-as-patches view of an amphibian metapopulation, gave four expected characteristics that such a system might be expected to possess. These included population

dynamics being primarily driven by processes occurring at breeding ponds, local extinctions and recolonisations being common, many local extinctions resulting from stochastic processes and population distribution being affected by limited dispersal ability. They suggested it was unlikely that all four conditions would apply to all systems and that a metapopulation structure may be more apparent than real. Donovan *et al.* (1995), for example, modelled a source-sink system but called it both source-sink and a metapopulation. It is therefore highly likely that a subset, or even all, of the labels used to describe populations and groups of populations could be applied to individual parts of the same landscape at any one time. It may be better to recognise the various effects that can occur rather than struggle to categorise the complete assemblage with a single term. Despite these issues, due to its widespread use, the term metapopulation is used within this thesis when considering the set of populations of a single species inhabiting one or more fragmented habitat patches within the modelled landscape.

### 2.4.3 The ‘Levins’ Model

The first metapopulation model was a single-species population based model which measured the rate of change in the fraction of occupied habitat patches (Levins 1969, 1970):

$$\frac{dP}{dt} = cP(1 - P) - eP$$

Where  $P$  is the fraction of occupied habitat patches,  $c$  is the colonisation rate and  $e$  the extinction rate.

As may be expected by this seminal model, there are some simplifications. The model assumes the landscape consists of isolated habitat patches with each patch considered either empty or occupied. The mean-field approximation applies (all occupied patches are considered equally connected to other occupied patches), hence colonisation is not affected by distance. Local extinctions and colonisations are considered slow compared to

demographic events and local dynamics are duly ignored. All patches are equal and the metapopulation survives in a colonisation-extinction equilibrium. Habitat fragmentation can be modelled (by increasing the extinction rate and reducing the colonisation rate), but the spatial structure of a real landscape cannot be accommodated (Hanski 1999; Akcakaya 2000; Keeling 2002). This type of model can be classed as spatially implicit (Hanski 1999).

Despite these restrictions, the Levins model has been instrumental in providing insights into the effects of habitat loss and fragmentation on population dynamics (Hanski 1999). The model is an example of the ‘strategic’ class of models, which are used to produce general ecological formalisations (Gillman and Hails 1997). The Levins model and those population models that immediately followed were usually single-species based and employed differential equations. (These models are not discussed here, but a useful description of Levins type spatially implicit models is provided in Hanski (1999).) As the field developed, there was a shift away from these continuous (i.e. differential equation based) models (Durrett and Levin 1994). Conservation biologists and others concerned with population dynamics and species persistence are now making increasing use of SEPMs which simulate the movement of individuals, such as Baudry *et al.* (2003) who used such a model to investigate landscape connectivity and Gardner and Gustafson’s (2004) model of animal dispersal, which was used to investigate the effects of landscape patterns and species-specific characteristics on dispersal success.

#### **2.4.4 Single vs. Multiple Species Modelling**

As the concept of biodiversity includes the interaction of species within the landscape (Section 1.1), it follows that studies into biodiversity conservation should consider more than one species. However, most metapopulation models are single species based (Dunning *et al.* 1995; Turner *et al.* 1995; Hubbell 2001) (Appendices C.1 and C.2). Notable exceptions to this are predator/prey models and those investigating inferior/superior competition, but even these are usually limited to two species (Appendix C.1). Developing a model that covers multiple species is a definite requirement, but is also a significant challenge (Turner *et al.* 1995). As an example, one of the possible results of single vs.

multiple species modelling is presented in Appendix D, in which two generic species inhabit a landscape that is subject to a 50% habitat loss halfway through the simulation. If each species is modelled separately, then both survive the habitat loss. If both species are modelled together, then only one survives. Due to the wide range of species types that can be modelled, making sense of the results and their applicability to biodiversity conservation would be problematic (Fahrig 1998). A possible development route could be to develop a model of a single species and extend it to cover additional species once its effectiveness is proven.

### 2.4.5 Dispersal Rules

One of the effects of habitat fragmentation is to isolate species in separate habitat patches. In order to reach areas of suitable habitat, individuals are forced to traverse uninhabitable and possibly inhospitable matrix habitat (Haydon and Pianka 1999; Zollner and Lima 1999a; Ricketts 2001). The degree to which fragmentation affects a particular dispersing species depends, in part, on its ability to locate nearby habitat patches. Thus dispersal success is thought to have a direct effect on population persistence (Gustafson and Gardner 1996; Schippers *et al.* 1996).

Dispersal in an individual-based SEPM is governed by a set of inter- and intra- patch dispersal rules. Dispersal in a real landscape is thought to be influenced by the spatial characteristics of that landscape and if the model is to reflect such influences, then dispersal rules should take account of spatial heterogeneity (Samways 1989; Wiens *et al.* 1997). Possibly as a result of risk-avoidance strategies, inter-patch movement paths tend to be straighter than intra-patch movements (Forman 1995; Wiens *et al.* 1997; Zollner and Lima 1999a). Data on this aspect of dispersal are scarce, but a variety of species, such as western harvester ants (*Pogonomyrmex occidentalis* Cresson) (Crist and MacMahon 1991), moose (*Alces alces* L.) (Pastor *et al.* 1997) and darkling beetles (*Eleodes obsoleta* Say) (Wiens *et al.* 1997), have been found to follow straighter paths when moving between habitat patches, than when foraging locally.

One possible way to model dispersal is by using a random walk, whereby individuals move around, or diffuse through, the landscape in convoluted paths in which each direction change is decided at random (Zollner and Lima 1999a). Such models are known as diffusion models but as no animal moves in this fashion their movement rules are somewhat unrealistic (Forman 1995). An extension of the random walk is the correlated random walk. With this type of dispersal, small turns are made at intervals, leading to a zig-zag movement across the landscape (Schippers *et al.* 1996; Tischendorf and Fahrig 2000a). The result is a nearly straight dispersal path and such paths are thought to maximise the chance of habitat detection over a perfectly straight one (Zollner and Lima 1999a). Other important factors affecting dispersal success include dispersal mortality and perceptual range (Lima and Zollner 1996; Schooley and Wiens 2003).

#### **2.4.6 Dispersal Mortality**

One method often used to incorporate dispersal mortality into grid-based models is to implement it as a probability of mortality, applied at each movement step. This is a useful technique as dispersal distances do not have to be directly modelled, allowing habitat structure and perceptual ability to have a direct effect on the overall dispersal mortality. Theoretical grid-based models typically use a range of per-step dispersal mortality probabilities of 0.0001 to 0.01 (Zollner and Lima 1999a; Tischendorf and Fahrig 2000a). Fahrig (1997) expanded the basic idea and used per-step mortality probabilities of 0.05 for habitat dispersal and 0.5 for matrix dispersal. One problem with these models is that the absence of a per-step scale prevents a useful comparison of their results. Per-step dispersal mortality is a required input, but needs to be realistic for the species and movement distances being modelled.



### 2.4.7 Perceptual Range

The distance over which a particular species is able to distinguish between different landscape elements, such as shelter and breeding quality habitat, has been variously defined as its 'radius of detection' or 'reactive distance' (Cain 1985; Adler and Nuernberger 1994), 'detection distance' (Fahrig 1988) or, more recently, its 'perceptual range' (Zollner and Lima 1997; Zollner 2000). For a dispersing individual, the shorter its perceptual range, the longer it spends in the matrix before locating a habitat patch. This increases the chance of dispersal mortality through factors such as resource depletion and increased risk of predation (Lima and Zollner 1996; Schooley and Wiens 2003). An individual species' perceptual range defines the spatial extent of the landscape for which movement decisions can be made, which in turn can be expected to influence population distribution. Perceptual range should therefore be a component of individual-based SEPM dispersal rules (Olden *et al.* 2004).

Little empirical evidence exists regarding the perceptual range of individual species (Lima and Zollner 1996; Zollner 2000). Work on small mammals has found perceptual ranges of up to 30 m for the root vole (*Microtus oeconomus* Pallas) (Andreassen *et al.* 1998) and up to 90 m, possibly 120 m, for the white-footed mouse (*Peromyscus leucopus*) (Zollner and Lima 1997), depending on the visual obstruction of the habitat. Perceptual ranges of 300 - 500 m have been found for the eastern fox squirrel (*S. niger* L.) and the grey squirrel (Zollner 2000). These estimates were based on visual perception, although other forms of perception, e.g. perception of polarised light in the pond slider turtle (*Trachemys scripta* Schoepff) (Yeomans 1995) and olfactory perception in the cactus bug (*Chelinidea vittiger* Uhler) (Schooley and Wiens 2003), are possible. Although it is intuitively likely that birds have the ability to detect landscape features at greater distances, no details of the actual perceptual ranges of birds were found in the literature.

Perceptual range has been included in several SEPMs in one form or another, but has rarely been explored. Saarenmaa *et al.* (1988), Doak *et al.* (1992), Turner *et al.* (1993), Adler and Nuernberger (1994), Turner *et al.* (1994) and Schippers *et al.* (1996) for example, all used a form of fixed perceptual range but did not discuss the effects of its inclusion.

Only three models that explored perceptual range were found: Cain (1985), Fahrig (1988) and Zollner and Lima (1999a). These models all varied perceptual range and found that, in general, increasing perceptual range increased dispersal success within artificial landscapes. Cain (1985) found that increasing perceptual range increased dispersal success when tested in conjunction with an increase in average movement length. Fahrig (1988) found that increasing perceptual range increased mean patch population size and that habitat spatial arrangement only had an important effect for intermediate levels of perceptual range. Zollner and Lima (1999a) in their study into the effectiveness of different movement algorithms in artificial landscapes found that increasing perceptual range increased the probability of dispersal success. The perceptual range mechanism in these models was based on a 360° field-of-view, except in Zollner and Lima (1999a), where the method was probably straight ahead in the direction of movement, although this was not made clear. The models by Cain (1985) and Zollner and Lima (1999a) were individual-based; that by Fahrig (1988) was population based. None of these three models explored the effects of perceptual range in conjunction with the amounts and/or configurations of suitable habitat on population sizes in real landscapes, or attempted to parametrise a particular species.

## **2.5 Problems with grid-based SEPMs**

### **2.5.1 Introduction**

Despite the constructional attractiveness of the coupled-lattice structure of grid-based SEPMs (Section 2.3.1), there are several disadvantages to using this modelling technique. The main problem is perhaps the requirement for detailed species-specific data. SEPMs require information on demographics and dispersal behaviour, which is often habitat-specific, about the species under consideration (Dunning *et al.* 1995; Ruckelshaus *et al.* 1996). These data are unfortunately not available for most species (Akçakaya 2000; Hubbell 2001).

To ensure that only ecologically interesting behaviour is exhibited, account must also be taken of artefacts arising from the mathematics of the model (Childress *et al.* 1996). There is also a temptation to create models that require too many variables. Apart from the problem of data availability, the sheer number of variables can lead to usability problems (Possingham 1995; Verboom *et al.* 2001). On the other hand, neglecting details could limit the model's applicability (Drechsler and Wissel 1998). Any imported data, e.g. from a GIS, also need to be current and accurate (Turner *et al.* 1995).

Other problems with individual-based models include applying models developed specifically for one landscape to other landscapes that appear superficially similar, but in fact are not (Alderman *et al.* 2004, reproduced in Appendix B.1) and applying models developed at one scale to inappropriate scales (Railsback 2001). Problems can also arise if individual and population parameters are confused, such as applying population based mortality probabilities to individuals (Railsback 2001).

Information at the patch level, such as the efficiency of a stepping stone or the colonisation level of an individual patch is difficult to extract. If the landscape is undergoing transformation, keeping track of patches as they are created, removed or coalesce, presents an additional problem. This was illustrated by Akcakaya (2000), who developed a model that tracked patches as they changed, by recording their lineage, but this method is impractical for a realistic landscape with several hundred or more patches. On the other hand, extracting results at the landscape scale, such as the mean number of individuals of a particular species inhabiting the landscape, presents no such problems (Durrett and Levin 1994).

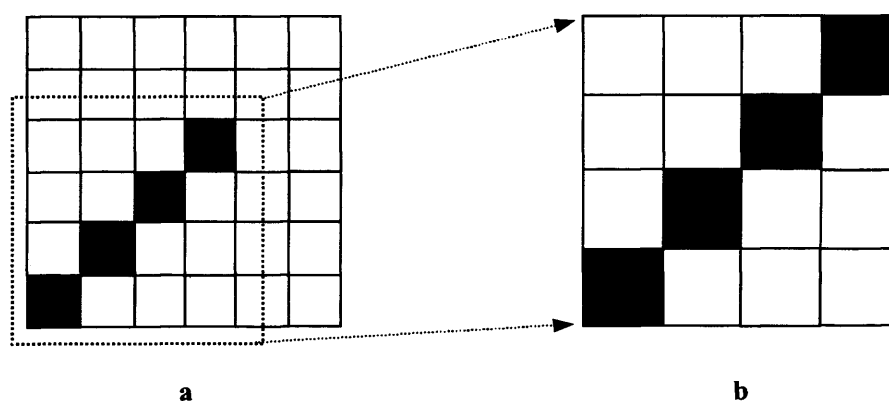
Pattern metrics are often used to present at least part of the output of SEPMS. Most metrics do not consider temporal effects and as a result give measures of 'frozen' landscapes, which encourages a static view of nature (Gustafson 1998). Researchers are therefore forced to use time-series of results from 'static' metrics (Moss and Davis 1994; Wu *et al.* 2000). The general sensitivity of landscape metrics to changing patterns is poorly understood and often overlooked by those using spatial measures to characterise landscape structure (Haines-Young and Chopping 1996). The availability of software capable of

calculating literally hundreds of indices has encouraged many researchers without special training in spatial analysis, to attempt to calculate and interpret pattern metrics (Gustafson 1998). One example of such software is the program Fragstats, which was developed solely to produce various landscape metrics from raster or vector habitat category maps (McGarigal and Marks 1995). As a result of its widespread use (e.g. Hargis *et al.* 1998, Thornton and Jones 1998, Tischendorf and Fahrig 2000a, Wu *et al.* 2000, Herzog *et al.* 2001 and Saveriaid *et al.* 2001, Tischendorf 2001), Fragstats can be considered a standard landscape spatial pattern quantification tool, but it and programs providing similar outputs, should not be used indiscriminately. Such programs also fail to consider the effects of pattern on any organisms inhabiting their landscapes and as such may be of limited use to conservationists. Inter-patch dispersal rates have been shown to be asymmetrical (Ferrerias 2001) and this is suggested as the probable major reason why population analysis with pattern metrics is often inconclusive (Gustafson and Gardner 1996). Whilst metrics are rarely used for temporal analysis, they are widely used for spatial pattern analysis and are further discussed in Appendix E.

### 2.5.2 Scale

Scale, or the area or time-span being studied, is an important issue in the field of landscape ecology, which should be given due consideration. Processes operate at different spatial and temporal scales, creating hierarchies of landscape patterns (Keitt 2000; Elkie and Rempel 2001), suggesting that multiple scales should be considered when exploring the persistence and stability of ecological processes (O'Neill *et al.* 1992). Elkie and Rempel (2001) found that forest harvest practices could create new landscapes that operate at a different scale from the natural landscape, which suggests that the success of an application depends on both identifying an appropriate scale and on extrapolating the findings across different scales (Gustafson 1998). Spatial scale is mentioned most often in the literature (Haines-Young and Chopping 1996), but temporal scale, although a vital element, is rarely covered. Turner (1990) gave early recognition of the need for considerable research to develop a better understanding of the relationships between scale, patterns and ecological processes, an issue later recognised by Li and Archer (1997).

Scale is a problem for grid-based SEPMs. The grain of the landscape is determined by the cell size, which must be relevant to the scale of the organism under consideration (Dunning *et al.* 1995). As species of different trophic levels tend to operate on different scales (Tischendorf and Fahrig 2000b; Elkie and Rempel 2001), multi-species grid-based SEPMs are usually limited to modelling species of similar trophic level (Appendix C.2). This limitation has the danger of producing a case-specific model, with the result that lessons learned are not transferable between models (Dunning *et al.* 1995; Hokit *et al.* 2001). The scale of the organism or process under consideration should therefore be taken into account, as an unwise choice could have major implications (Debinski and Holt 1999; Tischendorf and Fahrig 2000). Figure 2.1 gives an idea of the effects that choice of extent can have. The landscape in Figure 2.1a is incised with an unsuitable habitat type (shown in black), but the habitat is not fragmented (suitable habitat is shown in white). If a reduced area of the same landscape is taken (Figure 2.1b), the landscape is dissected and there is no connectivity from one side to the other. The choice of extent can therefore present two entirely different views of the same area and scale should therefore be considered when comparative analyses are undertaken, or when absolute values are used.



**Figure 2.1:** One of the effects that choice of extent can have on spatial pattern, using a grid-based landscape. Suitable habitat is shown in white and unsuitable cover type in black. Landscape *b* is a fragment of landscape *a*, resulting in the incision in *a* becoming a dissection in *b*.

## **2.6 Features Commonly Included in Existing SEPMs**

### **2.6.1 Introduction**

Before embarking on the development of a new model, it is essential to determine the characteristics and features of existing published models. Research of this nature should reveal the existence of a suitable model, to avoid ‘re-inventing the wheel’. This section of the chapter presents the results of surveys into the existing published models that were found to most closely meet the overall aim of this thesis (Section 1.3).

One of the problems encountered when trying to determine the classification of the surveyed models was similar to the problem of metapopulation classification discussed in Section 2.4.2. Hanski (1999) for example, referred exclusively to population models incorporating information on the geometry of landscapes as spatially realistic, whereas other authors would call such models spatially explicit. Another example is given by Fahrig (1998), who referred to population models based on GIS technology as spatially explicit habitat models, another exclusive term. This author takes the view, in line with Thomas and Kunin (1999), in that although model classification is useful as it enables results comparisons, trying to exactly classify models does not suit any real purpose and could well descend into arguments over semantics.

### **2.6.2 Common Characteristics and Uses**

#### *2.6.2.1 A Survey of Population Ecology Models*

To determine any common areas in their construction, a survey of published population ecology models (Section 2.2.1) was carried out. The results are presented in Appendix C.1. Of the 24 models surveyed, 14 (58%) were grid-based, with 13 of the 14 (93%) models fitting the SEPM category. The remaining ten models were based on non grid-based technologies, such as differential equations, markov chains and incidence functions. The

survey also revealed that eight of the 13 (62%) SEPM models were individual-based. With this type of model, the location of each individual is explicitly modelled, with movement rules forming a key element (Beissinger and Westphal 1998).

The results of the survey also revealed that 17 models (71%) were based on a single species. Of the remaining models, five (21%) were based on two species. These models investigated competition for habitat based on inferior/superior species. The survival of two species as metapopulations in these models relies on the inferior competitor finding unoccupied habitat by being a more effective disperser than the superior species. Two studies dealt with more than two species. Kerr *et al.* (2002) investigated diversity, using three strains (rather than species) of the bacterium *Escherichia coli* Escherich and had no landscape. Palmer (1992) modelled 10 species with different competitive and reproductive characteristics, living in a small ( $32 \times 32$  cell) landscape and investigated environmental variation rather than the effects of spatial structure. Another common group of models based on two species, but not surveyed here, concerns predator/prey interactions stemming from the Lotka-Volterra equations of competition. The literature on this field is voluminous (Hanski 1999) and is not of direct interest to this thesis.

#### 2.6.2.2 A Survey of SEPMs

In order to determine the characteristics of, and any common areas between, existing SEPMs, a survey of 24 published SEPMs (the majority of which were individual-based) was carried out. The results, including for comparison, the characteristics of PatchMapper (the model developed for this thesis), are presented in Appendix C.2.

Fourteen (59%) of the surveyed models used neutral maps, usually generated by the model itself. Seven (29%) models used realistic maps, usually imported from a GIS and three (12%) used both neutral and realistic maps. Sixteen (67%) models incorporated more than one habitat type, allowing variations in habitat quality to be modelled. Of these 16 models, nine (56%) allowed habitat availability and/or quality in one form or another to be varied during the simulation. Example uses of this feature included food source availability, habitat disturbance and habitat loss.

A range of different species were found to be modelled. Single specific species were modelled in five (21%) cases, and single generic species in 13 (54%) cases. Six (25%) models incorporated multi-species modelling. None of the models allowed for immigration into the study area. Four (17%) of the models incorporated perceptual range, but two of those used a perceptual range-like parameter rather than explicitly modelling habitat perception.

None of the models had user-selectable parameters. No model had a visual real-time (computer) output, although one purported to do so (Gardner and Gustafson 2004), but this aspect of their model was not discussed.

#### *2.6.2.3 Commonly Used Landscape Resolutions*

To determine any commonality between the resolution of modelled landscapes, a survey of published papers employing modelling with raster maps was undertaken. The results are presented in Appendix C.3. Of the twenty-four models surveyed, 22 (92%) used a square lattice and two (8%) used a hexagonal lattice. The square lattices ranged in resolution from  $16 \times 16$  to  $1024 \times 1024$ . Of these, two (9%) used the larger resolutions of  $800 \times 800$  and  $1024 \times 1024$  and 11 (50%) used resolutions between  $100 \times 100$  and  $200 \times 200$ . Fourteen (58%) studies concerned theoretical modelling, in that they did not use a real landscape. Ten (42%) studies used digitised representations of a real landscape and in all cases, the chosen resolution matched the scale of the data source. Studies concerning pure modelling tended towards resolutions of  $100 \times 100$  or less. Most studies digitising real landscapes used resolutions from  $100 \times 100$  to  $200 \times 200$ . The survey also revealed widely differing scales, from individual plant diameter to region-wide.



#### 2.6.2.4 Model Survey Summary

The results of the surveys suggest that most (published) population ecology models are SEPMs, with a bias towards modelling single generic-species inhabiting neutral landscapes. Such models are useful for determining general characteristics (Section 2.3.2), such as investigations into relative effects of habitat loss and fragmentation on the survival of a generic species, but are not useful for modelling specific case studies (Fahrig 1997; Fahrig 1998; Fahrig 2001; Ricketts 2001). The common resolution survey results suggested that most digitised landscape modelling uses square lattices, theoretical modelling studies use resolutions of  $100 \times 100$  or less and studies digitising real landscapes use resolutions of  $100 \times 100$  to  $200 \times 200$ . Despite the apparent commonality of map sizes comparisons are problematic, due to the widely differing scales.

## 2.7 Summary

Based on the review of relevant literature and existing (published) models presented in this chapter, it was determined that a model possessing the following characteristics would be required to meet the overall aim of this thesis (Section 1.3):

- Model both real and neutral landscapes
- Incorporate multiple habitat types
- Incorporate landscape transformation
- Model a real species, preferably more than one
- Be individual-based and incorporate realistic dispersal rules
- Generate a real-time (computer) visual output as well as stored results

Modelling real and neutral landscapes allows specific case studies and investigations into general effects to be undertaken (Sections 2.3.1 and 2.3.2). Modelling multiple habitat types increases realism by allowing the inclusion of habitat quality, rather than employing a

binary view of habitat/matrix (Section 2.3.3). To investigate and compare landscape and habitat management schemes, landscape dynamics should be modelled. If this were to include habitat quality dynamics, then the effects of habitat maturation and degradation could also be modelled (Sections 2.3.4 and 2.3.5). To apply the model to a specific landscape, real species should ideally be modelled (Section 2.4.4). To investigate the effects of landscape structure on population distribution and viability, the dispersal of individuals needs to be explicitly modelled (Section 2.4.5). To this end, the dispersal rules should incorporate elements such as dispersal mortality, perceptual range and field-of-view (Sections 2.4.6 and 2.4.7). To aid the acceptance of the model, a real-time visual output of the position of individuals should be possible (Section 2.2.2) and to enable post-simulation analysis, a set of numerical measures should be stored (Section 1.2).

The surveys of published models presented in Section 2.6 showed that a single model which provided all these features was not available, suggesting that a new one was required. To enable comparisons with existing models and theories, the new model should preferably be an extension of a commonly used type, in this case an SEPM combining a grid-based landscape with an individual-based population simulator (Section 2.2.2). The construction of the model, its application and analysis are described in the following chapters.

## 3. MODEL FRAMEWORK

### 3.1 Introduction

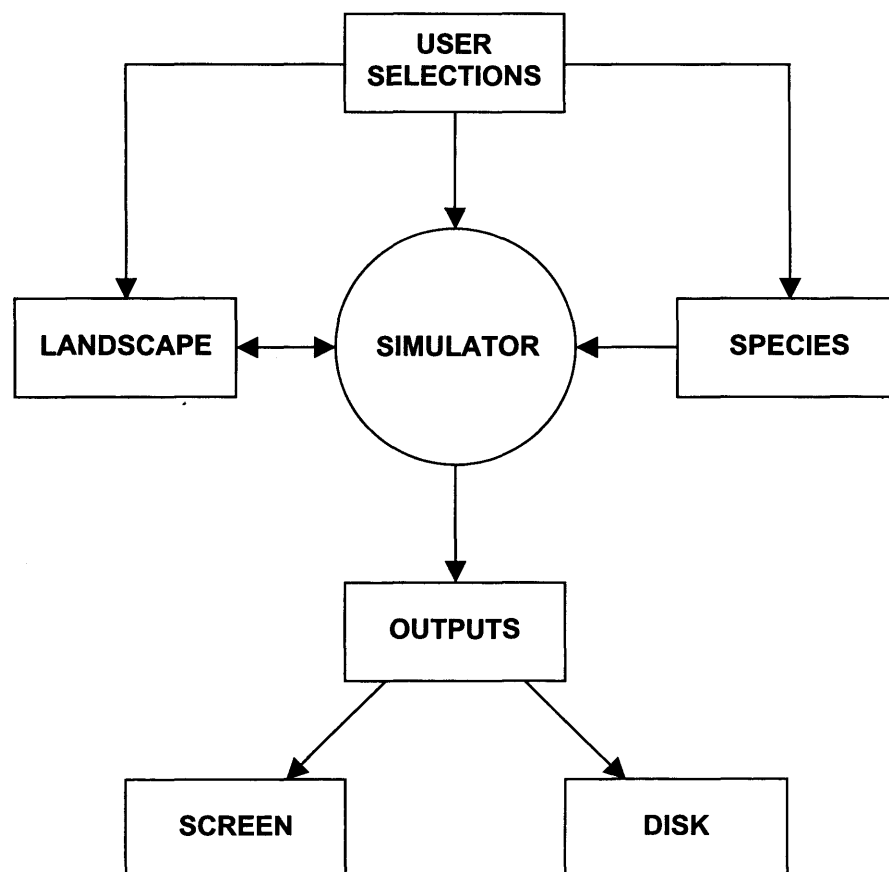
As stated in Section 2.7, a decision was made to design and build a new individual-based SEPM. The resultant model was called PatchMapper. This chapter describes the basic framework of the model. The following two chapters present the modelling of three different taxa, the model performance comparison tests and a set of sensitivity analyses.

### 3.2 Basic Principles

Some SEPM modelling approaches meet their requirements by combining existing packages, often with a custom built one (Rushton *et al.* 1997; Langevelde *et al.* 2000; Lurz *et al.* 2003; Macdonald and Rushton 2003). This method is unwieldy. Access to the source code and software licensing issues with the existing modules may make customisation difficult, as well as restricting use by other researchers. Building a new model allows for easy customisation during development and testing, meeting requirements as they arise. If care is taken with the choice of programming language and libraries, then software licensing issues can also be avoided.

Various programming languages are suitable for programming a SEPM, but if the model is to be widely used it must run on as many platforms as possible. Java, developed by Sun Microsystems, is an interpreted, object-oriented programming language (Wright 1998), which meets the requirements for portability (Appendix F). On the other hand, it has been suggested that for increased efficiency a procedural language such as C or Fortran would be more suitable, despite the loss in portability (Barnes and Hopkins 2003). It was decided to program the model in Java, as an acceptable compromise between portability and run-time efficiency.

A functional block diagram showing PatchMapper's main modules is given in Figure 3.1. Individuals of the chosen species inhabit the landscape, under control of the simulator module. The landscape can be either dynamic or static, with its structure directly affecting the behaviour of the modelled species. Populations are not directly modelled, but form as a direct consequence of the behaviour of the individuals. During the run, a real-time (computer) visualisation of the positions of individuals in the landscape is presented to the user. The results of the simulation, in the form of a set of landscape metrics and population demographics, are saved to disk and are also made available for direct display on the screen. The user's selections, entered via a set of interactive screens, control the overall simulation.

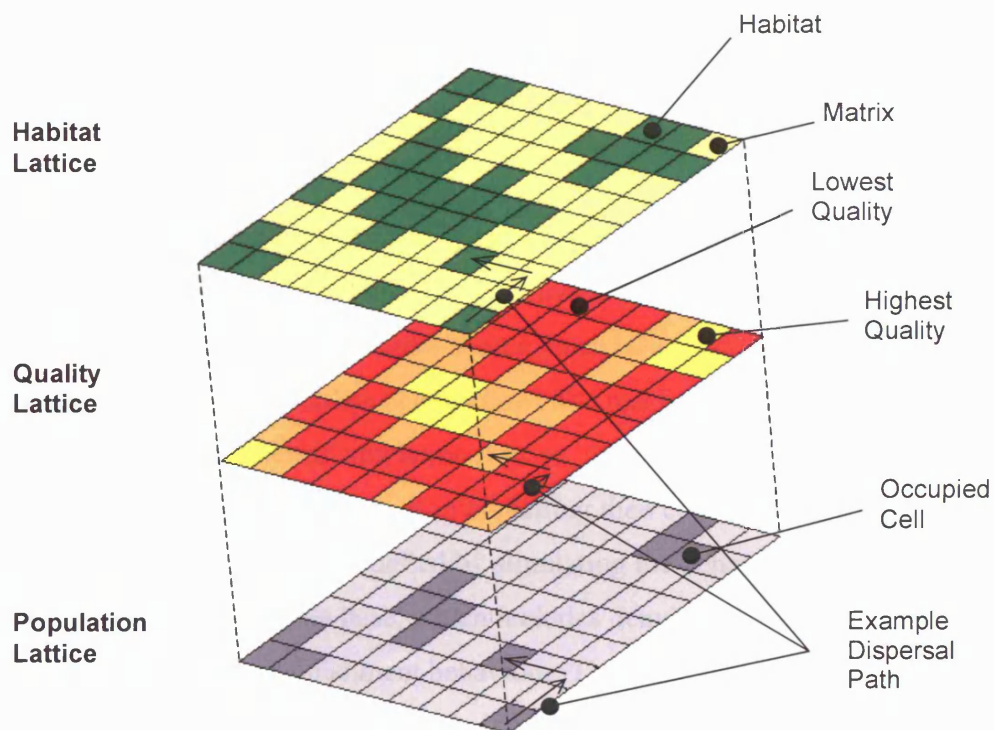


**Figure 3.1:** Functional block diagram of PatchMapper. The user's selections are entered via a set of interactive screens, as described in the text and Appendix I.

### 3.3 Model Structure

PatchMapper is based on a coupled-lattice design, encoded as a multi-dimensional array (Section 2.3.1). There are three lattices: habitat, quality and population (Figure 3.2). The habitat lattice contains a binary representation of habitat and matrix, in the form of a cartographic view of the landscape. The term matrix refers here to any area of the landscape that does not contain suitable breeding or foraging habitat, i.e. non-habitat.

The quality lattice has the same resolution as the habitat landscape, with four possible states, allowing the modelling of up to four levels of habitat quality. The population lattice contains details of the species being modelled, including information on residential status, occupancy status, territory size and demographic details. The exact use of the population lattice depends on the species being modelled (Appendix G.1).



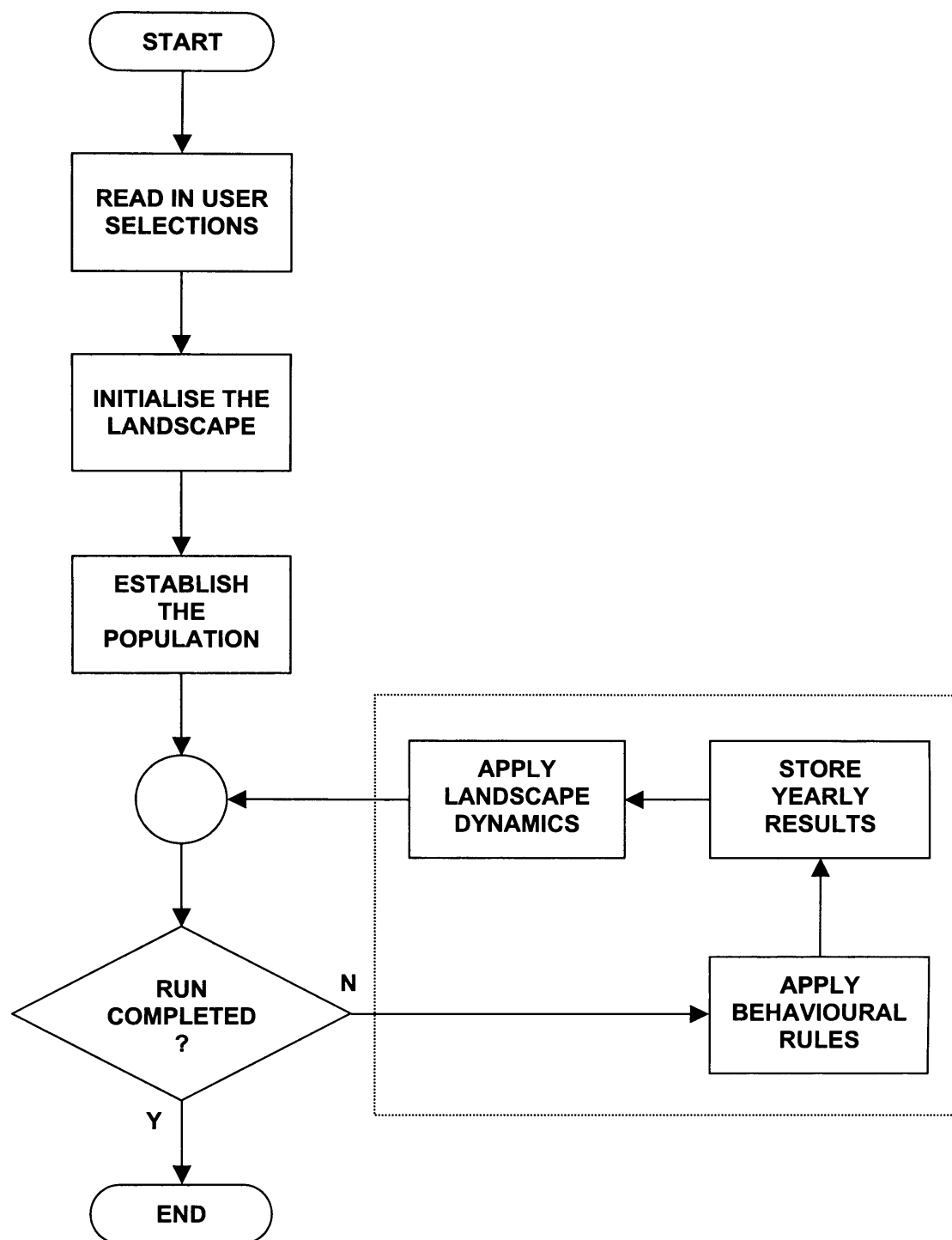
**Figure 3.2:** The coupled-lattice structure of PatchMapper, showing the habitat, quality and population lattices. The example dispersal path demonstrates the inter-lattice coupling. The various habitat and quality cell states are labelled. The darker shaded cells in the population lattice represent cells that are occupied and contain demographic details of the occupants.

During dispersal, reference is made to the habitat lattice and if the individual is on a habitat cell, reference is made to the corresponding cell in the quality lattice to determine behaviour appropriate to that quality level. In the case of the nuthatch (*Sitta europaea*) this could, for example, determine territory size (Matthysen 1990; Pravosudov 1993a; Bellamy *et al.* 1998).

Using different lattices for habitat and species modelling separates the algorithms, allowing changes in the landscape to be modelled without reference to the species' modelling algorithms. This forces a species to adapt to changes in habitat spatial arrangement and/or habitat quality as they are encountered. This method of modelling also allows different species to inhabit the same landscape and allows the same species to inhabit different landscapes, as selected by the user.

### 3.4 Overall Simulation Process

Figure 3.3 shows the overall simulation process. The required landscape is selected by the user and loaded under control of the simulator module. Landscapes can either be internally generated or imported from an external source (such as a GIS). Once the landscape is loaded, the population is established and allowed to reach equilibrium. This takes the form of a user-selectable number of simulation runs or 'pre-runs', during which no measurements are taken. The population modelling then continues for a user-selectable number of cycles. Species are modelled by simulating the behaviour of individuals, with reference to a behavioural rule base, which includes demographic characteristics as well as dispersal and territorial establishment behaviour. The exact nature of the rule base depends on the species being modelled. Results, in the form of a set of landscape metrics and demographic totals, are then recorded. Any landscape dynamics are next applied, allowing both the spatial structure and habitat quality of the landscape to be changed during the simulation. A counter keeps track of the current cycle and the sequence repeats until the required (user-selectable) number of cycles has been completed. The individual modules are described in more detail in the following sections.

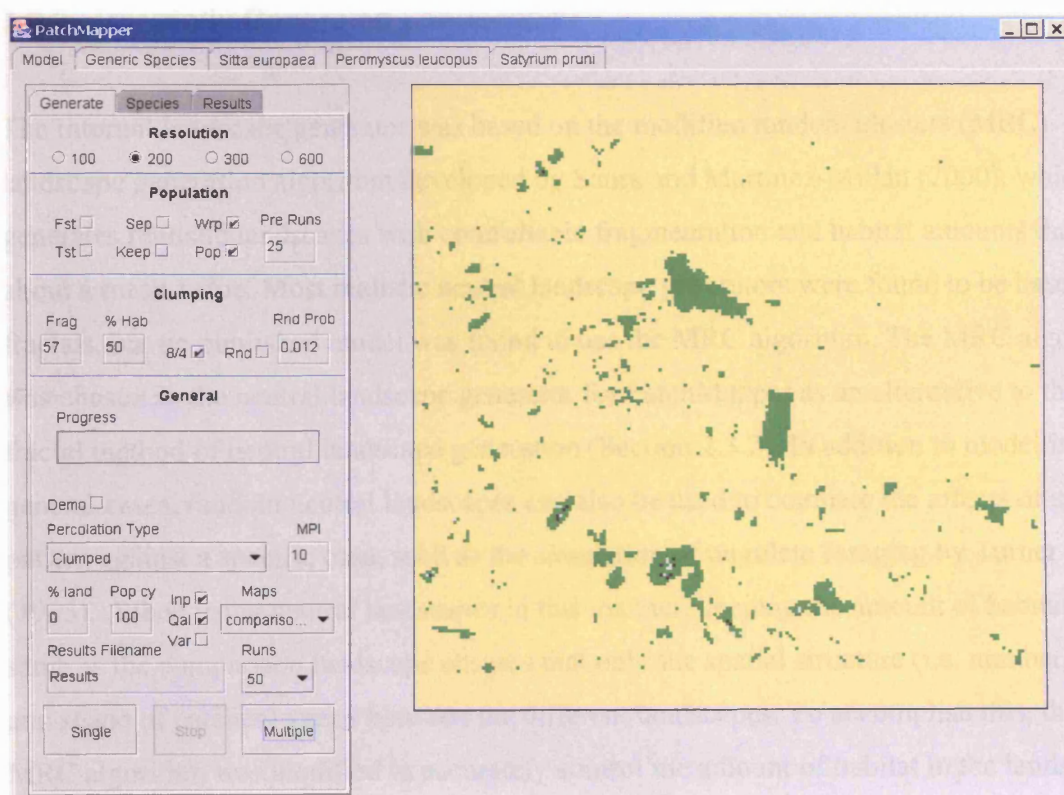


**Figure 3.3:** The overall simulation process. All the activities are under control of the simulation module. The processes within the dashed box show the main elements in the species simulation module. Landscape dynamics are only applied if selected by the user.

### 3.5 User Screens

The user initialises the simulation via a set of interactive screens. The main ‘model’ screen is used to control the simulation via three sub-screens labelled ‘generate’, ‘species’ and ‘results’. The ‘generate’ sub-screen allows control over the type of landscape to be loaded, landscape dynamics and model run time. The simulation is also started from this screen. Single or multiple runs are possible. A stop button is provided to allow the simulation to be halted at any time. The ‘species’ sub-screen allows selection of the species to be modelled and the ‘results’ sub-screen allows a choice of metric graphs to be displayed. The habitat and quality maps can be also displayed via controls on the ‘results’ sub-screen. Further screens are accessible from the main screen, allowing the user control over the species being modelled. Figure 3.4 gives an example ‘model’ screen, showing a landscape imported from a GIS. The control panel on the left hand side of the screen shows that the map is  $200 \times 200$  cells, a population has been selected and will run for 100 cycles after completing 25 ‘pre-runs’. The name of the loaded map is given. The user can specify a filename prefix to identify the saved results, which in Figure 3.4 has been set to ‘Results’. In this example the nuthatch is being modelled, with the black squares representing the current position of pairs of nuthatches and the white squares the position of single birds in the landscape. The display is dynamic and the positions of the individuals are updated with each cycle. All the user screens and controls are detailed in Appendix I.





**Figure 3.4:** An example ‘model’ user-screen, as described in the text.

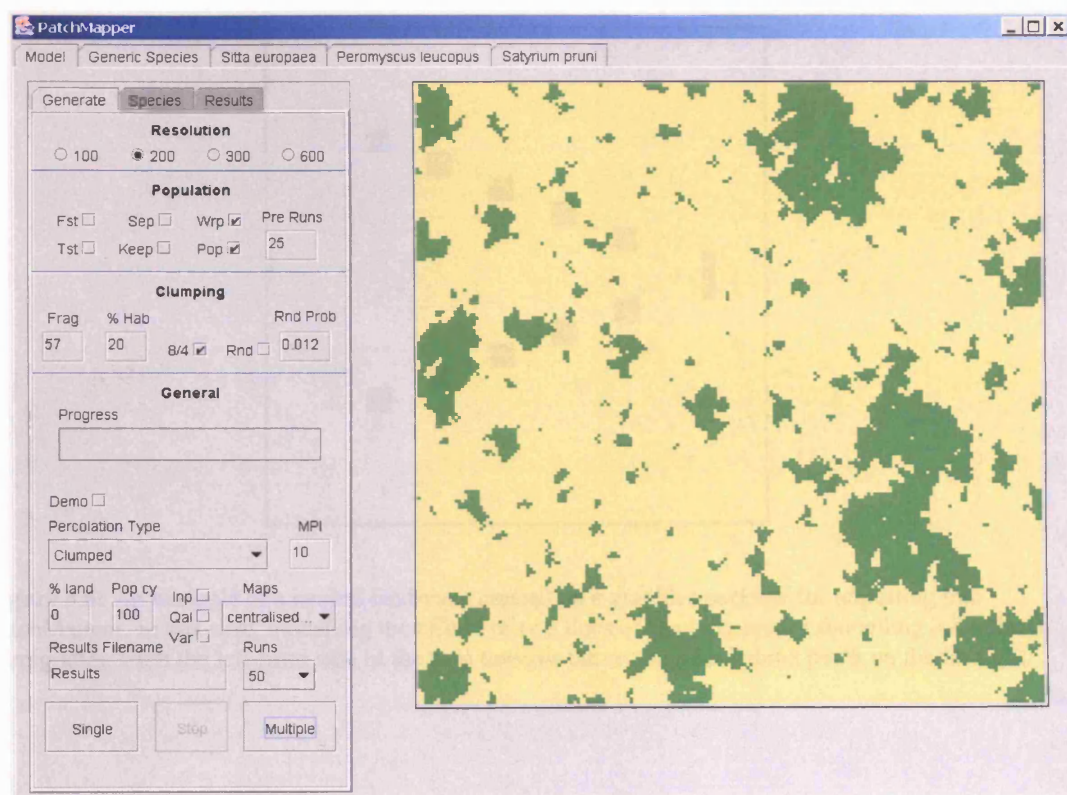
## 3.6 Landscape Modelling

### 3.6.1 Introduction

The habitat landscapes (Figure 3.2) are modelled in binary form (habitat and matrix), using a square celled lattice of  $100 \times 100$ ,  $200 \times 200$ ,  $300 \times 300$  or  $600 \times 600$  cells and can either be generated internally or imported. The landscape resolutions were chosen to span the range of commonly used SEPM landscape resolutions (Section 2.6.2.3). The internal landscape generator can be used to produce a set of random neutral landscapes for exploring general effects, whereas importing a landscape allows specific case studies to be undertaken. A method of changing both the habitat structure and the quality of the habitat during the simulation was also developed. These modules are explained further in the following sub-sections.

### 3.6.2 Internally Generated Landscapes

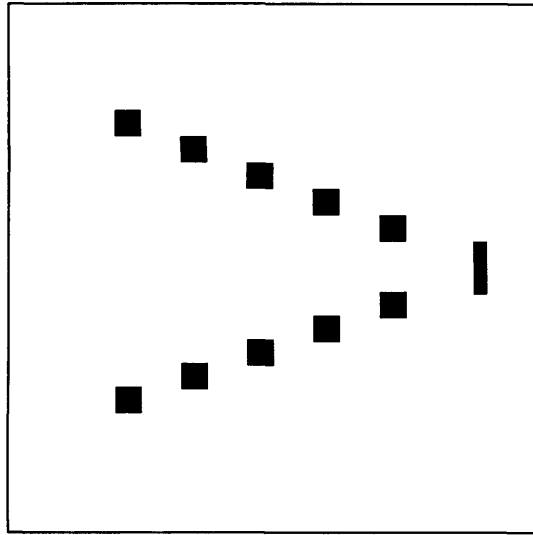
The internal landscape generator was based on the modified random clusters (MRC) landscape generation algorithm developed by Saura and Martínez-Millán (2000), which generates realistic landscapes with controllable fragmentation and habitat amounts that vary about a mean value. Most realistic neutral landscape generators were found to be based on fractals, but no published model was found to use the MRC algorithm. The MRC algorithm was chosen as the neutral landscape generator for PatchMapper as an alternative to the fractal method of neutral landscape generation (Section 2.3.2). In addition to modelling general cases, random neutral landscapes can also be used to compare the effects of spatial pattern against a specific case, such as the simulation of ungulate foraging by Turner *et al.* (1993). When using neutral landscapes in this manner, keeping the amount of habitat the same as the comparison landscape ensures that only the spatial structure (i.e. number, size and shape of patches) varies between the different landscapes. To accomplish this, the MRC algorithm was modified to accurately control the amount of habitat in the landscape to meet a ‘percentage habitat’ level, entered via the ‘% Hab’ input box (Figure 3.5). Once the initial landscape was generated, the required level of habitat cover was met by taking cells at the edge of patches at random and changing them and their eight neighbouring cells to either habitat or matrix to increase or decrease the habitat amount accordingly. Changing the neighbouring cells in addition to the selected cell kept the changes in line with the original clustering algorithm in preventing too many single-celled habitat or matrix patches. As a general control over the number of patches being generated, the ‘initial probability’ control used by Saura and Martínez-Millán (2000) was retained, labelled ‘Frag’ (Appendix I). This control allows the user to select the mean number of patches generated for a set of neutral landscapes. Figure 3.5 shows an example of an internally generated landscape.



**Figure 3.5:** An example of an internally generated neutral landscape with 20% total habitat cover. With a resolution of 40,000 cells ( $200 \times 200$  resolution), this gives a habitat area of 8,000 cells, with 315 habitat patches and 57 matrix patches (contiguous areas of non-habitat).

### 3.6.3 Imported Landscapes

To allow specific study areas and habitat configurations to be studied, landscapes can be imported from a GIS, be user-drawn with a graphics package or hand-drawn and scanned. Whatever the source, landscapes must be in 24-bit bitmap (.bmp) format and must match the required landscape resolution. Both habitat and quality landscapes can be imported, depending on the modelling requirements. Figure 3.6 gives an example of an imported neutral habitat landscape, drawn with a graphics package. The habitat and quality file formats are detailed in Appendix G.2.

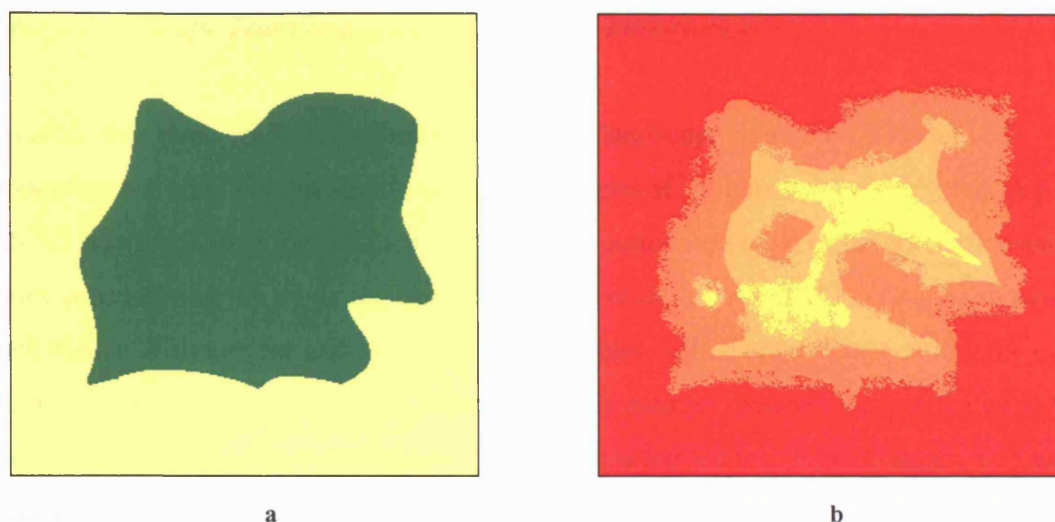


**Figure 3.6:** An example of a neutral landscape created on a graphics package for importing into PatchMapper. In this case, modelling the effects of two lines of stepping-stones funnelling individuals immigrating from the left-hand side of the map towards the rectangular habitat patch on the far right.

### 3.6.4 Modelling Habitat Quality

Within a particular habitat patch, it is likely that habitat quality will differ, resulting in variations in species density within the patch. To increase realism, the quality of a patch should therefore be modelled, in addition to its shape and location. To meet these requirements, PatchMapper can use two landscapes for each simulation, one for habitat structure and the other for habitat quality (Figure 3.2).

The exact use of the quality levels depends on the species being modelled, but one possible example could be to use the information in all three lattices (habitat, quality and population) to model territory size in relation to breeding habitat quality. Figure 3.7 gives an example of the habitat and quality landscapes used to model a fictitious wood. The utility of modelling habitat and habitat quality is further explored in Appendix H.



**Figure 3.7:** An example of the use of habitat and quality landscape modelling within PatchMapper. The habitat landscape models the shape of the wood (Figure 3.7a), with green (darker) representing habitat and yellow (lighter) representing the matrix. The quality landscape (Figure 3.7b) models habitat quality levels. The example here showing the four possible levels within the landscape, varying from unsuitable habitat shown in red (darkest) through to the most suitable type of habitat shown in yellow (lightest).

### 3.6.5 Modelling Landscape Dynamics

To reflect the dynamic nature of landscapes, PatchMapper was given the ability to model changes in the spatial structure of both habitat quality and the habitat itself. Two methods were provided: an internal landscape transformation algorithm and the controlled importation of a set of landscapes.

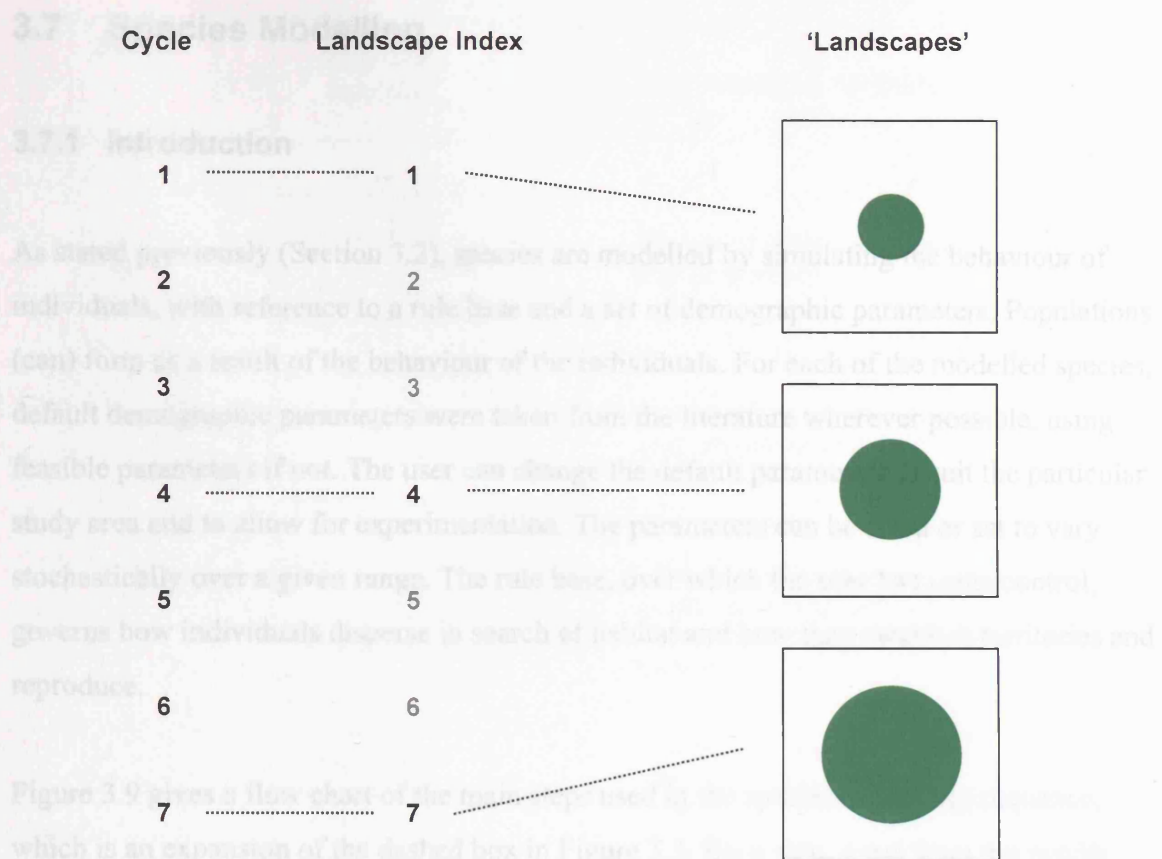
#### 3.6.5.1 Internal Landscape Transformation Algorithm

The internal dynamic modelling algorithm only affects the habitat lattice. Habitat cells at the edge of patches are selected at random and converted into matrix cells, reducing the amount of habitat in the landscape by a set (user-selectable) amount at each model cycle. Uses for this feature include investigating thresholds in neutral landscapes. The internal algorithm is limited due to a lack of control over which patches are affected, no option to increase habitat and the inability to model changes in quality. As such, it is unsuitable for modelling studies using real landscapes.

### 3.6.5.2 Landscape Transformation by Controlled Importation

To provide a more realistic method of modelling landscape dynamics, a system of importing different habitat and/or quality landscapes at set intervals was devised. A plain ASCII text file, called the 'landscape index' file, containing a list of numbers increasing in value representing the modelled cycle number, is required. A set of landscapes showing the new habitat structure for each of the modelled cycles is then created, appending the cycle number to the landscape filename. When the cycle counter matches the next value in the landscape index file, the corresponding landscape is loaded into PatchMapper. To model changes in the landscape, the user has only to draw up a set of landscapes and a landscape index file, a far more versatile approach than devising an algorithmic approach for each test scenario. Habitat area can increase, decrease or both. Scale and timing, from fine scale yearly changes through to drastic sudden changes in habitat cover are both under complete control of the user. Figure 3.8 gives an example of modelling a patch increasing in area over time. Extending the idea to the quality landscape enables changes in habitat quality to be modelled. Uses for this option include modelling habitat management schemes where habitat area may not change, but habitat quality does. A practical example could be exploring the effects of changes in forest rides on the wood white (*Leptidea sinapis* L.) butterfly. This method can also be used to model the simultaneous effects of habitat and habitat quality changes.





**Figure 3.8:** An example of modelling a patch increasing in size. As described in the text, whenever the cycle counter matches the next number in the 'landscape index' file, a new landscape is loaded, in this example at years 1, 4 and 7.

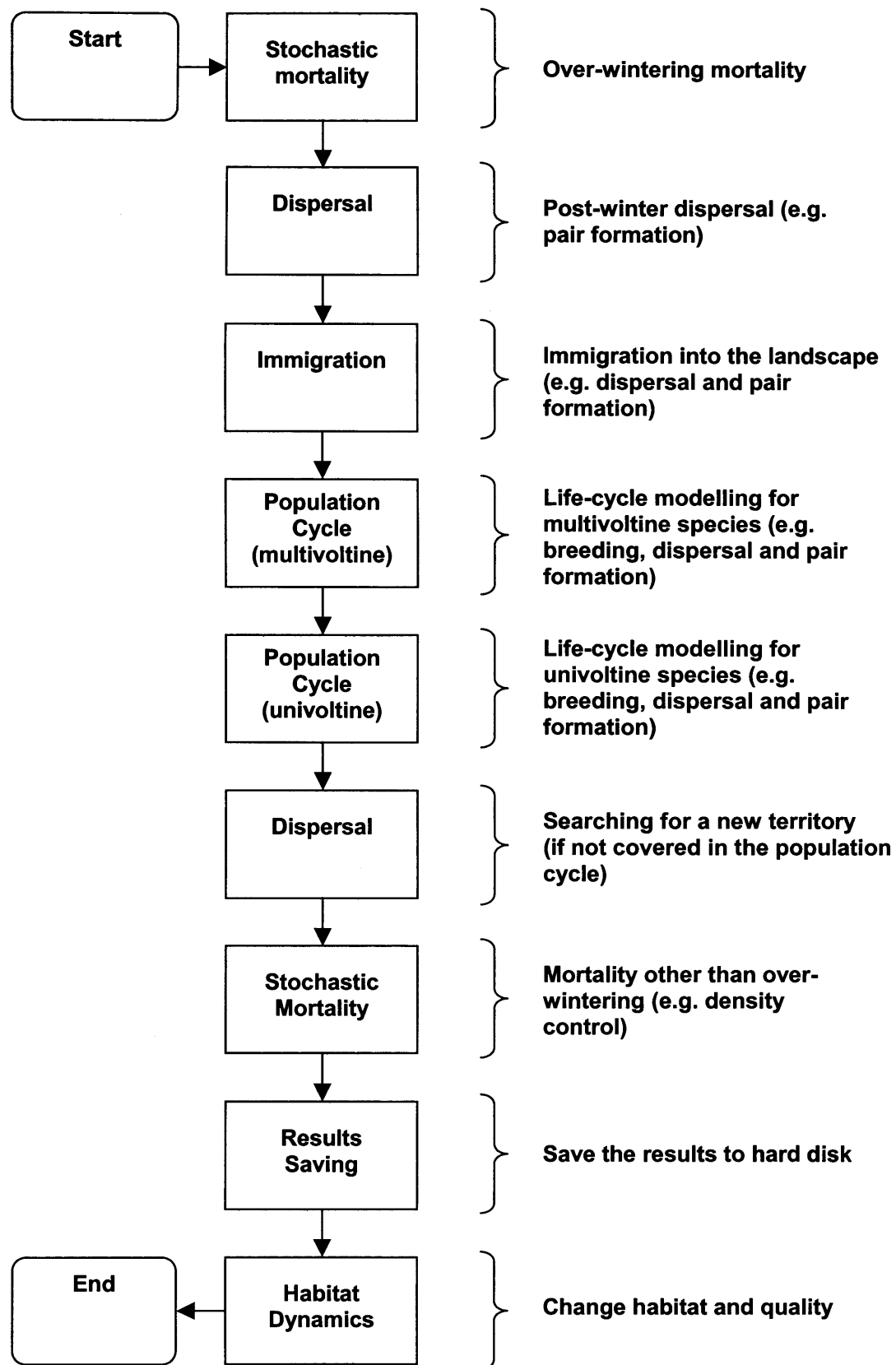
## 3.7 Species Modelling

### 3.7.1 Introduction

As stated previously (Section 3.2), species are modelled by simulating the behaviour of individuals, with reference to a rule base and a set of demographic parameters. Populations (can) form as a result of the behaviour of the individuals. For each of the modelled species, default demographic parameters were taken from the literature wherever possible, using feasible parameters if not. The user can change the default parameters to suit the particular study area and to allow for experimentation. The parameters can be fixed or set to vary stochastically over a given range. The rule base, over which the user has some control, governs how individuals disperse in search of habitat and how they establish territories and reproduce.

Figure 3.9 gives a flow chart of the main steps used in the species modelling sequence, which is an expansion of the dashed box in Figure 3.3. Each step, apart from the results saving and habitat dynamics steps, is implemented as an empty method (signature only) in a base species class. In this manner, the same controlling method is used for all species, with individual behaviour being modelled by overriding the appropriate methods in the individual inheriting species classes as required. Note that not all methods are used by all species.





**Figure 3.9:** The population modelling sequence, showing the methods provided in the base species class, along with a brief functional description. As described in the text, the methods have no body and are overridden in the individual inheriting species classes as required (if not overridden, no action is taken). (The 'results saving' and 'habitat dynamics' methods are implemented in the simulator module.)

### 3.7.2 Modelling Immigration and Perceptual Range

Immigration rate and direction and perceptual range are user-selectable, depending on the species being modelled. These parameters are rarely found in existing published SEPMs (Section 2.6.2) and were added to PatchMapper to increase realism and to allow the effects of landscape structure on population viability to be investigated.

In a real landscape, as dispersing individuals are unlikely to be constrained by arbitrary study area dimensions, they can be expected to both leave and enter the study area. This can be modelled with wrapped or reflective boundaries (Pulliam *et al.* 1992; Venier and Fahrig 1996; Butler 2003), but these approaches have the disadvantage that immigration rate and direction cannot be controlled. PatchMapper models emigration by ‘losing’ an individual once it crosses the landscape edge (an absorbing boundary). To model immigration into the landscape, from a nearby external source for example, both the rate and direction of immigration were made user-selectable. Immigration rate is modelled as an annual number of immigrants. Immigration direction can be from one of the cardinal or quadrantal compass points or from all points. Individuals enter the landscape from a position chosen at random along the selected landscape edge, sampled from a uniform distribution.

Published models using wrap-around or reflective immigration, such as Bachmap (Pulliam *et al.* 1992), may give misleading predictions. Reflective boundaries assume that an immigration source with a rate equalling the emigration rate at a particular point lies beyond the study area boundary at that point. Likewise, wrap-around boundaries assume that an immigration source, with a rate equalling the emigration rate at a particular point, lies at a point beyond the opposite study area boundary. Both cases are possible, but unlikely. Patch immigration and emigration rates are often asymmetrical (Gustafson and Gardner 1996; Ferreras 2001) and immigration direction and rate can have a large influence on population sizes (Alderman *et al.* 2004, reproduced in Appendix B.1), indicating that these inputs should be both separate and controllable, with the modelled landscape allowing emigration through absorbing boundaries.

Perceptual range, or the distance over which a particular species is able to distinguish between different landscape elements (Lima and Zollner 1996; Schooley and Wiens 2003), probably plays a key roles in species' response to habitat fragmentation. To further incorporate the possible effects of landscape structure on dispersal patterns (Travis and French 2000), a habitat perceptual range mechanism was added to the basic dispersal rules, allowing the disperser to move directly to the nearest suitable habitat patch if within the specified range. The perceptual range algorithm searched all cells within the user-selected range, fanning out progressively from the origin. Implicit in the concept of habitat perceptual range is the species' field-of-view, but published coverage of this subject is sparse (Section 2.4.7). The user can select perceptual range as a combination of a number of cells and three fields of view: straight-ahead, 90° or 180°. The perceptual range and field-of-view algorithms are further explained in Section 4.2.4.

### 3.7.3 Multi-Species Modelling

The species module employs inheritance and polymorphism, with run-time binding. The different species objects inherit their methods and variables from the base species class, enabling each species to have its own behavioural rule base. The user selects which species to model and at run time an instance of each selected species is placed in an array of species objects. Up to four species can be modelled simultaneously. The order in which each species is placed in the array is also user-selectable, allowing a more dominant species to establish a territory over a less dominant one. Inheriting from the base species class enables additional species to be added at a later date, without altering any existing code (apart from the user interface). A set of four generic species and three specific species: the nuthatch, the white-footed mouse (*Peromyscus leucopus*) and the black hairstreak (*Satyrrium pruni*) are currently modelled. Details of the modelled species are given in Chapter 4 and Appendices D and G.1.

## **3.8 Model Outputs**

### **3.8.1 Introduction**

The model outputs consist of a real-time (computer) display and a set of landscape pattern metrics and population demographics. The metrics and demographics are saved for future analysis and can also be displayed on the screen. The various outputs are further detailed in the following sub-sections.

### **3.8.2 Real-Time (Computer) Display**

Visual feedback of the simulation is a potentially important factor in aiding the acceptance of a SEPM (Section 2.2.2): the literature is, however, short on examples (Section 2.6.2). As stated earlier (Section 3.2), PatchMapper provides a real-time (computer) display of the positions of the individuals in the loaded landscape during the simulation (Figure 3.4), enabling a visual judgement of the effect of various habitat and habitat quality scenarios on the viability and distribution of the population. Another use for a graphical output is during program development, often providing indication of a programming error or poor parametisation that would otherwise probably be missed (Railsback 2001).

### 3.8.3 Landscape Pattern Metrics and Population Demographics

To allow a statistical analysis of the simulation results, sets of landscape pattern metrics and population demographics are calculated and saved to disk in the comma separated variable (.csv) format (for widespread compatibility), using a different file for each measure.

The chosen spatial measures included the commonly used pattern metrics revealed by the survey of commonly used metrics (Appendix E.3). The mean proximity index (MPI) was substituted for mean nearest neighbour metric, to allow some control over the measure (McGarigal and Marks 1995) and two further metrics were added: maximum patch area (Pmax) and the number of single and multi-celled patches (NP Split). These two additions were found to be useful during program development. All metrics, with the exception of total edge (TE) and the class area (Habitat CA) were calculated for both habitat and matrix patches (Table 3.1). The demographic measures provided were those found to be useful during program development and are listed in Table 3.2.

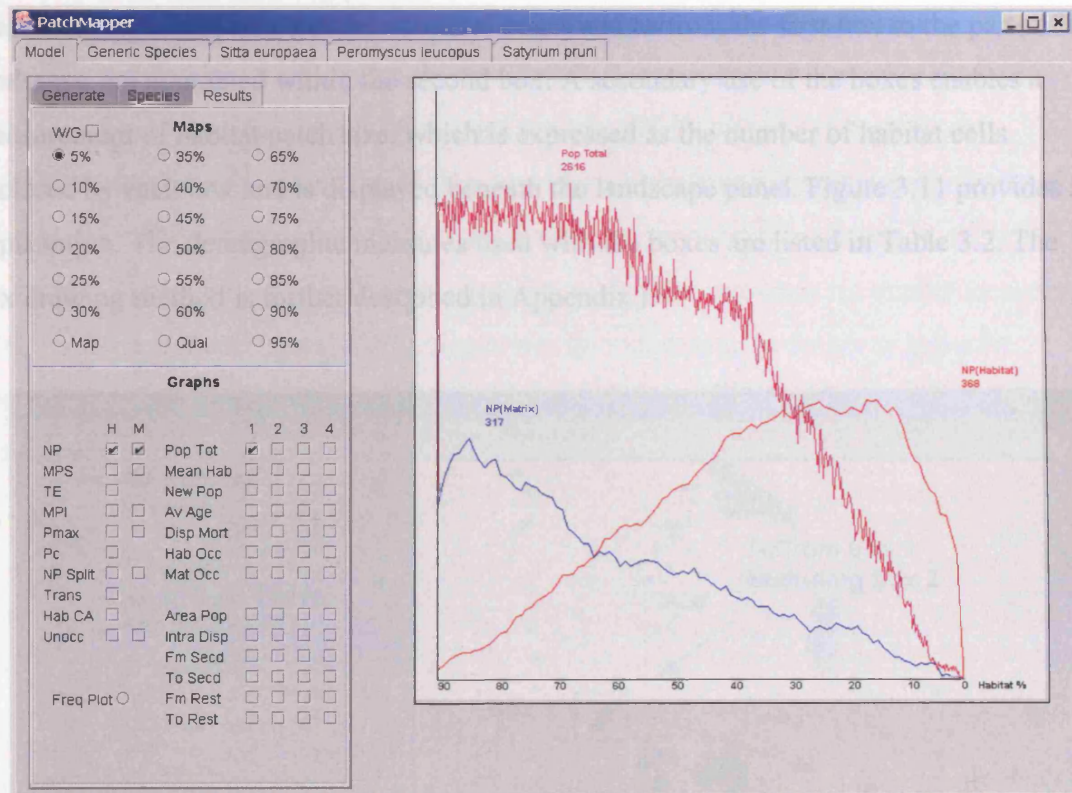
Pattern metric	Description
NP	Number of patches: Habitat and Matrix
MPS	Mean patch size: Habitat and Matrix
TE	Total edge
MPI	Mean proximity index: Habitat and Matrix
Pmax	Maximum patch area: Habitat and Matrix
Habitat CA	Total area of habitat
NP Split	Number of single and multi-celled patches: Habitat and Matrix

**Table 3.1:** The landscape pattern metrics recorded at the end of each (yearly) modelling cycle. The left hand column gives the labels used for the metrics on the 'Results' sub-screen (Figure 3.10; Appendix I).

<b>Population demographics</b>	<b>Description</b>
Pop Tot	Number of individuals in the landscape
Mean Hab	Population density per unit area of habitat
New Pop	Number of newly established territories following dispersal
Av Age	Average age of the population
Disp Mort	Level of dispersal mortality
Hab Occ	Number of occupied habitat or target habitat patches
Mat Occ	Number of occupied matrix or non-target habitat patches
Unocc	Number of unoccupied habitat patches
Area Pop	Number of individuals in the first box
Intra Disp	Number of successful dispersals within the first box
Fm Sec	Number of successful dispersals from the second to the first box
To Sec	Number of successful dispersals from the first to the second box
Fm Rest	Number of successful dispersals from outside the second box to the first box
To Rest	Number of successful dispersals from the first box to outside the second box

**Table 3.2:** The population demographic measures recorded at the end of each (yearly) modelling cycle. The left hand column gives the labels used for the metrics on the ‘Results’ screen (Figure 3.10; Appendix I). The population demographics are recorded separately for each species. The first and second boxes are drawn by the user and are explained in the text (Section 3.8.4) and Appendix I).

The 'Results' sub-screen enables the user to display a graph of the different measures (Figure 3.10). This option is meant for a quick visual comparison as although multiple measure can be displayed, the y-axis scaling varies across the measures.



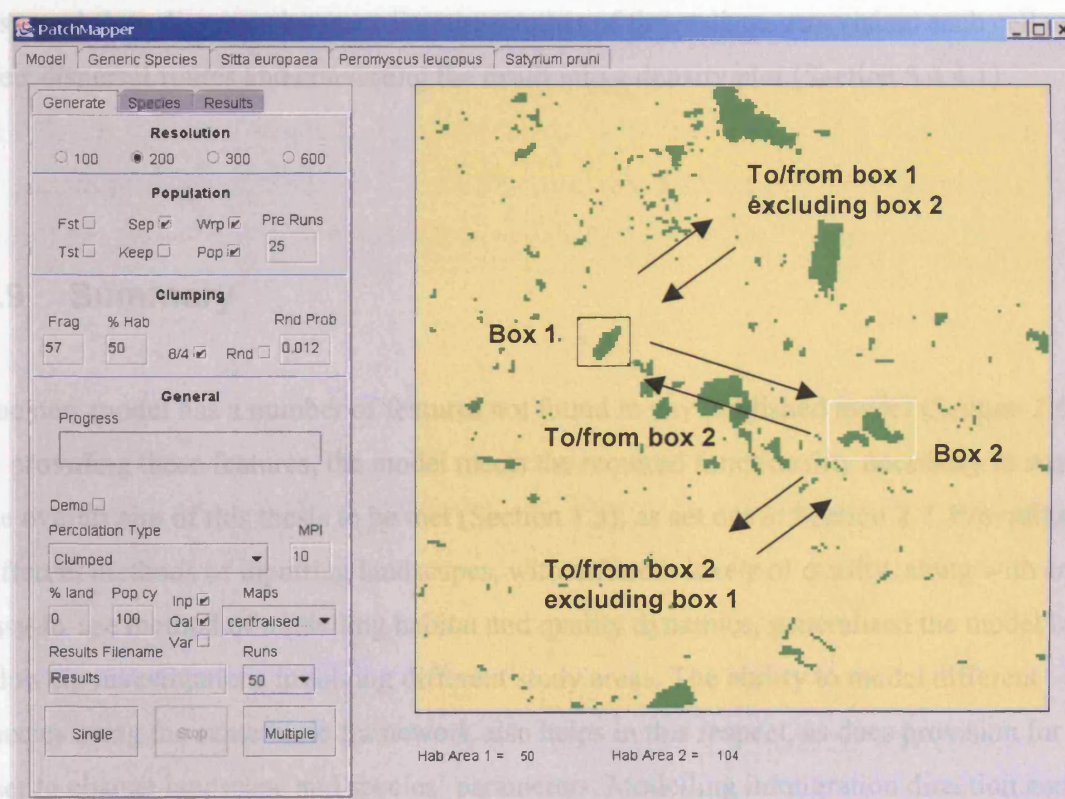
**Figure 3.10:** The 'results' user-screen, showing graphs for the number of habitat and matrix patches, along with the number of individuals in the landscape. In this example, a generic species is being modelled in an internally generated neutral landscape, with the landscape changing from 90% to 0% habitat coverage during the simulation. The figure also shows the other metric graphs that can be displayed.

### 3.8.4 Recording Patch Demographics

Designing an individual-based SEPM to measure population demographics for the whole landscape is accomplished by keeping running totals. Measuring population demographics for a particular patch cannot be easily undertaken in the same manner (Section 2.5.1). If the model is to be useful then it must be able to work with different landscapes. Patch sizes and positions vary and the large numbers of patches in a typical fragmented landscape means that the size and location of each patch cannot realistically be recorded. As an example, the



20 × 20 km ‘centralised’ landscape described in Section 4.3.2, which was used for some of the nuthatch model tests, has 235 woods. To overcome this problem, a facility to enable the user to draw two boxes over the loaded landscape was devised. The first box, displayed in black, is used for recording population size; the second one, displayed in white, enables the measurement of dispersal between the two boxes and to/from the first box to the parts of the landscape not contained within the second box. A secondary use of the boxes enables a measurement of habitat patch size, which is expressed as the number of habitat cells enclosed by each box and is displayed beneath the landscape panel. Figure 3.11 provides an explanation. The demographic measures used with the boxes are listed in Table 3.2. The box drawing method is further described in Appendix I.



**Figure 3.11:** A screen shot of a landscape imported from a GIS showing the principles behind the user-drawn boxes. The different measures allow separation of immigration and emigration rates, allowing dispersal flow patterns and population sinks and sources to be identified.



### 3.8.5 Recording Dispersal Flow Paths

By recording the paths travelled by dispersing individuals, dispersal flow diagrams can be created, which can be used to predict the existence of inter-patch dispersal flow paths and the effects of habitat changes on those paths. Following a literature search, only one individual-based SEPM was found to use a dispersal flow diagram to predict dispersal in a real landscape. Schippers *et al.* (1996) used their model Gridwalk to construct an ‘accumulated walking pattern’ to predict the effect of landscape barriers on the dispersal pattern of 10,000 european badgers (*Meles meles* L.), from a single starting point within the landscape. Their model was not used to predict inter-patch dispersal. To enable an analysis of inter-patch dispersal flow, PatchMapper was provided with an option to generate dispersal flow diagrams by recording the number of times dispersers visited each cell on their dispersal routes and converting the result into a density plot (Section 5.4.4.1).

## 3.9 Summary

The new model has a number of features not found in any published model (Section 2.6.2). In providing these features, the model meets the required functionality necessary to enable the overall aim of this thesis to be met (Section 1.3), as set out in Section 2.7. Providing different methods of inputting landscapes, with different levels of quality, along with an easy-to-use method of modelling habitat and quality dynamics, generalised the model by allowing investigations involving different study areas. The ability to model different species using the same basic framework also helps in this respect, as does provision for the user to change landscape and species’ parameters. Modelling immigration direction and rate into the study area, in conjunction with absorbing landscape boundaries, enables study area immigration to be taken into account in a realistic manner. Incorporating perceptual range increases realism by allowing spatial structure to directly affect population viability and distribution. Modelling in this manner, by simulating individual behaviour and allowing the structure of the landscape to govern population distribution, removes the need to explicitly model essentially unviable and potentially restricting parameters, such as the

fraction of individuals entering or leaving individual patches and dispersal distance functions (redistribution kernels). The provision of real-time (computer) and saved numerical outputs widens the potential audience by enabling visual demonstrations, as well as statistical analyses.

SEPMs should be portable (Turner *et al.* 1995). The best choice of programming language to meet this requirement is Java. It is (currently) free and without restrictions on program deployment. Java's *write once, run many* paradigm means that a single version of the program will run on any operating system for which a Java Virtual Machine has been developed (Appendix F). Currently, these include Linux, Macintosh OS, Solaris and the various flavours of Microsoft Windows.

The resultant model, PatchMapper, is offered as a portable, generalised individual-based SEPM, which can be adapted to different scenarios by providing a wide range of user-selectable parameters. The next chapter describes the modelling of the nuthatch, the white-footed mouse and the black hairstreak as representatives of three major taxonomic groups.

## 4. SPECIES MODELLING

### 4.1 Introduction

This chapter presents the modelling of three species: the nuthatch (*Sitta europaea*), the white-footed mouse (*Peromyscus leucopus*) and the black hairstreak (*Satyrrium pruni*). These species were chosen as they belong to three different classes with differing ecological requirements. The nuthatch is a univoltine species, in which juveniles disperse to form mutually exclusive territories. The white-footed mouse is a multivoltine species, with a requirement for a home range rather than a territory. The black hairstreak is a univoltine species, which has no requirement for either a territory or a home range. If the model can cope with three distinctly different taxa, albeit from the same kingdom, it would confirm the robustness of the modelling and demonstrate its wider application to other species in similar taxa. In addition to descriptions of the models, applications and performance comparisons are also described. A sensitivity analysis of the models is presented in the next chapter.

### 4.2 Modelling the Nuthatch

#### 4.2.1 Introduction

The scarcity of the nuthatch in an area in eastern England, centred on Monks Wood (52°24'N, 0°14'W) in Cambridgeshire, has been the subject of several studies (e.g. Hinsley *et al.* 1995; Bellamy *et al.* 1998). The study by Bellamy *et al.*, compared predictions of wood occupancy generated by a model using a different technology to PatchMapper, with observed occupancy levels. While expanding its range in the U.K. since the 1970s (Gibbons *et al.* 1993), and in other parts of Cambridgeshire since the 1980s (Bircham *et al.* 1994; Clark 1996), the nuthatch is still scarce in the Monks Wood area. The main reason for this absence was thought to be the fragmented nature of suitable habitat and its isolation from other nuthatch populations (Bellamy *et al.* 1998).

Taking into account the demographic and behavioural characteristics of the nuthatch and the availability of landscape and habitat occupancy data, including a suitable published comparison modelling study, the nuthatch was selected as the first species to be modelled with PatchMapper's individual-based SEPM approach.

Nuthatches were modelled by applying behavioural rules to each individual bird. Territories were established, pairs formed and breeding undertaken, with reference to landscape structure and habitat quality (Section 3.3). The nuthatch model has two main sections: demographic and behavioural modelling and landscape and territory modelling. The individual components of the model are described in the following sub-sections. Figure 4.1 shows the user-screen for the nuthatch model.

**Figure 4.1:** The 'nuthatch' user-screen, where the user selects suitable demographic, territorial and dispersal parameters. The various controls are detailed in Appendix I.

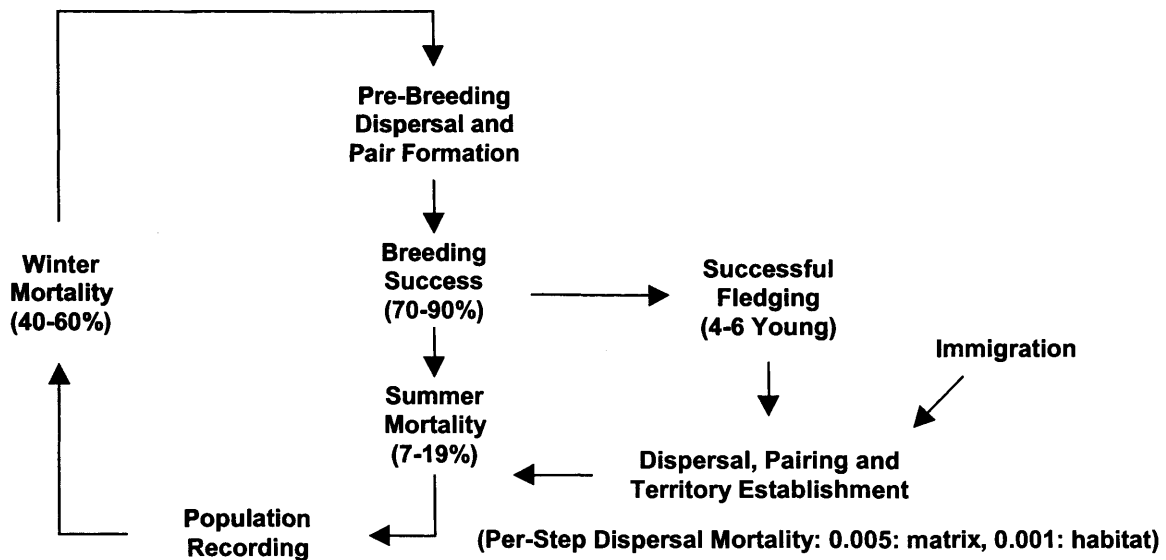
### 4.2.2 Lifecycle Stages and Parameters

Resident in the UK, the nuthatch is a small (c. 22-26 g) cavity-nesting, woodland passerine bird species (Nilsson 1976), which has been shown to be sensitive to forest fragmentation (Enoksson *et al.* 1995; Bellamy *et al.* 1998). The species lives in pairs throughout the year, in mutually exclusive territories (Nilsson 1987; Matthysen 1990; Wesolowski and Stawarczyk 1991; Matthysen and Adriaensen 1998). Widely distributed throughout Europe and Asia (Pravosudov 1993a; Matthysen 1998), breeding takes place in spring and the species is usually single brooded (Nilsson 1987; Wesolowski and Stawarczyk 1991). Juvenile nuthatches disperse from the natal site and establish new territories and begin pair formation in late summer (Nilsson 1987; Pravosudov 1993b). Dispersal from the natal patch, in search of suitable quality breeding habitat is common in fragmented habitat (Matthysen *et al.* 1995; Matthysen and Currie 1996). Mortality is highest in the winter (Nilsson 1987; Matthysen 1990), leaving territory vacancies. In early spring, a period of pre-breeding dispersal provides a chance for any singleton individuals to form pairs and to occupy existing territories or to form new ones, as appropriate (Matthysen 1989a; Pravosudov 1993b). Territories are usually established before March, when breeding starts (Matthysen 1989b). Once settled, nuthatches are extremely sedentary (Nilsson 1987; Paradis *et al.* 1998).

These characteristics, employing parameters taken from the literature (Table 4.1), were used to model the behaviour of each individual bird. The overall model flow is given in Figure 4.2, which also shows the default nuthatch parameters used for the nuthatch tests described in this thesis. Locations of nuthatches are stored in the population lattice (Figure 3.2), the structure of which is presented in Appendix G.1. The simulation was based on a yearly cycle, with population size, dispersal mortality, average age and other demographic statistics recorded at the end of each cycle. To model stochastic variation in the demographic and environmental parameters, the summer and winter mortality probabilities, along with the breeding success probability and the number of successfully fledged young were sampled from a uniform distribution between the upper and lower limits given in Figure 4.2.

Territory size (ha)	Winter Mortality (%)	Summer mortality (%)	Annual mortality (%)	Breeding success (%)	Mean brood size/female	Mean fledged young/female	General study area	Reference
			50				Belgium	Matthysen (1986)
	46	15	54	72% (SD=16.5)		3.72 (SD = 1.5)	Sweden	Nilsson (1987)
		7-19	58-64				Belgium	Matthysen (1989a)
	30-60		50				Belgium	Matthysen (1990)
2.08 (Good Habitat)			40-50	58-89 72 (Sweden) 83 (SW Germany) 91 (U.K.)	6.2		Poland	Wesolowski and Stawarczyk (1991)
30 (21-41)			32.8 (mean)				Siberia	Pravosudov (1993b)
				57.5 (41.9-78.2)	5.97 (4.83-7.4)	5.11 (3.6-6.33)	Siberia	Pravosudov (1993a)
			43			4.26	Belgium	Matthysen <i>et al.</i> (1995)
1-2 (Good Habitat)							U.K.	Bellamy <i>et al.</i> (1998)
					6-8		Belgium	Currie and Matthysen (1998)
1.58-1.85				75	6.5	5	Belgium	Matthysen and Adriaensen (1998)

**Table 4.1:** Published sources of demographic and territorial characteristics of the nuthatch used to parametrise PatchMapper's nuthatch simulator. The parameters used for the simulations in this study are given in Figure 4.2.



**Figure 4.2:** The nuthatch lifecycle as modelled by PatchMapper. The steps were implemented as methods in the nuthatch class, which are called during the simulation process via the base species class (Section 3.7.1). The immigration input allows individuals to disperse from distant sources into the study area. The figures refer to the parameters used for the tests in this thesis, based on published data (see text and Table 4.1) and during the simulation vary stochastically over their ranges, as described in the text. Note that absorptive landscape boundaries are employed, which means that emigration occurs as part of the simulation process and is therefore not explicitly modelled.

### 4.2.3 Movement Rules

Searching for fragmented habitat within a landscape involves searching a heterogeneous space for a habitat patch. The detection of a patch is paramount and dispersal mortality, together with habitat perceptual range and an efficient search algorithm, are likely to play a significant part in successful dispersal. Searching for a suitable vacant territory involves searching within a homogenous space (the patch) and making decisions based on gender-based territory availability, bringing a different set of behavioural responses into play. Dispersal mortality is likely to be lower than in the open and habitat perceptual range is less likely to be useful. To accommodate these differences, two movement algorithms were employed, covering inter- and intra- patch movement.

## 4.2.4 Inter-patch Movement

### 4.2.4.1 Basic Principles

In the model, dispersing nuthatches search for habitat by traversing the matrix with a correlated random walk (Section 2.4.5), combined with a per-step dispersal mortality and user-selectable perceptual range and field-of-view. On leaving the natal site, individuals are each assigned a dispersal direction, chosen at random from the set of cardinal and quadrantal directions. On leaving the patch, dispersers ‘look’ for habitat within an arc of  $180^\circ$ , and up to a distance determined by a user-selectable perceptual range. If a habitat patch is detected, the disperser moves directly to that patch. If not, it resumes the search, dispersing in a random direction. During the simulation, individuals may disperse from natal patches or immigrate into the study area from the landscape boundary. In both scenarios, dispersers are searching for a suitable vacant territory and therefore use the same inter-patch movement rules. When a habitat patch is encountered, it is searched for good quality breeding habitat. If none is found, the search is resumed for a new patch. If good quality breeding habitat is found, then depending on its occupancy status, a new territory is established, a pair formed or, if no suitable vacancy exists, the disperser is forced to search for further suitable habitat within the wood, or to search the matrix for another wood. As described in Section 3.7.2, absorptive landscape boundaries are modelled, together with user-selectable immigration rate and direction. Immigration takes place in ‘late summer’ (Figure 4.2). An individual nuthatch enters the landscape from a position chosen at random along a landscape edge, sampled from a uniform distribution (Section 3.7.2). Gender alternates for each immigrant. Immigration rate is modelled as a yearly number of immigrants (the rate was fixed for the nuthatch tests described in this thesis).

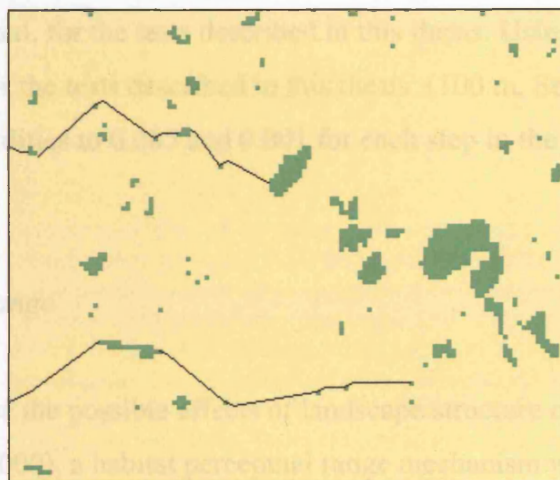


#### 4.2.4.2 Correlated Random Walk

To create the correlated random walk, the disperser moves one cell in the ascribed dispersal direction followed by one cell in an orthogonal direction, determined at random from a uniform distribution:

$$\text{Orthogonal Direction} = \begin{cases} \text{Left} & P < 0.5 \\ \text{Right} & P \geq 0.5 \end{cases}$$

At the scale of the grid, the resulting inter-patch dispersal paths represent nearly straight ‘zig-zags’ across the landscape. The scale chosen for modelling the landscape (1 cell = 1 ha, Section 4.3.2) meant that features smaller than 1 ha could not be modelled. During dispersal across the matrix, it is likely that a nuthatch would take shelter in single trees or small woods and the actual dispersal path would therefore most likely be more ‘zig-zag’ than straight. To illustrate the results, Figure 4.3 shows the dispersal paths taken by two birds entering the left hand side of the landscape.



**Figure 4.3:** The dispersal paths of two birds undertaking the correlated random walk as they immigrate into a landscape. (Both the habitat and quality landscapes shown in Figure 4.8 were used to create this example.) The top trace shows a bird successfully reaching a wood containing suitable ‘good’ quality breeding habitat (Table 4.2). The lower trace shows a bird reaching an unsuitable habitat patch and perishing in the process.

#### 4.2.4.3 Dispersal Mortality

The predator most likely to be encountered by dispersing nuthatches is the sparrowhawk (*Accipiter nisus* L.), although other avian predators such as kestrel (*Falco tinnunculus* L.) and hobby (*F. subbuteo* L.) may also be a threat (Newton 1986). Vulnerability, once pursued, would be greater in the open than in woodland.

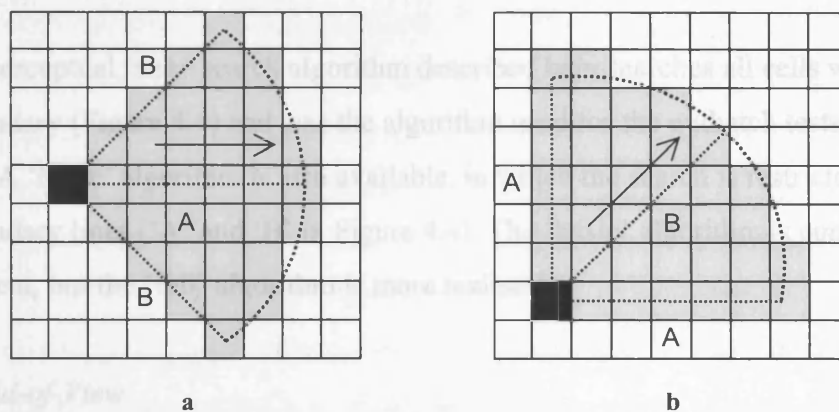
Dispersal in PatchMapper is modelled as cell-to-cell movement. Dispersal mortality is modelled by applying a probability of mortality at each movement step, by sampling from a uniform distribution. Only two examples of per-step dispersal mortality covering small birds were found in the literature. Pulliam *et al.* (1992) used probabilities of 0.04, 0.08 and  $0.4 \text{ km}^{-1}$  and Liu *et al.* (1995) who used  $0.08 \text{ km}^{-1}$ , both modelling Bachman's sparrow (*Aimophila aestivalis* Lichtenstein) using the Ecocon model. Reflecting the lack of dispersal data, Pulliam *et al.* (1992) chose their values to span the range of values thought feasible for the species. Taking these findings into account, in conjunction with published dispersal mortality rates (Section 2.4.6), per-step dispersal mortality probabilities equivalent to  $0.05 \text{ km}^{-1}$  were chosen for dispersal within the matrix and  $0.01 \text{ km}^{-1}$  for within-habitat dispersal, for the tests described in this thesis. Using these values at the modelled step size for the tests described in this thesis (100 m, Section 4.3.2), set the per-step dispersal probabilities to 0.005 and 0.001 for each step in the matrix and habitat respectively.

#### 4.2.4.4 Perceptual Range

To further incorporate the possible effects of landscape structure on dispersal patterns (Travis and French 2000), a habitat perceptual range mechanism was added to the basic inter-patch dispersal rules, allowing the disperser to move directly to the nearest wood within the specified range (Section 2.4.7). The distance at which a disperser perceives a wood should represent their actual habitat perceptual range, but such data are not known for the nuthatch (or for many other species) and are difficult to estimate (Wennergren *et al.* 1995). Unless stated otherwise, a distance of 2 km was an assumed suitable perceptual

range for the nuthatch tests described in this thesis. This distance corresponded to the maximum distance over which a human observer in a similar landscape was able to clearly identify woods (pers. obs.). To simulate nuthatches flying at canopy height, the observations were taken from hilltops.

The perceptual range algorithm searches all cells within the user-selected perceptual range (Figure 4.4). At the chosen modelling scale, 1 cell represented 1 hectare (Section 4.3.2), giving a selectable perceptual range to the nearest 100 m. The algorithm examines all cells within range, fanning out progressively from the origin, with the bird moving to the habitat cell nearest the origin. If more than one cell is found at the same distance, a random choice is made to avoid any directional biasing.



**Figure 4.4:** Example search coverage for a disperser with a six-cell perceptual range, using a 90° field of view, when moving in a cardinal direction (Figure 4.4a) and a quadrantal direction (Figure 4.4b). The black cell is the search origin. Dashed lines A, B and the arc form the search area boundaries. The searched cells are shown shaded. Lines marked A and B are all the same length, but cover a different number of cells. The search length, in number of cells, for the 'A' lines is taken from the user-selected perceptual range, with the search length for the 'B' lines calculated as described in the text. The perceptual range algorithm selects the other cells to search, based on the 'A' and 'B' search lengths and the 'ahead' search direction. The solid arrow shows the movement direction, which also forms the 'ahead' search direction.

Although the perceptual range is entered as a number of cells, this refers to the number of cells in the cardinal directions (the 'A' lines in Figure 4.4). Due to the limits of a square grid, the linear distance covered by a given number of cells in a quadrantal direction is greater than that in a cardinal direction. In order to overcome this problem, the following formula was applied to the selected perceptual range:

$$45^\circ \text{ Range (no. cells)} = \frac{\text{Selected Range (no. cells)}}{\sqrt{2}}$$

The answer, rounded to the nearest integer, forms the number of cells used for the 'ahead' search distance (the 'B' length in Figure 4.4b) when moving in a quadrantal direction. The same formula is applied, for the same reasons, to set the number of cells for the 45° search boundaries when moving in a cardinal direction (the 'B' lengths in Figure 4.4a).

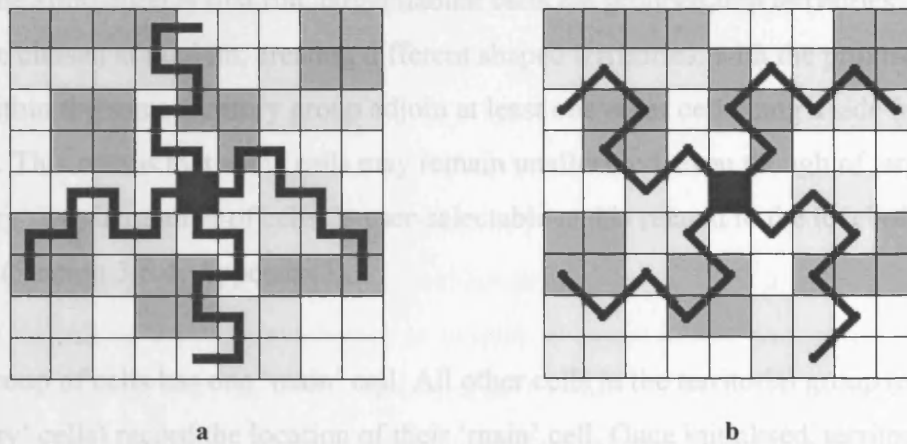
The 'full' perceptual range search algorithm described here searches all cells within the search boundary (Figure 4.4) and was the algorithm used for the nuthatch tests described in this thesis. A 'basic' algorithm is also available, in which the search is restricted to the search boundary lines ('A' and 'B' in Figure 4.4). The 'basic' algorithm is computationally more efficient, but the 'full' algorithm is more realistic.

#### 4.2.4.5 *Field-of-View*

Implicit in the concept of habitat perceptual range is the species' field-of-view (Section 2.4.7). Visual acuity in birds varies with the size and structure of the eye, but it is thought that birds with laterally positioned eyes have greatest acuity in their lateral rather than forward vision (Erichsen 1985). Behavioural adaptation, such as head movements, can also alter the direction and width of the field-of-view. In order to explore the effects of field-of-view in conjunction with perceptual range on dispersal paths, user-selectable options of straight-ahead, 90° or 180° fields of view were provided. The straight-ahead option, which searches a 1-cell wide strip in the movement direction (along line 'A' in Figure 4.4a), is labelled '0' on the user screens (Appendix I). Unless stated otherwise, the nuthatch model tests described in this thesis employed a 90° field-of-view (Figure 4.4), as a compromise between computational efficiency and ensuring that the cell coverage was a factor in the resultant model behaviour.

### 4.2.5 Intra-patch Movement

The intra-patch movement algorithm models the localised dispersal undertaken by single birds as they attempt to form pairs prior to breeding (Figure 4.2). Within the patch, visual perception may be of lesser importance for pair formation and territorial establishment than non-visual traits, such as auditory cues. Starting from its current position, the bird searches for a suitable (same gender) vacancy, up to a user-selectable search depth in each of the cardinal and quadrantal directions. To prevent any directional bias, the cardinal and quadrantal directions are chosen at random. The search continues until all directions, up to the search depth, are exhausted. If a suitable vacancy is not found, the bird moves through the patch, repeating the search at each step. Movement through the patch and for the depth search is cell by cell, using a correlated random walk to maximise search success, as per the inter-patch dispersal algorithm (Section 4.2.4). The search is confined to the patch and perceptual range is not employed. To keep the linear search distance the same for all directions, within the limits of a square grid, the same formula that is applied to the quadrantal perceptual range search boundaries (Section 4.2.4), is applied to the search depth in the quadrantal directions. The result is a complete search of all habitat cells (in the current patch), within a distance up to the search depth from the path through the patch. Dispersal mortality is not applied for the search steps, due mainly to a lack of data on this aspect of nuthatch behaviour, but it is applied for each movement step through the patch. Figure 4.5 shows an example search pattern.



**Figure 4.5:** Example intra-patch search paths showing the cardinal (Figure 4.5a) and quadrantal (Figure 4.5b) directional search paths for an 8-cell search depth. The two sets of directions are separated here for clarity. A searcher will look in all directions, moving to the first found suitable vacancy (as described in the text). The shaded cells represent 4-cell territories as described in the text (Section 4.2.6). The search algorithm covers all territories within the search depth range. The reduced search length for the quadrantal search paths ensured no directional bias, as detailed in the text.

#### 4.2.6 Landscape and Territory Modelling

Nuthatch territory size depends on habitat quality, increasing as quality decreases (Matthysen 1990; Pravosudov 1993a; Bellamy *et al.* 1998). To accommodate these features, the landscape was modelled as a combination of target habitat, non-target habitat and matrix. Target habitat represents suitable breeding habitat. Non-target habitat represents habitat that is unsuitable for occupation by the species (but which may initially be perceived by the species as being suitable). The matrix element represents all other areas. Even though certain patches within the study area may have been identified as containing habitat of suitable quality for occupation by the modelled species, such patches will most likely contain a mixture of both target and non-target habitat. This method of landscape modelling enables habitat quality spatial structure to directly affect population distribution and viability.

When the simulation is first run, target habitat cells are grouped into territories. Suitable cells are chosen at random, creating different shaped territories, with the proviso that all cells within the same territory group adjoin at least one other cell along a side (rather than a corner). This means that some cells may remain unallocated, even though of target habitat. Territory size, in number of cells, is user-selectable and is related to the level of habitat quality (Section 3.6.4; Appendix I).

Each group of cells has one 'main' cell. All other cells in the territorial group (called 'territory' cells) record the location of their 'main' cell. Once initialised, territories do not change, reflecting observations that territorial boundaries change little throughout the year (Matthysen 1986; Wesolowski and Stawarczyk 1991; Pravosudov 1993a). The 'main' cell is also used to store occupancy details, such as gender, age of each occupant and whether the territory is occupied by a pair or has a vacancy (Appendix G.1). During dispersal, a nuthatch locates a target habitat cell. Information is gleaned from the territory's 'main' cell, either directly if on the 'main' cell, or indirectly by obtaining its location from a 'territory' cell. If a suitable (same gender) vacancy exists, then the territory is occupied and marked as such in the 'main' cell. If not, the dispersing nuthatch moves on in search of further suitable habitat (Section 4.2.4.1). Territory information is stored in the population lattice (Appendix G.1) and an example of territory formation is given in Figure 4.5.

## 4.3 Nuthatch Model Application and Performance Comparison

### 4.3.1 Introduction

The following sections describe the application of PatchMapper to the modelling of population viability of the nuthatch in a real landscape. The aims of this study were twofold. Firstly, to investigate whether an individual-based SEPM could produce more realistic predictions than those of a published analytical model (Bellamy *et al.* 1998). Secondly, to use the model to evaluate the importance of immigration in maintaining the existing nuthatch population in a real landscape and to determine how much new habitat would be required to decrease this reliance on immigration and to create a self-sustaining regional population.

In the comparison study (Bellamy *et al.* 1998), observed numbers of breeding pairs in woods in the Monks Wood study area were compared with predictions from an analytical model (defined below) originally developed in the Netherlands to predict nuthatch abundance in fragmented woodland (Schotman and Meeuwsen 1994). Bellamy *et al.* (1998) found that the number of breeding pairs predicted by the Dutch model was lower than that expected from habitat area alone. The nuthatch is noted as being sensitive to isolation (e.g. Enoksson *et al.* 1995; Matthysen *et al.* 1995), but despite taking this into account, the analytical model still predicted a higher occupancy than that observed.

Analytical models are here defined as those that model species, or populations, using difference, differential or other methods, rather than by the direct simulation of a species' (individual or population) behaviour. Examples of analytical models fitting this definition include dynamic, matrix, regression analysis and variance models (Jeffers 1982).



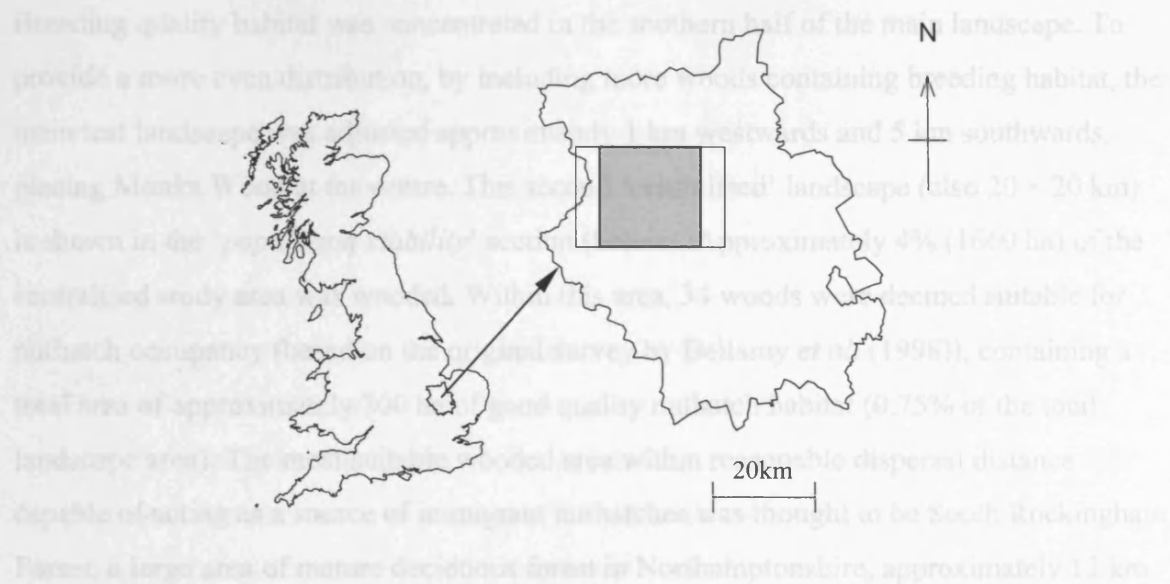
The Dutch model used regression equations based on landscape data from 96 woods distributed across an arable landscape, to estimate both the probability of a wood being occupied by breeding nuthatches and the expected number of breeding pairs (Schotman and Meeuwsen 1994). The model was revised to reflect the reduced woodland cover and lower density of hedges and tree rows in the Monks Wood study area, compared to the landscape of the Dutch work (Bellamy *et al.* 1998). The revised equation for the expected number of breeding pairs is:

**Equation 4.1** 
$$N = e^{[-4.23 + 1.34 \ln(A+1) + 0.45 \ln(H)]}$$

Where  $N$  is the number of breeding pairs,  $A$  is the area of suitable quality habitat (ha) within a wood and  $H$  is the area of suitable habitat (ha) within a 3 km radius of the wood.

### 4.3.2 The Study Area

The main study area used for these investigations was in west Cambridgeshire, in eastern England (Figure 4.6). It was based on the study area of Bellamy *et al.* (1998), but was trimmed to 20 × 20 km (40,000 ha) to match the model input requirement for ‘square’ landscapes. This ‘main’ landscape (shown in the ‘*model comparison*’ section below) was used for comparison with the analytical model. Approximately 4% (1570 ha) of this reduced area was wooded. A survey of the original study area conducted by Bellamy *et al.* (1998), using the habitat classification criteria given in Table 4.2, deemed 28 woods (totalling 512 ha) suitable for possible nuthatch occupancy, totalling approximately 261 ha (0.65% of the total landscape area). The matrix comprised intensive arable farmland, with large fields bounded by hedgerows (usually well trimmed) with few individual mature trees or rows of trees (Bellamy *et al.* 1998).



**Figure 4.6:** Location of the 20 × 20 km main study area (darker shading) in relation to the 20 × 25 km study area used by Bellamy *et al.* (1998), within the county of Cambridgeshire in eastern England, UK (redrawn from Bellamy *et al.* 1998).

All the landscapes used for the nuthatch modelling tests in this thesis were based on a 200 × 200 cell grid, which for the study area dimensions of 20 × 20 km gives a modelled scale of 1 cell = 1 ha. All suitable breeding quality habitat was modelled using the 'good'

Category	Suitability	Breeding density (pairs ha <sup>-1</sup> )	Habitat definition (dbh = diameter at breast height)
0	Very poor	0.05	No trees > 20 cm dbh. Few deciduous trees.
1	Poor	0.05	No deciduous trees > 25 cm dbh.
2	Tolerable	0.2	Some suitable sized trees (> 30 cm dbh including conifers), few oaks but at least beech, birch or aspen, or small oaks (25-30 cm dbh).
3	Good	0.5	Either (a) no or few oaks, but otherwise suitably sized trees (beech, elm, aspen, ash, birch, > 30 cm dbh), or (b) mixed forest with conifers (trees > 35 cm dbh) and deciduous trees (> 25 cm dbh).
4	Very good	1	Fewer oaks (but still some > 30 cm dbh), less beech/hazel/extra food than category 5.
5	Excellent	1	Big (> 40 cm dbh) oaks, elms and beech and/or hazel (or other winter food sources).

**Table 4.2:** The method of habitat quality classification used by and adapted from Bellamy *et al.* (1998) to identify habitat suitable for breeding nuthatches in the study area. Categories 3 - 5 are suitable habitat for nuthatches, 0 - 2 are marginal habitat.

Breeding quality habitat was concentrated in the southern half of the main landscape. To provide a more even distribution, by including more woods containing breeding habitat, the main test landscape was adjusted approximately 1 km westwards and 5 km southwards, placing Monks Wood at the centre. This second ‘centralised’ landscape (also  $20 \times 20$  km) is shown in the ‘*population viability*’ section (below). Approximately 4% (1660 ha) of the centralised study area was wooded. Within this area, 34 woods were deemed suitable for nuthatch occupancy (based on the original survey by Bellamy *et al.* (1998)), containing a total area of approximately 300 ha of good quality nuthatch habitat (0.75% of the total landscape area). The most suitable wooded area within reasonable dispersal distance capable of acting as a source of immigrant nuthatches was thought to be South Rockingham Forest, a large area of mature deciduous forest in Northamptonshire, approximately 12 km to the west of the main study area.

All the landscapes used for the nuthatch modelling tests in this thesis were based on a  $200 \times 200$  cell grid, which for the study area dimensions of  $20 \times 20$  km gives a modelled scale of 1 cell = 1 ha. All suitable breeding quality habitat was modelled using the ‘good’ habitat quality classification, which gives such habitat a potential breeding density of  $0.5 \text{ pairs ha}^{-1}$  (Table 4.2).

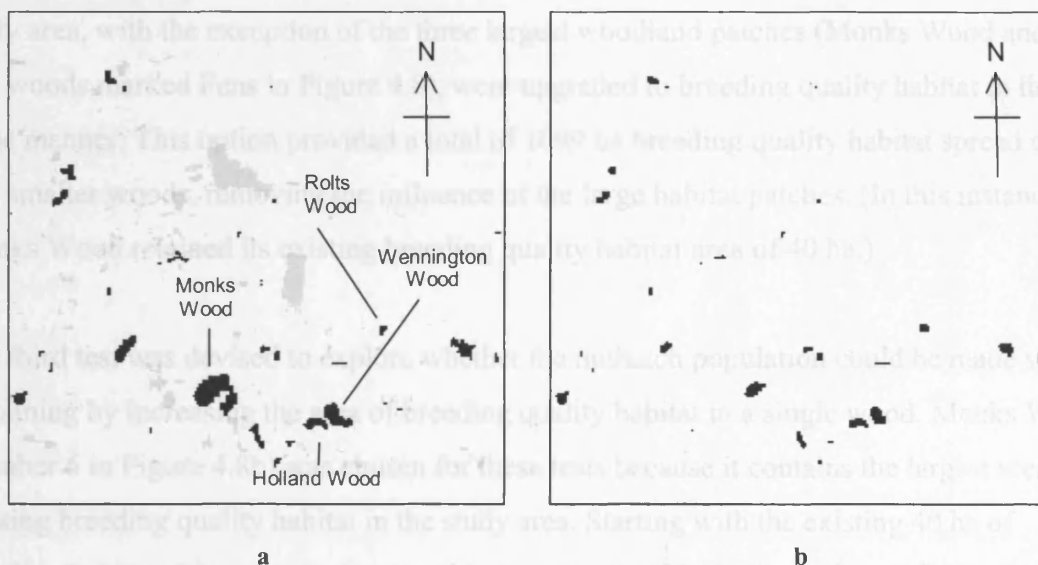
### 4.3.3 Methods

#### 4.3.3.1 Introduction

Firstly, the predictions of PatchMapper were compared to those of the revised Dutch analytical model, and to observed numbers of nuthatches in target woods (*model comparison tests*). Secondly, the importance of immigration into the study area and the effects of increasing the area of good quality habitat on nuthatch population persistence were examined (*population viability tests*). The nuthatch model was parametised with the values given in Table 4.1.

#### 4.3.3.2 Model Comparison

The model comparison tests used the main study area (Figure 4.7). The most likely direction of immigration into the study area is westerly (from South Rockingham Forest), but the immigration rate itself is unknown. The comparative tests therefore took the form of a sensitivity analysis, measuring the mean population sizes in Monks, Holland, Wennington and Rolts Woods for immigration rates (from outside the study area) from 0 to 60 birds per annum. The upper range limit of 60 birds was thought to be well above the most likely actual rate, with the test thereby spanning the actual rate. Tests were run with the presumed nuthatch perceptual range of 2 km (Section 4.2.4.4), with each test run recording the mean population size in each wood over 10,000 yearly cycles. To enable a model comparison, the revised analytical model equation (Equation 4.1) predicting the expected number of breeding pairs was used to predict the number of pairs in Monks, Wennington, Holland and Rolts Woods. Due to the reduced time spent in the matrix, it was expected that the population sizes would rise in line with immigration rate.



**Figure 4.7:** The two main landscapes used in PatchMapper for the comparison tests. The 'habitat' landscape (Figure 4.7a) is a binary representation of the landscape comprising wooded areas (potential habitat) and matrix. For illustration, woods containing breeding quality habitat are shown in black, with all other woods shaded light grey. Woods of particular relevance to the study are individually labelled. The 'quality' landscape (Figure 4.7b) represents areas of habitat of sufficient quality to contain nuthatch territories. Data extracted from survey results by Bellamy *et al.* (1998).

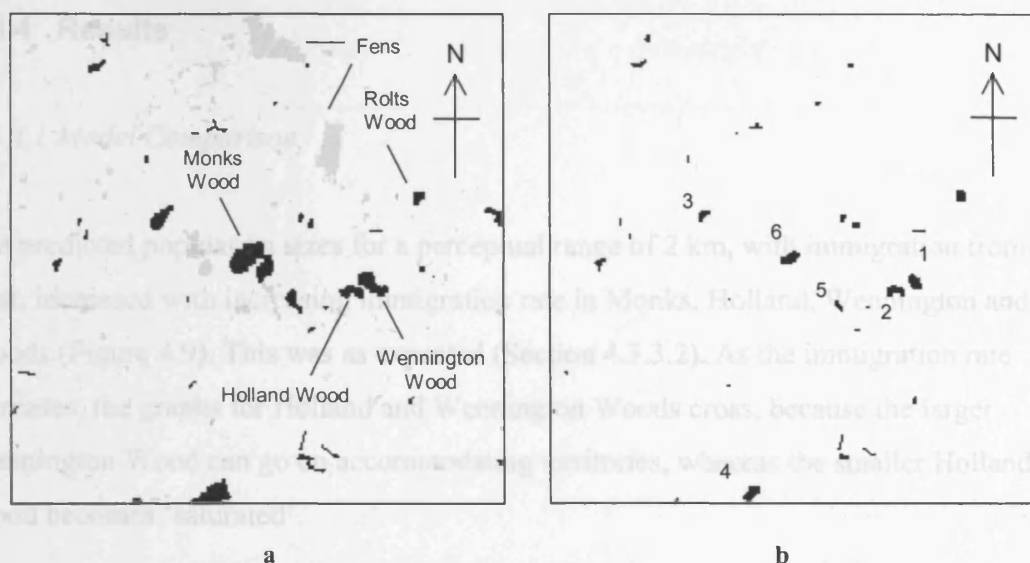
#### 4.3.3.3 Population Viability

To investigate the role of immigration in population persistence, the model was run using the main landscape (Figure 4.7), with no immigration (from outside the study area).

Emigration still applied, meaning that birds were lost as they crossed the study area boundary. For each test, the landscape was seeded with the maximum possible number of nuthatches and consisted of 100 runs of 100 yearly cycles per run, with the results being used to calculate the mean time to extinction for the study area population.

To determine the effects of increasing the amount of good quality habitat in the study area on the long-term viability of the nuthatch population, three tests using the centralised landscapes (Figure 4.8) were carried out. In the first test, the six largest woods containing breeding quality habitat were selected and the area of existing breeding habitat therein increased (Figure 4.8a), i.e. quality was improved in existing woods, but without any increase in the total area of woodland. In each of the numbered woods in Figure 4.8b, breeding quality habitat area was increased as shown in Table 4.3, until it occupied the whole area of each wood. In the second test (the 'All Small' option), all the woods in the study area, with the exception of the three largest woodland patches (Monks Wood and the two woods marked Fens in Figure 4.8), were upgraded to breeding quality habitat in the same manner. This option provided a total of 1099 ha breeding quality habitat spread over 232 smaller woods, removing the influence of the large habitat patches. (In this instance, Monks Wood retained its existing breeding quality habitat area of 40 ha.)

The third test was devised to explore whether the nuthatch population could be made self-sustaining by increasing the area of breeding quality habitat in a single wood. Monks Wood (number 6 in Figure 4.8b) was chosen for these tests because it contains the largest area of existing breeding quality habitat in the study area. Starting with the existing 40 ha of breeding habitat, this area was increased in increments of 10 ha (equating to five nuthatch territories) up to the maximum existing wood area of 157 ha. The mean fraction of remaining population was calculated for each increase in area of breeding habitat at 25, 50, 75 and 100 years after the start of the simulation.



**Figure 4.8:** The habitat and quality centralised landscapes used with PatchMapper for the population viability tests. The habitat landscape (Figure 4.8a) is a binary representation of the landscape, comprising woods (potential habitat) and matrix. For illustration, woods containing breeding quality habitat are shown in black, with all other woods shaded light grey. Woods of particular relevance to the study are individually labelled. The quality landscape (Figure 4.8b) represents the areas of habitat of sufficient quality to contain nuthatch territories. Data extracted from survey results by Bellamy *et al.* (1998).

Option	Existing total area (ha)	Existing breeding habitat area (ha)	Increased breeding habitat area (ha)	Cumulative breeding habitat area (ha)
Current, all woods	1660	298	0	298
Wood 1	72	30	42	340
Wood 2	35	20	15	355
Wood 3	50	20	30	385
Wood 4	85	32	53	438
Wood 5	32	14	18	456
Wood 6	157	40	117	573

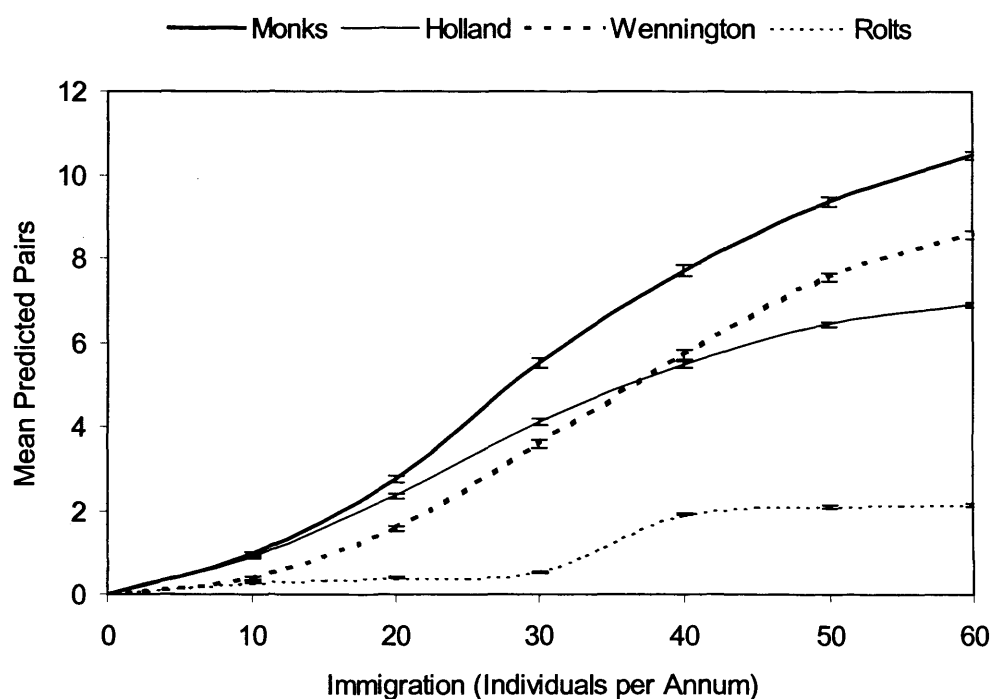
**Table 4.3:** Woodland and nuthatch breeding habitat areas in the whole study area, and for each of the numbered woods identified in Figure 4.8b. The 'increased breeding habitat area' column gives the increase in breeding area for each identified wood. The 'cumulative breeding habitat area' column gives the total amount of breeding habitat in the whole study area as habitat quality in each wood is increased. The 'Current, all woods' option represents the baseline areas of all woodland and breeding quality habitat, as shown in Figure 4.8.

### 4.3.4 Results

#### 4.3.4.1 Model Comparison

The predicted population sizes for a perceptual range of 2 km, with immigration from the west, increased with increasing immigration rate in Monks, Holland, Wennington and Rolts Woods (Figure 4.9). This was as expected (Section 4.3.3.2). As the immigration rate increases, the graphs for Holland and Wennington Woods cross, because the larger Wennington Wood can go on accommodating territories, whereas the smaller Holland Wood becomes 'saturated'.

The maximum observed numbers were 2 pairs in Monks Wood, 1 pair in Wennington Wood and 0.5 pairs in Holland and Rolts Woods. The comparison paper (Bellamy *et al.* 1998) gives potentially misleading results in that the given analytical predictions lists 63 pairs for Monks Wood, 22 pairs for Wennington Wood and 3.5 pairs for Rolts Wood (no results were given for Holland Wood). Prior to the submission of the paper in Appendix B.2 (but after publication of Alderman *et al.* (2004), reproduced in Appendix B.1), it was revealed that the analytical model predictions were based on the whole of the wood area and not the area of breeding quality habitat (Bellamy pers. com.). The predictions of the analytical model were recalculated by this author, using the breeding quality habitat areas modelled by PatchMapper, and are given in Table 4.4, along with the observed pairs and PatchMapper's predictions.



**Figure 4.9:** Predicted population size (mean number of pairs) in Monks, Holland, Wennington and Rolts Woods, as a function of immigration into the study area, using the main landscape (Figure 4.7). Perceptual range was set to 2 km. The error bars give 95% confidence intervals.

Wood	Area of good quality breeding habitat (ha)	Area of suitable habitat within a 3 km radius of the wood (ha)	Analytical model predicted pairs	Observed pairs	PatchMapper predicted pairs
Monks	40	33.9	11	2	1 - 2
Wennington	30	3.58	2-3	1	0.5 - 1
Holland	20	78.54	6	0.5	1-2
Rolts	15	24.95	2-3	0.5	0.5

**Table 4.4:** Predictions of the analytical model (Equation 4.1) used by Bellamy *et al.* (1998) to calculate the number of breeding pairs of nuthatches in Monks, Wennington, Holland and Rolts Woods. The areas of breeding quality habitat and the areas of suitable habitat within a 3 km radius of each wood were taken from Bellamy *et al.* (1998). Also included are the observed pairs and the predictions from PatchMapper for 10 - 15 immigrants (Section 4.3.5).

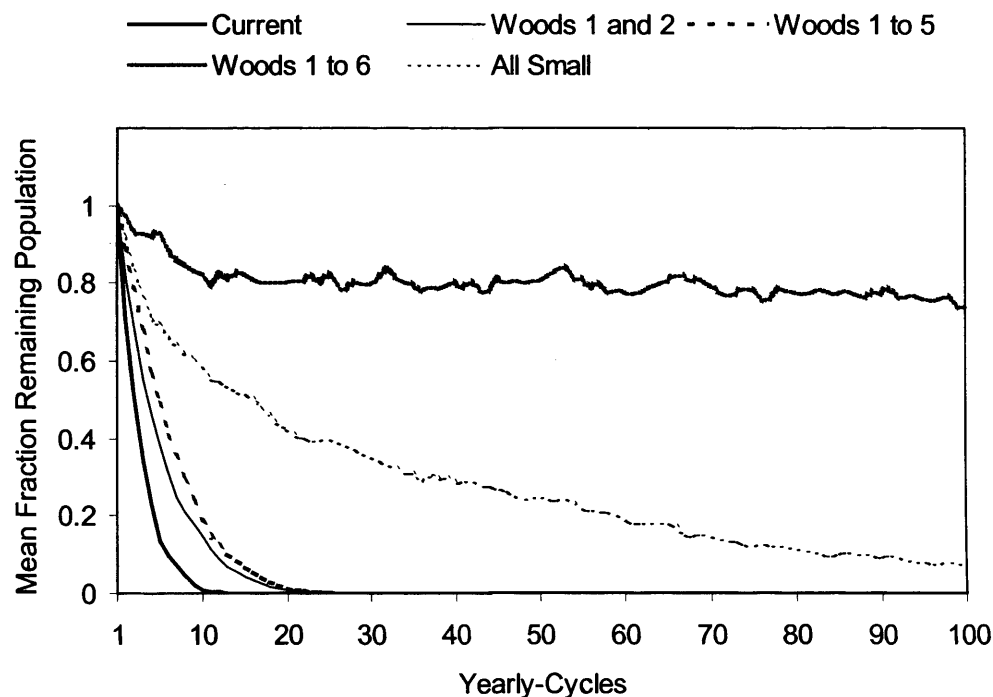


#### 4.3.4.2 Population Viability

The population viability test revealed that without immigration, the study area population became extinct after a mean of 8 years  $\pm$  0.5 years (95% C.I. over 100 runs). Therefore, immigration into the main study area was a vital factor in maintaining the existing nuthatch population and needed to be included in the model.

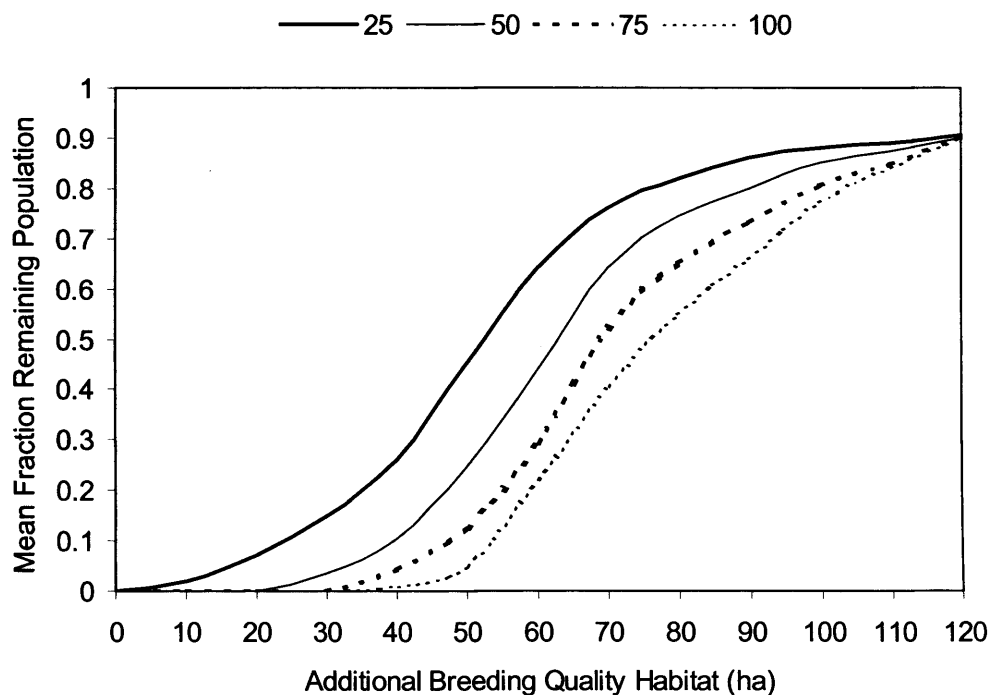
The results of increasing the area of breeding habitat in selected woods are given in Figure 4.10. For clarity, not all results are shown. With the current amount of breeding quality habitat, the population lasted approximately 10 years. This increased to approximately 20 years when breeding habitat in woods 1 to 5 (Figure 4.8b) was increased to occupy the whole of each wood. However, the population only became self-sustaining over the long-term, when the amount of breeding habitat in Monks Wood (wood number 6) was also increased to occupy the whole wood.

The 'All Small' option provided the largest increase in breeding quality habitat of the three tests (1099 ha compared with 573 ha for the 'wood 6 option' (Table 4.3)). Of the 232 woods altered by this option, 117 were below 2 ha and hence too small to support a breeding pair, 90 woods were from 2 - 10 ha, leaving 25 woods above 10 ha. Young produced in the smaller woods have little option but to disperse through the matrix, with all the dangers that that entails (plus the possibility of leaving the study area). Despite the large overall increase in breeding quality habitat, the structure of the landscape therefore prevented the nuthatch population from becoming self-sustaining over the long-term under this option.



**Figure 4.10:** The mean fraction of remaining population in the study area, resulting from increasing the area of good quality habitat in selected woods (Figure 4.8b), as per the legend. Perceptual range was set to 2 km.

The results of increasing the area of breeding quality habitat in Monks Wood alone are given in Figure 4.11. The results showed a lower threshold at an addition of approximately 40 - 50 ha, with an upper threshold of approximately 65 - 75 ha. The thresholds were essentially the same for each of the recorded yearly intervals. The lower threshold represents the increase in breeding habitat area required to enable the nuthatch population to overcome the effects of demographic and dispersal mortality. Increasing the area above this threshold increases emigration from Monks Wood to the surrounding woods, thereby increasing the 'self-sustainability' of the study area population. This carries on until saturation occurs at an upper threshold.



**Figure 4.11:** The mean fraction of remaining population in the study area, at 25, 50, 75 and 100 years (as per the key), resulting from increasing the area of breeding habitat in Monks Wood. Perceptual range was set to 2 km.

#### 4.3.5 Discussion

PatchMapper's predictions, using a presumed nuthatch perceptual range of 2 km and a range of westerly immigration rates (from Rockingham Forest), over-estimated the mean population sizes for Monks, Wennington and Rolts Woods at the higher immigration rates (Figure 4.9). To match the observed numbers of nuthatches in the study area, the model required an annual immigration rate of about 10 - 15 birds (Table 4.4), which seems not unrealistic (Hinsley pers. com.). However, care must be taken over these results as the work was based on feasible, but unvalidated, parameters.

The population viability tests demonstrated that, as suspected, the fragmented structure of the existing suitable habitat in the study area was incapable of supporting a nuthatch population without external immigration. The current landscape is effectively acting as a sink. Information on nuthatch distribution in eastern England obtained from local county bird reports and atlas data (Gibbons *et al.* 1993; Bircham *et al.* 1994; Clark 1996) revealed two likely sources of immigrant nuthatches. The main source is probably South Rockingham Forest, which lies some 12 km to the west of the study area, the other is a more wooded area to the northwest of Peterborough and of the study area (Smith and Gilbert 2002). With immigration rate affecting the predicted population sizes in target woods (Figure 4.9), identification of these sources and their likely emigration rates are necessary to increase the accuracy of PatchMapper's predictions.

Three 'habitat management' plans were tested, all with the aim of reducing the reliance of the resident nuthatch population on immigration, by increasing woodland habitat quality, rather than total woodland area (Section 4.3.3.3). This approach avoids problems of land acquisition, which would be costly, if possible at all, in many landscapes, and might also decrease the time taken to achieve the desired habitat quality. The first two plans had little effect until Monks Wood was included (Figure 4.10). Without changing Monks Wood, the population still declined, even when all woods except the largest three (the 'All Small' option) were improved. This suggested that the largest suitable wood in the area (Monks Wood) was a key feature and that, for this study area, improving the quality of core woods would be more effective than improving that of smaller, more dispersed ones.

The third plan revealed that a lower threshold of approximately 40 - 50 ha of the unsuitable habitat in Monks Wood was required to mature and/or be managed to increase quality, to enable the study area nuthatch population to become largely self-sustaining and less reliant on immigration (Figure 4.11). Increasing the amount of breeding quality habitat above this threshold increases emigration from Monks Wood to the surrounding woods, thereby increasing the 'self-sustainability' of the study area population. This carries on until the whole wood is converted to breeding quality habitat, with saturation starting to occur at the upper threshold of 65 - 75 ha. These results were based on a perceptual range of 2 km; the effect of perceptual range on population viability is the subject of a separate study.

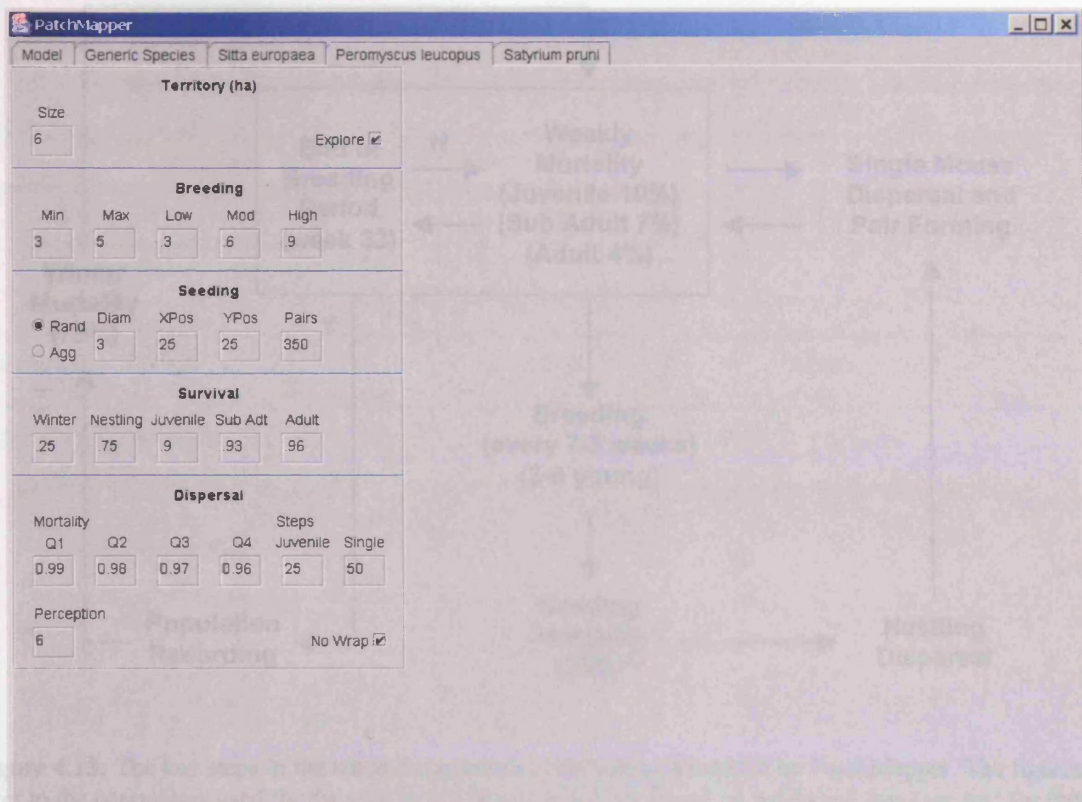
The results from the model are based on a static landscape. In reality, the current population may be a result of historical changes in landcover. In this study area, this was not thought to be a problem as historically the county of Cambridgeshire has been poorly wooded, less than 1.5% cover, until the mid 20<sup>th</sup> century (Smith and Gilbert 2002). Recent increases (up to about 4%) in woodland cover will not have altered the distribution of breeding habitat for nuthatches, as the trees will not have reached a sufficient size.

## **4.4 Modelling the White-Footed Mouse**

### **4.4.1 Introduction**

To investigate the practicality of modelling a multivoltine species with the individual-based approach of PatchMapper, the white-footed mouse was chosen as the second species to be modelled. The decision was aided by the availability of two published modelling studies that investigated the role of habitat corridors on the size of a metapopulation of white-footed mice (Henein and Merriam 1990; Anderson and Danielson 1997). Both models used different technologies to PatchMapper, thereby enabling a useful performance comparison.

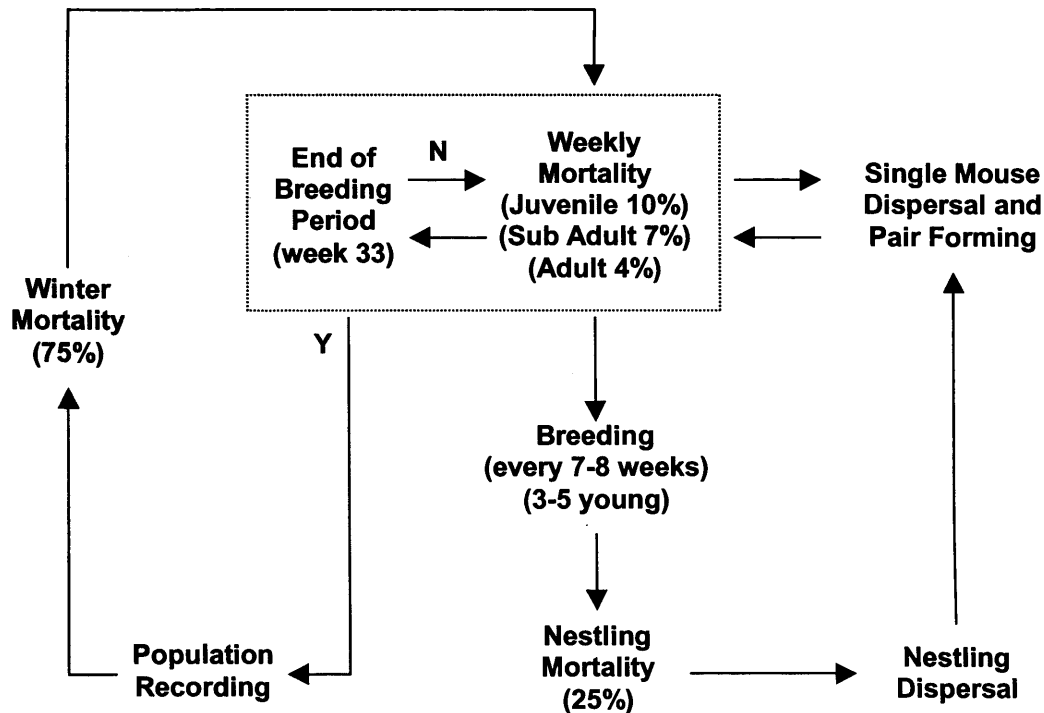
White-footed mice were modelled by applying behavioural rules to each individual mouse, as per the nuthatch (Section 4.2.1). Figure 4.12 shows the user-screen for the white-footed mouse model and Figure 4.13 gives the main steps in the modelled lifecycle. Each step was implemented as a method in the white-footed mouse class, which was called from the base species class (Section 3.7.1). The main elements of the model are described in the following sub-sections, followed by a performance comparison with the two published models.



**Figure 4.12:** The 'white-footed mouse' user-screen, where the user selects suitable demographic, territorial and dispersal parameters. The various controls are detailed in Appendix I.

#### 4.4.2 Lifecycle Stages and Parameters

The white-footed mouse is widely distributed in North America, from the Atlantic coast to the Rocky Mountains, and in brushy areas, but occasionally found in open areas. Mostly nocturnal, the species has a home range of 0.1 to 1.6 ha, reaching an approximate maximum density of 30 mice ha<sup>-1</sup> in the summer. It is a multiparous species, with females having from two to four or more litters per year. The breeding season typically lasts from spring to autumn, but may be all year-round in the warmer parts of its range. Pairs are formed for the breeding season and new mates are sought if one partner dies. Litter size varies from one to eight, but is usually three to five. Young are weaned at two to three weeks and become sexually mature at seven to eight weeks. These data are taken from Timm and Howard (1994). Breeding is bimodal, with peaks at the start and end of the season (Hewison and Merriam 1990). On dark nights in open ground, perceptual range is thought to be under 30 m, increasing to 90 m and possibly



**Figure 4.13:** The key steps in the white-footed mouse lifecycle as modelled by PatchMapper. The figures refer to the parameters used for the tests in this thesis, which are based on published data (see text for further details).

#### 4.4.2 Lifecycle Stages and Parameters

The white-footed mouse is widely distributed in North America, preferring wooded or brushy areas, but occasionally found in open areas. Mostly nocturnal, the species has a home range of 0.1 to 1.6 ha, reaching an approximate maximum density of 37 mice  $\text{ha}^{-1}$  in the summer. It is a multivoltine species, with females having from two to four or more litters per year. The breeding season typically lasts from spring to autumn, but may be all year-round in the warmer parts of its range. Pairs are formed for the breeding season and new mates are sought if one partner dies. Litter size varies from one to eight, but is usually three to five. Young are weaned at two to three weeks and become sexually mature at seven to eight weeks. These data are taken from Timm and Howard (1994). Breeding is bimodal, with peaks at the start and end of the season (Henein and Merriam 1990). On dark nights in open ground, perceptual range is thought to be under 30 m, increasing to 90 m and possibly



to 120 m, with increasing illumination (Zollner and Lima 1997, 1999a; Mech and Zollner 2002). On dark nights, perceptual range reduces to possibly 10 m in fields with mature crops (Zollner and Lima 1997). The default demographic parameters used for the tests described in this thesis are given in Table 4.5.

Parameter	Value	Reference
<b>Mortality Probabilities:</b>		
Weekly Juvenile (0-5 weeks)	0.1	Henein and Merriam (1990)
Weekly Sub-adult (6-8 weeks)	0.07	''
Weekly Adult (> 8 weeks)	0.04	''
Nestling	0.25	''
Winter	0.75	''
Per-step Dispersal (quality based)	0.001 - 0.004	See text and Table 4.7
Breeding Period (number of weeks)	33	Henein and Merriam (1990)
Breeding Probability:	0.7 - 0.9	Henein and Merriam (1990)
Litter Size	3 - 5	Timm and Howard (1994)
Home Range / Territory Size (ha)	0.06	See text
Perceptual Range (m)	90	Mech and Zollner (2002)

**Table 4.5:** Published sources of demographic and territorial characteristics of the white-footed mouse, used to parametrise PatchMapper's white-footed mouse simulator. To enable a useful performance comparison, the Henein and Merriam referenced parameters were chosen to match those used by their model (Section 4.4.5.1).

To enable a comparison of predictions with the two published models described in Section 4.4.5, the white-footed mouse annual life-cycle was based on a 33-week cycle. For each 'week', individuals are aged and an age-based mortality probability applied. To simplify the model, breeding times, juvenile dispersal and pair forming were synchronised to set weeks during the cycle (Table 4.6). Three breeding probabilities, applied at set week numbers, were used to model the bimodal breeding pattern (Table 4.6). The breeding week numbers were chosen to allow five breeding cycles during a 'year', accommodating adult

breeding rates and allowing young born in the spring and summer to breed in the same year (Timm and Howard 1994). The dispersal and juvenile pair forming week numbers matched the species demographics to the chosen breeding week numbers. A winter mortality probability is applied to all individuals at the end of the 33-week breeding cycle, with any survivors being carried forward to the next breeding cycle.

Parameter	Value	Reference
Breeding Period (number of weeks)	33	Henein and Merriam (1990)
Breeding Probability:	0.7 - 0.9	Henein and Merriam (1990)
High (week numbers 2, 30)	0.9	See text
Medium (week numbers 9, 23)	0.8	''
Low (week number 16)	0.7	''
Breeding Week Numbers	2, 9, 16, 23, 30	''
Juvenile Dispersal Week Numbers	1, 8, 15, 22, 29	''
Sub-Adult Dispersal Week Numbers	5, 12, 19, 26, 33	''

**Table 4.6:** The week numbers during the yearly active breeding period of 33 weeks, when the bimodal breeding probability and synchronised breeding, dispersal and juvenile pair forming are applied. As an example of the life-stage sequence, a mouse is born in week 2, leaves the nest at week 8 as a juvenile, pair forms and settles in a territory as a sub-adult at week 12 and breeds as an adult at week 16. Modelled life stages therefore overlap.

#### 4.4.3 Territory Modelling

A species' home range can be defined as the area over which that species moves during the course of its normal daily activities (Burt 1943), whilst a territory can be defined as an area from which other individuals are partially or totally excluded (Begon *et al.* 1996). White-footed mice have home ranges, rather than territories (Timm and Howard 1994), which presented a problem for the model, in that home ranges often overlap and population density per unit area varies (Section 4.4.2). At the modelled scale, it is possible for more than one pair to occupy the same cell, which needed to be taken into account when modelling population distribution.

The chosen array, or lattice (Section 3.3), data type imposes a limit on the number of available bits for each cell, limiting the number of pairs that can occupy a particular cell. Employing 'larger' data types or extending the array dimensions would extend the limit, but with the number of pairs per cell only becoming known at run-time, choosing the array size becomes problematic. A ceiling could be placed on cell pair-occupancy, fixing the array size, but as not all cells would be at maximum capacity, this would artificially restrict population distribution and would result in inefficient memory usage. Implementing a method whereby memory requirements were adjusted dynamically during run-time would also be possible, but with a significant increase in model complexity. To overcome these problems, the white-footed mouse was modelled using territories, with a combination of 'main' and 'territory' cells, as per the nuthatch model (Section 4.2.6; Appendix G.1). Territory size was based on the white-footed mouse's home range. All the landscapes used for the white-footed mouse tests in this thesis were based on a  $300 \times 300$  grid, which was calculated to give a modelled scale of 1 cell = 0.01 ha. Six cells were used for each territory, which gives 16 six-cell territories per ha (96 cells). With one pair per territory, this results in a maximum density of 32 individuals per ha, closely matching the given maximum density of  $37 \text{ mice ha}^{-1}$  (Section 4.4.2).

#### 4.4.4 Modelling Dispersal

##### 4.4.4.1 *Inter-Patch Dispersal*

If the dispersing mouse (juvenile or adult) reaches the edge of a patch without locating a suitable vacancy, it enters the matrix. When in the matrix, a search is carried out for the best quality cell within the user-selectable perceptual range. The default perceptual range chosen for the white-footed mouse tests described in this thesis was 90 cells, which corresponds to a distance of 90 m (i.e. 1 cell = 0.001 ha) (Section 4.4.3). This distance is at the higher end of the suspected perceptual range of the white-footed mouse in open ground at dusk (Section 4.4.2). As the white-footed mouse uses visual perception (Zollner and Lima 1999b), the quality-search algorithm was based on the perceptual range algorithm

used for the nuthatch model (Section 4.2.4.4). The algorithm enables a dispersing white-footed mouse to navigate the landscape with reference to landscape quality, being attracted to the highest found quality cell within its perceptual range. Locations of individual white-footed mice are stored in the population lattice (Section 3.3), the structure of which is detailed in Appendix G.1.

#### *4.4.4.2 Intra-Patch Dispersal*

When juveniles reach the dispersal age of three weeks, they leave the natal cell (Table 4.6). At this stage they are unable to breed and cannot therefore form pairs. Whilst in the habitat patch, juveniles undertake a search using the same depth-based intra-patch search algorithm as per the nuthatch model (Section 4.2.5), but modified to look for a vacant ‘territory’ cell. If a vacancy exists, then the ‘territory’ cell is marked as occupied. If not, then the dispersing mouse moves on in search of a further vacant ‘territory’ cell. Once settled, the mouse stays put in its ‘territory’ cell, progressing from juvenile (3 - 5 weeks) to the sub-adult stage (6 - 8 weeks). On reaching adulthood (> 8 weeks), the mouse disperses to attempt to form a pair, by searching for a suitable vacancy in a ‘main’ cell.

Dispersal mortality was applied as each movement step, by sampling from a uniform distribution (Section 2.4.6). Data on dispersal mortality of the white-footed mouse was not available, so a subjective choice was made, based on probabilities typically used by grid-based models, such as those by Zollner and Lima (1999a) and Tischendorf and Fahrig (2000a) (Table 4.7).

Parameter	Value	Reference
Dispersal Mortality:	0.001 - 0.004	See text
Habitat	0.001	
Good quality corridors	0.002	
Poor quality corridors	0.003	
Matrix	0.004	

**Table 4.7:** Per-step dispersal mortality for the various habitat quality probabilities used for the white-footed mouse model comparison and sensitivity analysis tests (Section 4.4.5.2; Section 5.5).

#### 4.4.5 A Comparison with two Published Models

##### 4.4.5.1 Introduction

As stated earlier (Section 4.4.1), a search of the literature revealed two studies using models to investigate the role of habitat corridors on the size of a metapopulation of white-footed mice. One study was by Henein and Merriam (1990), the ‘H&M model’, the other by Anderson and Danielson (1997), the ‘A&D model’. One of the aims of the models was to determine whether the quality of connections among patches affected the size of a metapopulation. The general conclusion of both models was that both the quality of corridors and their arrangement in a landscape influenced the size of a metapopulation. Connectivity is considered an important element of population viability in landscapes containing fragmented habitat (With *et al.* 1997; Boudjemadi *et al.* 1999). It was therefore decided to compare predictions from the individual-based SEPM modelling method of PatchMapper, with the analytical, individual-based spatially-implicit approach of the H&M and A&D models.

The H&M model was based on age-classes and tracked groups of nestlings, juveniles, subadults and adults over a 33-week breeding period. Nestlings graduated from juveniles through sub-adults to adults. A proportion of juveniles, subadults and adults was selected for inter-patch emigration via corridors. The emigration corridor was selected at random. Dispersal and mortality rates varied for age class and season. The model was deterministic, with no density dependence. The model was run for ten (simulated) years, with an overwintering mortality applied at the end of each 'year'.

The A&D model simplified the H&M model to concentrate on the effects of corridors on metapopulation size. Intra-year and age-specific dynamics were not modelled; the model had no age-classes, used the same parameters for all individuals, with a yearly-cycle incorporating overwintering mortality.

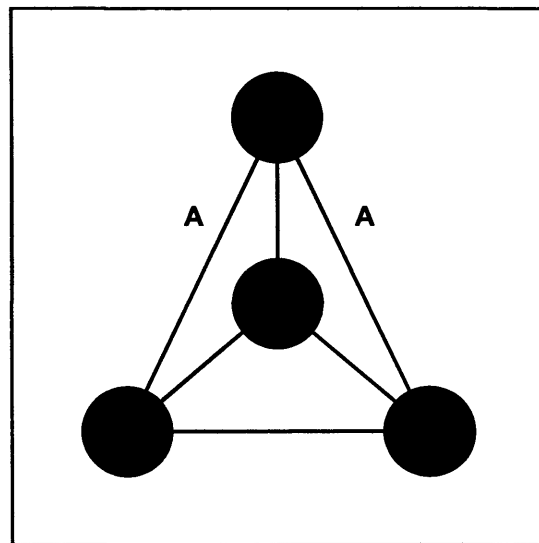
Both models used a set of artificial landscapes consisting of four habitat patches. The patches were connected with various combinations of no corridors, low quality corridors and high quality corridors. Varying the quality of the connection represented different degrees of 'resistance' to inter-patch dispersal, modelled as a dispersal mortality probability. Only the patches were habitable. Dispersal for both models was density independent and movement was only allowed between patches along high or low quality corridors. A corridor survival rate based on corridor quality was applied for each inter-patch movement. Dispersers entering the matrix did not survive.

H&M's analytical approach used complex demographic modelling, which allowed for asynchronous pregnancies and graduation between age stages. PatchMapper's white-footed mouse model simplified this, with synchronised demographic events and the substitution of territories for home ranges. In terms of realistic formulation, PatchMapper lies between the H&M and A&D models.

#### 4.4.5.2 Landscape Modelling

The landscape was modelled as a combination of habitat patches and matrix, with four possible quality levels (Section 3.6.4). In this case, the quality levels determined dispersal mortality, instead of territory size as with the nuthatch model (Section 4.2.6). Territories only existed in habitat patches, which were assigned the highest quality. The matrix was assigned the lowest quality. Corridors were assigned one of two intermediate quality levels. Dispersers were thus ‘encouraged’ to move between patches, by virtue of the connecting corridors, with higher quality connections having lower dispersal mortality and hence favouring dispersal over the lower quality corridors and matrix.

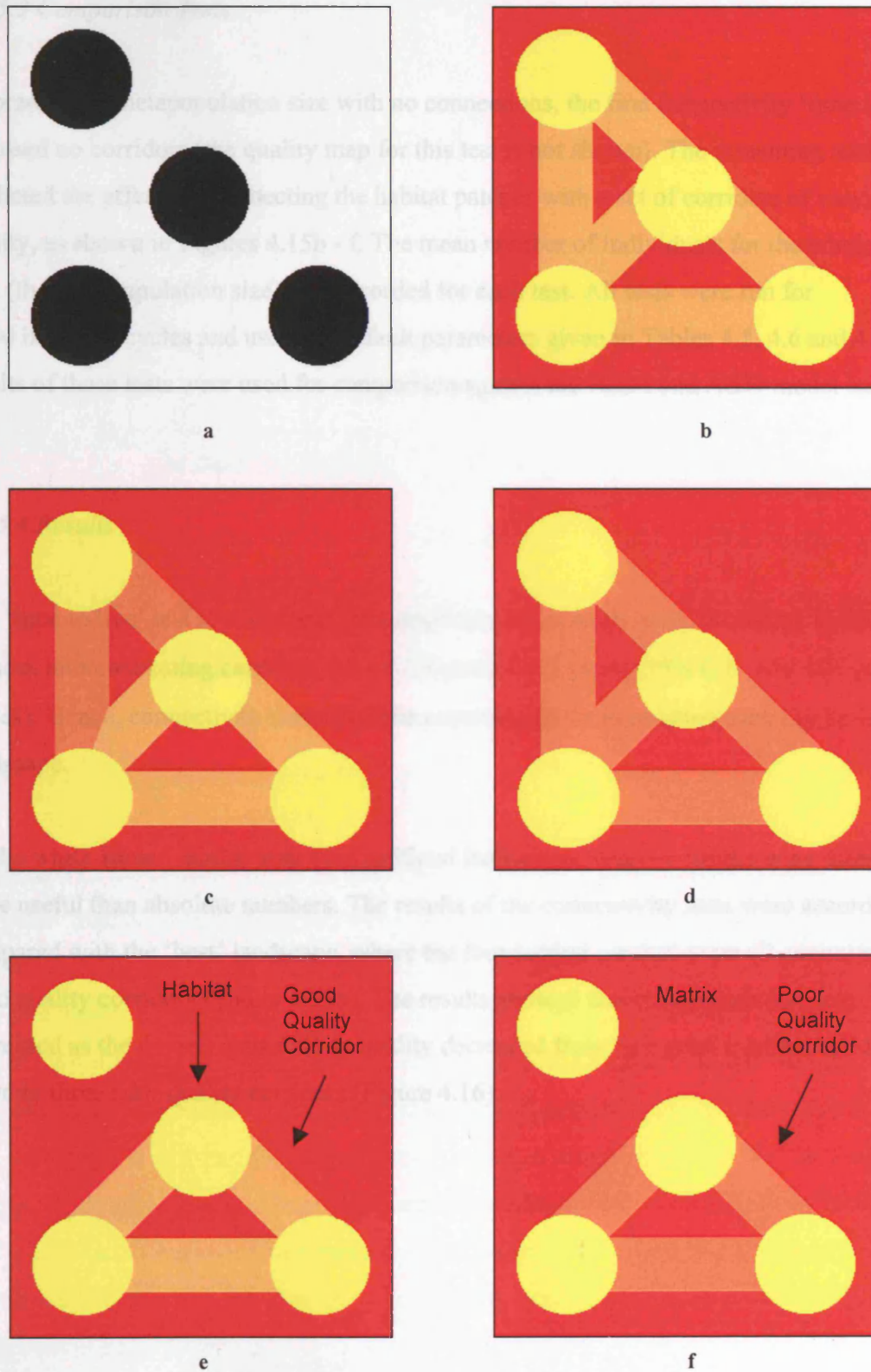
The H&M and A&D models used the same basic landscape, comprising a set of four habitat patches linked with a set of corridors (Figure 4.14). These landscapes were not a problem for the comparison models, as they did not directly simulate inter-patch movement. With PatchMapper modelling individual dispersal, the two corridors marked ‘A’ in Figure 4.14, passed too close to the centre patch. Dispersers moving along these corridors would ‘spot’ the central patch and due to it being of higher quality than the corridor, would move directly to it, failing to complete their journey. To avoid this problem, the basic landscape was altered by moving the top patch to the left (Figure 4.15a). This allowed a similar configuration to that of the base studies, with four habitat patches linked with corridors wide enough to facilitate individual movement, but without attraction to the central patch.



**Figure 4.14:** The basic landscape used in the H&M and A&D comparison models. The lines represent the possible inter-patch connections. Paths 'A' show the connections that could not be used as corridors for the test landscapes used in this study, as described in the text.

The H&M model tests used 32 different corridor configurations, whereas the A&D model tests used 50. The configurations for PatchMapper were limited to six, comprising the configurations shown in Figure 4.15, together with a no-corridor option. The tests described in this thesis were limited to investigations into how the quality of inter-patch connections affected the size of a metapopulation, rather than to provide an exact match with the wider aims of the comparison studies, which included the effects of the numbers of corridors and their arrangement. The landscapes were modelled using habitat and quality landscapes, as described in Section 3.3, with the habitat landscape consisting of four round patches as shown in Figure 4.15a. Different quality maps were used to provide the inter-connecting low or high-quality corridors (Figures 4.15b - f).





**Figure 4.15:** The habitat (a) and quality landscapes used for the white-footed mouse comparison tests. Four habitat patches were joined with 'all good' (b), 'three good with two poor' (c), 'all poor' (d), 'three good' (e) and 'three poor' (f) quality corridors, providing a set of landscapes with varying connectivity. The colours used for the various qualities are shown in e and f.

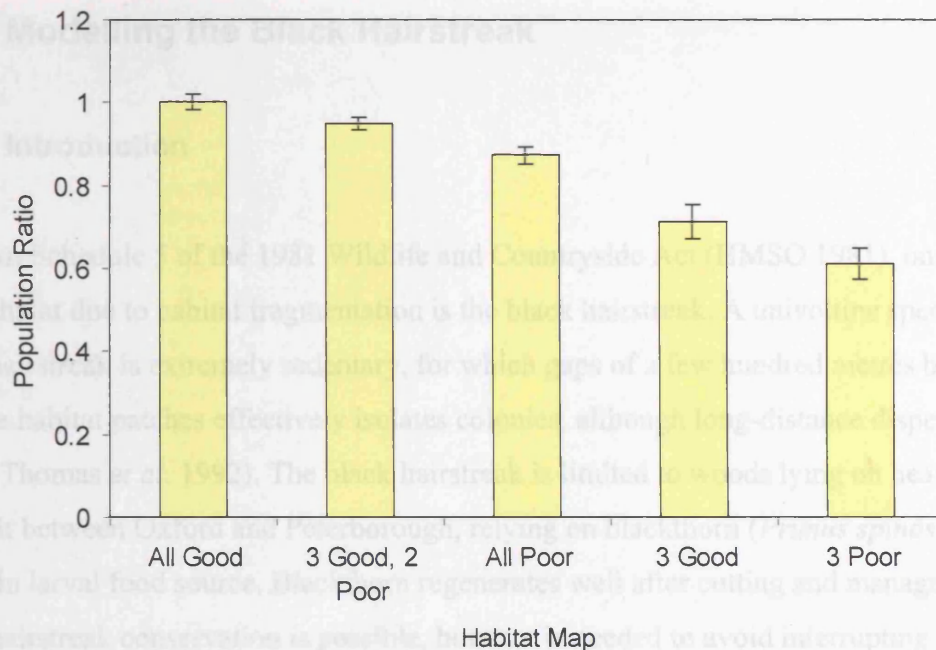
#### *4.4.5.3 Comparison Tests*

To predict the metapopulation size with no connections, the first connectivity ‘time to live’ test used no corridors (the quality map for this test is not shown). The remaining tests predicted the effects of connecting the habitat patches with a set of corridors of varying quality, as shown in Figures 4.15b - f. The mean number of individuals for the whole study area (the metapopulation size) was recorded for each test. All tests were run for 1,000 breeding cycles and used the default parameters given in Tables 4.5, 4.6 and 4.7. The results of these tests were used for comparison against the H&M and A&D model tests.

#### *4.4.5.4 Results*

The ‘time to live’ test revealed that the population in the study area (the metapopulation) without interconnecting corridors, lasted  $1.5 \text{ years} \pm 0.5 \text{ years}$  (95% C.I. over 100 yearly cycles). Hence, connectivity was a definite requirement for population viability in the test landscape.

As the white-footed mouse tests used artificial landscapes, relative results were thought more useful than absolute numbers. The results of the connectivity tests were accordingly compared with the ‘best’ landscape, where the four habitat patches were all connected with good quality corridors (Figure 4.15b). The results showed that metapopulation size decreased as the overall connectivity quality decreased from five good quality corridors down to three poor quality corridors (Figure 4.16).



**Figure 4.16:** The mean predicted population size (individuals) for the various connectivity scenarios (Figure 4.15c - f), relative to the base option of connecting all patches with good quality corridors, the 'all good' option (Figure 4.15b). The error bars give 95% confidence intervals.

#### 4.4.5.5 Model Comparison Results Discussion

The results of the connectivity tests were consistent with those of H&M and A&D, in that the overall size of a metapopulation was affected by the quality of the inter-patch connecting corridors (Figure 4.16). The results also revealed that connecting all the patches with low quality corridors was better than connecting with just three good quality corridors. (Note that movement in the matrix was allowed with PatchMapper, but not with the two comparison models.) This suggests that connecting all patches is better than connecting a few, even if the fewer corridors are of higher quality. A comparison with the 'time to live' test results revealed that any connection was better than having no connections (Section 4.4.5.4). For a landscape with a fixed number of connections, increasing the quality of the connection, as seen with the three good vs. the three poor corridors (Figure 4.16), increased the predicted population size.

## 4.5 Modelling the Black Hairstreak

### 4.5.1 Introduction

Listed in Schedule 5 of the 1981 Wildlife and Countryside Act (HMSO 1981), one species under threat due to habitat fragmentation is the black hairstreak. A univoltine species, the black hairstreak is extremely sedentary, for which gaps of a few hundred metres between suitable habitat patches effectively isolates colonies, although long-distance dispersal does occur (Thomas *et al.* 1992). The black hairstreak is limited to woods lying on heavy clays in a belt between Oxford and Peterborough, relying on blackthorn (*Prunus spinosa* L.) as the main larval food source. Blackthorn regenerates well after cutting and management for black hairstreak conservation is possible, but care is needed to avoid interrupting its lifecycle (Thomas 1974). Species action plans for regional counties call for the linking of existing black hairstreak sites, adding more habitat and encouraging effective management of blackthorn. The challenge is to identify optimum spatial arrangements of interconnected existing and new sites, along with any adverse consequences of the various options. It was decided to model the black hairstreak to investigate the applicability of the individual-based SEPM approach of PatchMapper to meeting this challenge.

The black hairstreak was modelled with a combined population and individual-based model, linked to a dynamic model of blackthorn, its main larval food source. Figure 4.17 shows the user-screen for the black hairstreak model. The species and food source models are described in the following sub-sections.



**PatchMapper**

Model: Generic Species Sitta europaea Peromyscus leucopus Satyrium pruni

**General**

Ceiling ☐ Hab Col ☒  
 Qual ☐ Hab Only ☐ Var Qual ☐ Hab Ageing ☒

**Breeding**

Var ☒  
 Eggs/Fem Min Max Eggs/Step Min Max Dec Age  
 90 80 100 45 40 50 20

**Seeding**

Var Hab Age ☒  
 • Rand Diam XPos YPos Cells Eggs/Cell Age Pw  
 ○ Agg 3 25 25 500 1000 4

**Mortality**

Var ☒  
 Egg Low High Pupae Low High  
 35 25 35 80 60 80  
 Instar 1 45 30 60 Instar 2 45 30 60  
 Instar 3 45 30 60 Instar 4 45 30 60

**Dispersal**

Init Disp Mort Prob Immigration Direction  
 5 0.02 0.05 Allow ☐ 50 Random  
 Trails ☐ 100 I ☐ C ☐

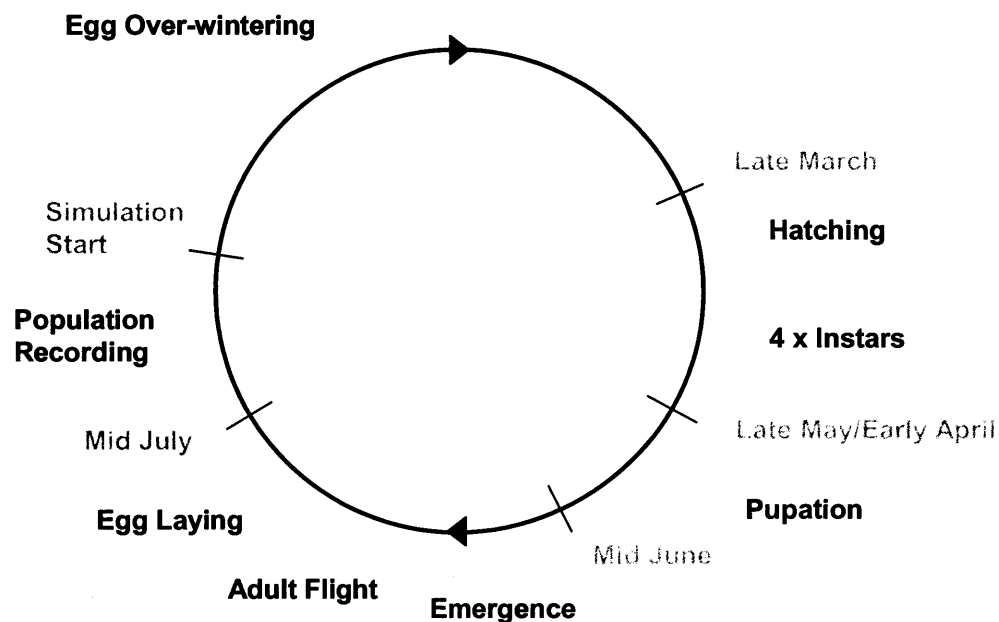
**Figure 4.17:** The ‘black hairstreak’ user-screen, where the user selects suitable demographic, territorial and dispersal parameters. The various controls are detailed in Appendix I.

## 4.5.2 Lifecycle Stages and Parameters

### 4.5.2.1 Modelling the Lifecycle

The female black hairstreak lays single eggs, mainly on blackthorn, from mid to late July. These hatch the following spring, usually from late March to early April. There are four larval instars of approximately 15 days duration. Pupation takes place in late May and lasts for three weeks. Egg laying takes place following emergence over a four week period from mid to late June onwards. These data were taken from Thomas (1974) and Bourn and Warren (1998).

The overall species model flow is given in Figure 4.18. The different steps were implemented as methods in the black hairstreak class, which is called from the base species class (Section 3.7). Population size, dispersal mortality, average age and other demographic statistics are recorded after each cycle of the model. Lifecycle stage mortality and other demographic characteristics are user-selectable. The model can be either deterministic or stochastic. To model stochastic variation, mortality and other demographic parameters are sampled from a uniform distribution between upper and lower (user-selectable) limits given in Table 4.8 (as per the nuthatch model, Section 4.2.2). The habitat modelling tests described in Section 4.5.3 used the stochastic option and the values given in Table 4.8.



**Figure 4.18:** The major stages in the black hairstreak lifecycle as modelled by PatchMapper. The simulation cycle starts in August. Population statistics are recorded at the end of each cycle, following egg laying.

Parameter	Value	Reference
Mortality Probabilities:		
Egg Over-wintering	0.25 - 0.35	Thomas (1974)
Instar (1-4)	0.3 – 0.6	”
Pupae	0.6 – 0.8	Bourn and Warren (1998)
Per-step Dispersal	0.02	See text
Eggs per female	90 - 100	”
Eggs laid per step	45 - 50	”
Eggs per cell ceiling	1000	”
Initial Dispersal (steps)	5	”

**Table 4.8:** The black hairstreak demographic parameters used for the model tests in this thesis.

Given that the black hairstreak is not territorial and taking into account its sedentary nature, the natal clump can be regarded as its home range. Due to the difficulty of modelling home ranges with individual-based lattice models (as described in the white-footed mouse model, Section 4.4.3), it was decided to model the black hairstreak life-cycle stages, except for emergence and egg laying, as a population. The demographic parameters for the life-cycle stages were applied to the number of eggs inhabiting each habitat cell, resulting in a single number representing the successful emergent population for that cell.

#### 4.5.2.2 Dispersal Modelling

Most metapopulation models assume a random walk for butterfly dispersal (Conradt *et al.* 2001). However, some studies have revealed that *Maniola jurtina* L. and *Pyronia tithonus* L. disperse in petal-like loops, based on the starting point, suggesting a systematic search pattern (Conradt *et al.* 2000; Conradt *et al.* 2001). Studies on the cabbage butterfly *Pieris rapae* L. suggest linear flight paths with a random dispersal direction (Jones *et al.* 1980; Root and Kareiva 1984). Perceptual range data for butterflies are sparse, although a range of 100 to 150 m is suggested for *Maniola jurtina*, whereas a range of less than 1 m is suggested for *Pieris rapae* (Fahrig and Paloheimo 1987; Conradt *et al.* 2000). Due to the lack of data for the black hairstreak, dispersal is modelled as a random walk, with no perceptual range. A dispersing individual undertakes a (user-selectable) number of ‘initial’ dispersal steps during which settlement cannot occur. This ensures the disperser does not lay eggs directly on its starting position, allowing the population to spread throughout the natal patch when modelling local dispersal (Section 4.5.2.3). This mechanism also gives the disperser a chance to clear the natal patch when modelling landscape-scale dispersal (Section 4.5.2.4). Following the ‘initial’ dispersal, the disperser moves at random until habitat is found or dispersal mortality occurs.

#### 4.5.2.3 Modelling Local-Scale Dispersal

Emergence and egg-laying stage modelling is based on individual females. Assuming a 50/50 gender split (Thomas 1974), the number of emergent black hairstreak is halved. Females then lay eggs and/or disperse. To represent local dispersal, the female lays a (user-selectable) number of eggs per step, moving to adjacent habitat cells to lay more eggs until all eggs (user-selectable) have been laid. To incorporate a density dependence factor, the number of eggs that can be laid in one cell (during a year) is limited via a user-selectable ‘ceiling’ input. Due to the lack of behavioural data for this species, for the tests in this thesis, the arbitrary, but feasible, values given in Table 4.8 were chosen for the egg-laying parameters.



#### 4.5.2.4 *Modelling Landscape-Scale Dispersal*

Despite its suggested sedentary nature, black hairstreak dispersal is not, however, limited to the natal clump, as evidenced by an introduced colony in Surrey that is known to have spread at a rate of approximately 1 km per decade (Thomas *et al.* 1992). To accommodate this characteristic, at the start of the emergence stage, individuals (female) are given a small (user-selectable) chance to disperse in search of another clump of blackthorn. This method of dispersal was not used for the tests in this thesis.

### 4.5.3 **Habitat Modelling**

#### 4.5.3.1 *Habitat Management Schemes*

The black hairstreak lays its eggs mainly on mature blackthorn, with other *Prunus* species being used on occasion. Blackthorn has a maximum lifespan of approximately 50 years and although just protecting the breeding areas should ensure a colony life for 20 to 50 years (Thomas 1975), habitat management is required if long-term survival is to be achieved. New habitat has to be created before the existing blackthorn becomes unusable. Due to the sedentary nature of the black hairstreak, new habitat should either be created close to existing colonies or by regenerating a portion of the existing habitat on a rotational basis. Cutting back helps to regenerate blackthorn, producing a thicker clump on re-growth. Blackthorn also spreads through suckering. Several blackthorn management schemes are suggested in the black hairstreak species-action plan (Bourn and Warren 1998). As an example, one recommendation is that only 25% of suitable areas are cleared at any one time, with subsequent cutting carried out on a 40 to 50 year rotation (Thomas 1975). To maximise realism, a conservation model of the black hairstreak should therefore include a model of blackthorn, incorporating habitat ageing and a habitat management scheme. Both these elements were included in the black hairstreak model.

#### 4.5.3.2 *Modelling Habitat Ageing and Management Schemes*

To model habitat ageing, each cell containing blackthorn has an age counter (Appendix G.1), which is reset when habitat is created and incremented after each yearly cycle. To model the requirement for mature blackthorn, settlement is not allowed until the blackthorn is greater than seven years old (Bourn and Warren 1998). When the blackthorn is greater than 20 years old it is subjected to an age-related exponential mortality probability (the older the blackthorn, the more likely it is to become moribund). When the blackthorn dies, any resident black hairstreak population also dies.

The ‘landscape transformation by controlled importation’ feature of PatchMapper (Section 3.6.5.2) was used to model a selection of habitat management schemes (Section 4.5.4). In this case, different quality maps were loaded at user-selectable years, representing areas of newly created habitat. When loaded, the areas covered by the new quality maps were cleared of any existing black hairstreak populations and their age counters reset. (The ageing algorithm allows colonisation only when the habitat matures.)

#### 4.5.3.3 *Modelling Habitat at the Landscape Scale*

A second habitat modelling method based on a habitat map representing woods and a quality map representing clumps of blackthorn within the woods is available and is intended for modelling at the landscape scale. This method dispenses with the temporal blackthorn modelling and habitat management schemes and could be used, for example, to model the effects of habitat placement on inter-patch and wood dispersal. Due mainly to the lack of data on this aspect of black hairstreak behaviour, this method of habitat modelling was not used for the habitat management tests described in this thesis.

## 4.5.4 Habitat Management Scheme Comparisons

### 4.5.4.1 Introduction

As no black hairstreak models were found in the literature, a comparison with published results was not possible. Black hairstreak habitat management is carried out at the local scale. One example being a Wildlife Trust reserve at Glapthorn Cow Pasture (52°30'N, 0°31'W) in Northamptonshire (UK), in which an area of blackthorn is managed by cutting rides and small glades. The blackthorn is also fenced to prevent damage by deer (Bourn and Warren 1998). To match the current management schemes, the possible application of PatchMapper to the modelling of habitat management on a local scale was investigated, using a set of theoretical habitat management schemes. The tests are described in the following sub-sections.

These tests were designed to provide some measure of the effectiveness of modelling the black hairstreak in conjunction with a dynamic habitat model, rather than as a realistic scenario. The relative results of the simulations are of interest here, hence the unlikely (but not impossibly) shaped landscape and replacement strips (Section 4.5.4.2). For the same reason, no scale is given. Each test was run 100 times, for 150 yearly cycles per run. The mean patch population size was recorded for each year for each test option. To simulate the effects of abandoning the management schemes, habitat replacement arbitrarily ceased at the end of year 96.

### 4.5.4.2 Habitat Management Schemes

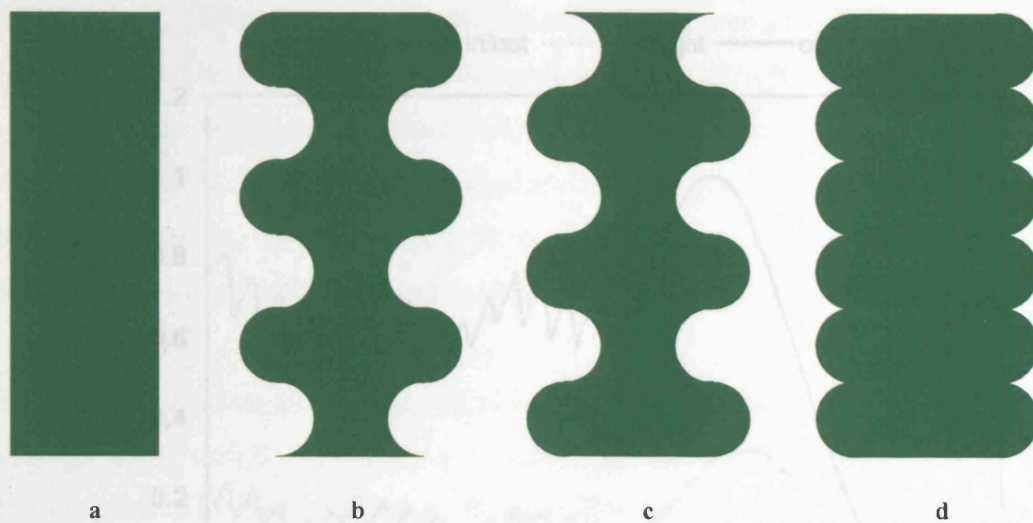
Three different habitat management schemes were devised. A rectangular patch was created and divided into seven equal strips (Figure 4.19). At four yearly intervals, each strip was replaced in turn with new habitat, giving a 28-year rotation.

1	2	3	4	5	6	7
---	---	---	---	---	---	---

**Figure 4.19:** The test blackthorn patch showing the strip divisions. Strips were renewed every 4 years in rotation, starting at strip 1. Each strip was therefore replaced every 28 years.

The first ‘straight’ test replaced each rectangular strip with another rectangular strip, giving straight borders between new and existing habitat (Figure 4.20a). The second ‘in/out’ test replaced each strip with a new strip of the same basic width as the rectangular strip, but which indented into and was indented by, the existing habitat. This method gave an irregular edge to the replacement strips, keeping some existing habitat within the general borders of the new patch. To ensure that all habitat was eventually replaced, the strip shape was reversed on each rotation (Figures 4.20b - c). The third ‘out’ test replaced each strip with one that indented only the existing habitat, giving an irregular edge to the new/existing habitat boundary (Figure 4.20d), but without keeping any existing habitat within the borders of the replacement habitat patch.

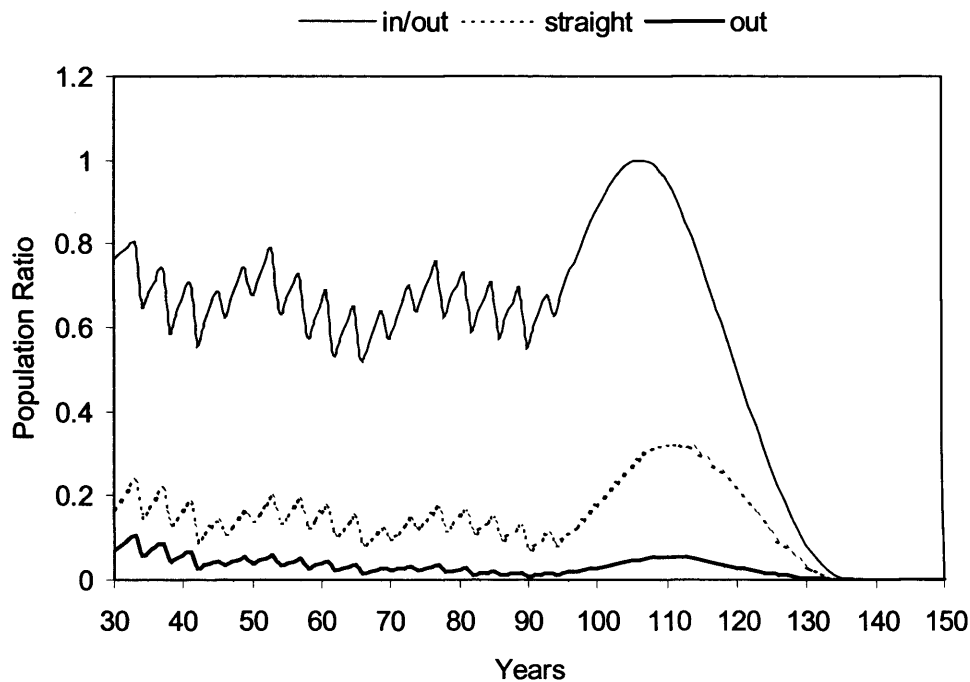
The tests in this thesis used the local-scale dispersal algorithm (Section 4.5.2.3), employing five initial dispersal steps (Section 4.5.2.2). Due to the lack of data on dispersal mortality, a probability of 0.02 per step was applied (Table 4.8), a subjective choice in line with other theoretical grid-based models incorporating per-step dispersal mortality (Section 2.4.6).



**Figure 4.20:** The replacement strip shapes. The basic strip shape (Figure 4.20a) gave straight boundaries between existing and new habitat. Sinuate edged strips (Figures 4.20b and c) and the crenate edged strip (Figure 4.20d) were designed to give irregular boundaries, as described in the text. The indentations were exaggerated to demonstrate the underlying principle.

#### 4.5.4.3 Results

As the black hairstreak tests used artificial landscapes, relative results were thought more useful than absolute numbers. The results were accordingly presented as a comparison with the ‘in/out’ scenario, which predicted the greatest population size. The results revealed that the size of the study blackthorn patch population was directly affected by the different management schemes (Figure 4.21). The ‘in/out’ scenario was far more effective (up to four times) in maintaining the population size than the other two options. The ‘out’ option was the poorest performer. Prior to year 96 when the management schemes were terminated, the overall trend for each scenario’s patch population was towards extinction. The introduction of each new strip caused a decline in the population, which then built up until the next new strip was introduced, resulting in a ‘jagged edge’ to the population curves up to year 96. In each case, with the cessation of the management schemes at year 96, the population rose to a peak and then declined to extinction as the blackthorn aged and became moribund.



**Figure 4.21:** The mean patch population recorded for the three management scenarios described in the text, from years 30 to 150. The settling down period (years 1 to 29) is not shown for clarity. The y-axis is labelled to provide a relative comparison. All management schemes were abandoned after year 96.

#### 4.5.4.4 Habitat Management Schemes Discussion

The habitat management tests revealed that with the ‘out’ scenario providing the worst performance, just having an irregularly shaped new habitat strip was not enough to guarantee success (Figure 4.21). The most effective of the three schemes was to provide an irregular edge which indented existing habitat with new habitat and left some existing habitat intact (the ‘in/out’ scenario), matching the recommended habitat management method of cutting irregular indentations into the blackthorn (Thomas 1975). These findings show that PatchMapper can be used to test habitat management schemes on a local scale and that even small variations on a theme can have a significant difference.

The 'hump' in population size after the cessation of the management schemes is of interest (Figure 4.21). The initial rise in population size, lasting up to ten years or more after cessation of the management scheme, may suggest that habitat management was having a detrimental effect. As the blackthorn aged and became moribund, the population declined to extinction, taking up to 30 years to do so. Unless long-term records are kept, these trends may not be noticed, with recovery possibly becoming unachievable if left too late.

These results suggest that an understanding of both black hairstreak and blackthorn ecology, along with the inter-species dynamics, is essential for effective conservation management of the black hairstreak. These findings were similar to those of Bergman and Kindvall (2004), who found that it was essential to combine landscape dynamics with stochastic population modelling when making a population viability analysis (PVA) of the *Lopinga achine* butterfly in Sweden. Their PVA was carried out using a model that combined a stochastic incidence function metapopulation dynamics model with a 'deterministic phenomenological' model of habitat succession, a different technique to the individual-based SEPM approach of PatchMapper.

## 4.6 Chapter Summary

The first part of this chapter described the modelling of the univoltine nuthatch, followed by a case study, in which PatchMapper was applied to a real landscape and its predictions compared with those of a regression model and with observed numbers (Section 4.3.3.2). PatchMapper was found to be capable of producing a closer match to the observed population sizes than the regression model (Section 4.3.4.1). The nuthatch model was further tested with three habitat management plans (Section 4.3.3.3), which found that the largest suitable wood in the area (Monks Wood) was a key feature (Section 4.3.4.2).

The second part of the chapter described the application of PatchMapper to modelling the population viability of the multivoltine white-footed mouse inhabiting a landscape of habitat patches interconnected with corridors of various qualities. The performance of PatchMapper matched the findings of two published modelling studies, which used the same landscape but a different technology (Section 4.4.5.5).

To further test the generality of PatchMapper, a third species, the univoltine black hairstreak, was modelled. Belonging to a different taxon to the nuthatch and white-footed mouse, the black hairstreak was modelled as a population-based species, with dispersing female individuals. The model was tested with several habitat management plans, which used the dynamic landscape capability of PatchMapper and demonstrated the applicability of PatchMapper to modelling with dynamic habitat (Section 4.5.4).

The white-footed mouse and black hairstreak tests were designed to judge the applicability of PatchMapper's individual-based SEPM approach to modelling species other than univoltine territorial forest birds (such as the nuthatch), rather than as an in-depth modelling study of a particular species. The next chapter presents a sensitivity analysis of the nuthatch, white-footed mouse and black hairstreak models.



## 5. SENSITIVITY ANALYSES

### 5.1 Introduction

Following the model descriptions and comparisons presented in the previous chapter, this chapter presents a performance evaluation of the species' models, in the form of a set of sensitivity analyses. The nuthatch (*Sitta europaea*) model is first evaluated, followed by the white-footed mouse (*Peromyscus leucopus*) and the black hairstreak (*Satyrrium pruni*) models. The nuthatch model section includes a demonstration of the utility of dispersal flow diagrams.

### 5.2 Nuthatch Model Sensitivity Analysis

#### 5.2.1 Introduction

The nuthatch test sequence started with a set of demographic sensitivity analyses, i.e. investigating the response of the model to variations in the modelled demographic parameters (*demographic sensitivity analyses*). The remainder of the analyses explored the model's response to variations in the inputs that directly affect the population viability of the (modelled) nuthatch in fragmented habitat (*immigration direction*, *perceptual range* and *field-of-view* tests). All the neutral landscapes used in these tests were created with PatchMapper's internal landscape generating algorithm (Section 3.6.2). The centralised habitat and quality landscapes described in Section 4.3.2 were used for the 'real landscape' tests.

## 5.2.2 Demographic Sensitivity Analyses

The main aim of the demographic sensitivity analyses was to evaluate the response of the model to changes in modelled nuthatch demographic parameters. A secondary aim of the tests was to evaluate the response in the general case alongside that of a specific case; hence the tests used both a set of neutral landscapes and the centralised landscape (Figure 4.8). The nuthatch model is based on stochastically varying parameters (Section 4.2.2). To provide a controlled testing environment for the sensitivity analyses, the nuthatch parameters were set to the defaults given in Table 5.1, creating a deterministic model. Each tested parameter was varied in turn, a recognised SEPM evaluation technique (Bart 1995; Dunning *et al.* 1995). The mean landscape population over 10,000 yearly cycles was recorded for each tested parameter. Table 5.2 lists the tested parameters and their range of variation.

Parameter	Value	Parameter	Value
<b>Nuthatch</b>		<b>Landscape</b>	
Young	5	Frag	44
Breeding success	80	%Hab	4
Winter survival probability	0.5		
Summer survival probability	0.87	<b>General</b>	
Perceptual range (km)	2	Var	Off
Field-of-view (degrees)	90	Immigration rate	30
Matrix dispersal mortality	0.005	Immigration direction	Westerly
Habitat dispersal mortality	0.001		

**Table 5.1:** The default deterministic parameters used for the nuthatch demographic sensitivity analyses. The ‘Nuthatch’ parameters govern nuthatch behaviour and are described in Section 4.2.2 and Appendix I (Section I.4). The ‘Landscape’ parameters control the structure of the internally generated neutral landscapes and are described in Section 3.6.2 and Appendix I (Section I.2.3). The ‘Var’ parameter controls variable or fixed immigration rates (set to fixed for these tests) and is described in Appendix I (Section I.4). The immigration level was set to 30 individuals per year in order to elicit measurable responses.

Parameter	Tested range	Actual range
Territory size (cells) (1 cell = 1 ha)	0 - 10	2
Breeding success probability	0 - 1	0.7 - 0.9
Fledged young	0 - 10	4 - 6
Winter survival probability	0 - 1	0.4 - 0.6
Summer survival probability	0 - 1	0.81 - 0.97
Matrix per-step dispersal mortality probability	0 - 0.1	0.001
Habitat per-step dispersal mortality probability	0 - 0.1	0.005

**Table 5.2:** The tested parameters and their range of variation. For comparison, the actual range of the parameters used for the nuthatch model tests are also given.

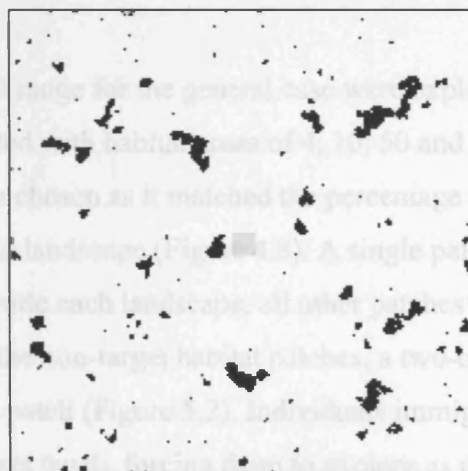
The set of neutral landscapes had a similar number of patches, habitat and quality area to that of the centralised landscape (Table 5.3). A different neutral landscape was used for each tested value, resulting in 100 different landscapes per test.

Parameter	Centralised landscape	Neutral landscapes
Number of habitat patches	235	227 (SD = 18.73, n = 500)
Total habitat area	1660 ha	1600 ha
Total quality area	300 ha	288 ha

**Table 5.3:** A comparison of the centralised and neutral landscape characteristics

### 5.2.3 Immigration Direction

Within a heterogeneous landscape, successful inter-patch dispersal is required in order to locate suitable quality breeding habitat. In this case, the presence and abundance (or absence) of nuthatches occupying a particular wood is likely to be, at least in part, a function of the direction of immigration into the study area. To test this hypothesis, a comparison of population sizes in a wood located in the centre of two types of landscape, subjected to immigration, were undertaken. The first test used a set of neutral landscapes consisting of non-target habitat (habitat not of sufficient quality to contain nuthatch territories) patches. A single 100 ha patch of target habitat (habitat of sufficient quality to contain nuthatch territories) was placed at the centre of each landscape, an area too small to support a nuthatch population without immigration. To avoid coalescence with non-target habitat patches, a two-cell wide strip of matrix was placed around the target patch (Figure 5.1). The total habitat area and mean number of generated patches for each landscape was set to match those of the centralised landscape (Figure 4.8), which was used for the second test. The mean number of pairs in the habitat patch for the neutral landscapes, and in Monks Wood for the centralised landscape, were recorded for annual immigration rates of 10, 20 and 30 individuals into the study area. Immigration direction was from an external source, located at each of the cardinal and quadrantal compass points (one direction per test). All tests were run for 100 runs of 100 yearly cycles, with a perceptual range of 2 km and a 90° field-of-view. The neutral tests used a total of 2,400 different landscapes (8 immigration directions, 3 immigration rates and 100 landscapes per test). If spatial arrangement affects dispersal flow, then these tests would be expected to show some directional bias when used with a specific landscape. As the neutral landscapes comprised a set of different spatial arrangements, any biasing in the results for these landscapes should cancel out, resulting in an unbiased response for the general case.



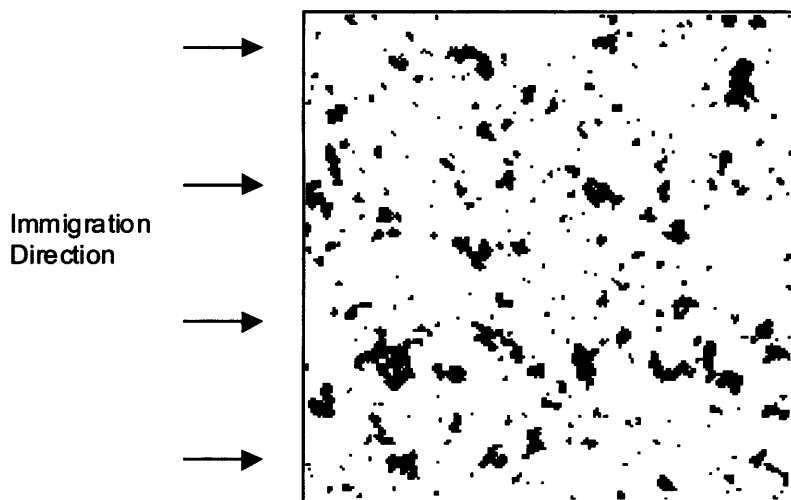
**Figure 5.1:** A sample neutral landscape, from the set of 2,400 used for the immigration direction tests. The total habitat area for each landscape was 4% (1,600 cells) with a sample mean number of patches of 219.66 (SD = 19.69,  $n = 500$ ). As a comparison, the centralised habitat landscape (Figure 4.8) had 235 patches. The shaded patch in the centre of the landscape is the target habitat patch. Landscape resolution was  $200 \times 200$  cells, representing a  $20 \times 20$  km landscape, matching the resolution of the centralised landscape.

#### 5.2.4 Perceptual Range

The overall aim of these tests was to establish whether or not perceptual range should be included as an input to individual-based SEPMs. Given the lack of empirical knowledge concerning perceptual range and the paucity of models using perceptual range (Section 2.4.7), it was thought worth exploring the effects of modelling this input. If perceptual range has a significant effect on population sizes within fragmented habitat, then its inclusion will increase the realism of models simulating the inter-patch movement of residential, territorial birds (in the UK). To evaluate the response in the general case alongside that of a specific case, the tests used a set of neutral landscapes and the centralised landscape (Figure 4.8).

#### 5.2.4.1 *Perceptual Range for the General Case*

The effects of perceptual range for the general case were explored with a set of random neutral landscapes, created with habitat areas of 4, 10, 50 and 70% of the total landscape area. The 4% option was chosen as it matched the percentage cover (target plus non-target habitat) of the centralised landscape (Figure 4.8). A single patch of target habitat was placed at the right hand side each landscape, all other patches were non-target habitat. To avoid coalescence with the non-target habitat patches, a two-cell wide strip of matrix was placed around the target patch (Figure 5.2). Individuals immigrated into the landscape from the side opposite the target patch, forcing them to explore as much of the landscape as possible in search of suitable habitat. To ensure that the size of the target habitat patch population was solely a function of immigration level and non-target habitat structure, and to avoid any misleading results created by internally generated dispersers, the target patch was made small enough to ensure it could not support a population without immigration.



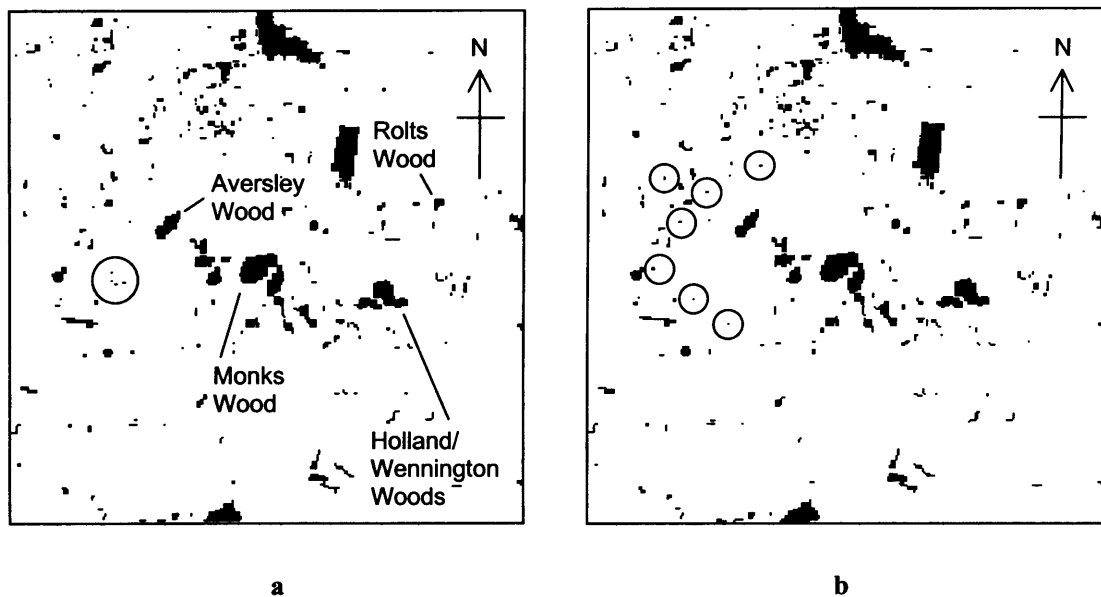
**Figure 5.2:** An example of a neutral landscape with 10% total habitat area used for the general case perceptual range tests. The target quality patch is the grey rectangle on the right hand side of the landscape.

Each set of tests was run with perceptual ranges from 0 to 7 km, using a 90° field-of-view, with a yearly immigration rate of 30 individual birds. A total of 100 landscapes was generated for each perceptual range tested, with each landscape modelled for 100 yearly cycles. The mean number of pairs in the target habitat patch was recorded for each set of tests.

#### 5.2.4.2 Perceptual Range for a Specific Case

It is perhaps intuitive that increasing perceptual range increases the size of the population in target woods. For the general case, this would be expected to hold true, but to establish whether this presumption held true for all cases, two comparative tests were devised. The first test used the centralised landscape given in Figure 4.8. For the second test, four 1 ha woods (the smallest possible at the modelled scale of 1 cell = 1 ha) were removed from the centralised landscape and seven 1 ha woods added to it, to form the ‘adjusted’ landscape of Figure 5.3b. All the ‘adjusted’ woods were non-target habitat (that is, the same quality landscape of Figure 4.8b was used for both tests). Although somewhat contrived, this scenario could represent felling and planting and/or maturing of existing woods and as such was thought feasible.

Both tests were run with perceptual ranges from 0 to 10 km, using a 90° field-of-view. Each test was run for 10,000 yearly cycles, with 30 immigrants per year from a westerly direction. The mean number of pairs in Aversley, Monks, Holland and Wennington and Rolts Woods (Figure 5.3a) were recorded for each test. Also recorded for each of the target woods was successful settlement by immigrant birds entering the landscape and successful settlement by birds immigrating from other woods within the landscape.



**Figure 5.3:** The centralised landscape (Figure 5.3a) with no adjustments and the ‘adjusted’, landscape, with four patches removed and seven added (Figure 5.3b). The circled patches in Figure 5.3a were removed and the circled patches in Figure 5.3b were added. The woods of relevance to the perceptual range tests are labelled in Figure 5.3a. Due to their close proximity, Holland and Wennington Woods were grouped together.

### 5.2.5 Immigration and Perceptual Range

If perceptual range is a factor in guiding dispersers towards distant woods and reducing dispersal mortality, then varying the perceptual range should have an effect on population size. To test this hypothesis, the mean population size in Monks Wood for the centralised landscape (Figure 4.8) was recorded for perceptual ranges from 0 to 20 km, a 90° field-of-view and westerly immigration rates of 10, 20, 30, 40 and 50 individuals per annum. Each test was for 10,000 yearly cycles.

### 5.2.6 Field-of-View

When traversing the matrix, it seems likely that for a given perceptual range, the wider a dispersers' field-of-view, the greater its chances of detecting a habitat patch and hence the lower its chances of dispersal mortality. When directly simulating dispersal, the modelled field-of-view is therefore likely to have an effect on predicted population sizes in target woods, which would presumably increase with increasing field-of-view. As field-of-view is an element of perceptual range (Section 3.7.2), increasing both factors should also increase dispersal success.

The effects of varying the field-of-view for the general case were explored with a set of random neutral landscapes. These were similar in structure to those generated for the perceptual range tests (Figure 5.2), but with a total habitat area of 4% of the landscape area, matching the percentage cover (target plus non-target habitat) of the centralised landscape (Figure 4.8). Individuals immigrated into the landscape from the side opposite the target patch, forcing them to explore as much of the landscape as possible in search of suitable habitat. Each landscape was run for 100 yearly cycles, with an immigration rate of 30 birds per annum for fields of view of straight-ahead, 90° and 180°, over perceptual ranges from 0 to 7 km. A total of 100 landscapes were generated for each tested field-of-view/perceptual range combination. The mean number of pairs in the target habitat patch was recorded for each set of tests.



To compare the effects of varying the field-of-view in a real landscape with those in neutral landscapes, immigration into the centralised landscape was modelled with fields of view of straight-ahead, 90° and 180°, over perceptual ranges from 0 to 7 km. Each test was run for 10,000 yearly cycles, with a westerly immigration rate of 30 birds per annum, recording the mean number of pairs in Monks Wood.

To explore any possible directional effects of field-of-view on dispersal success, the immigration direction tests (Section 5.2.3) were repeated for fields of view of straight-ahead, 90° and 180°, with a perceptual range of 2 km and an immigration rate of 20 birds per annum. These tests used the centralised landscape (Figure 4.8). As with the immigration direction tests, some directional bias would be expected with the real landscape, but none with the set of neutral landscapes (Section 5.2.3).

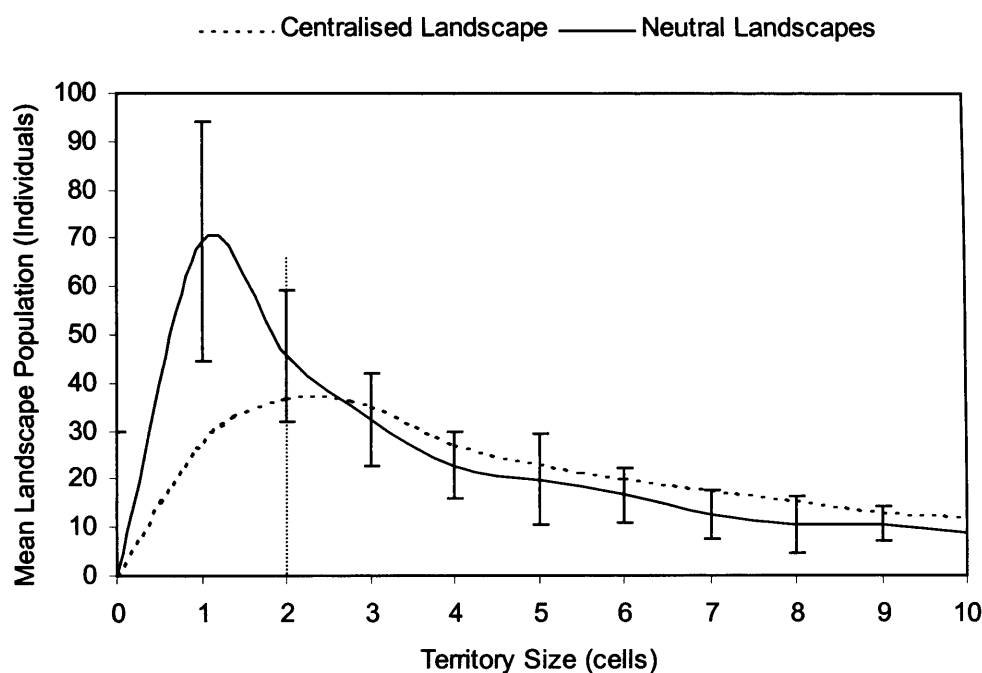
## **5.3 Nuthatch Model Sensitivity Analysis Results**

### **5.3.1 Demographic Sensitivity Analysis**

The results of the demographic sensitivity analyses are presented as a set of graphs showing the mean landscape population resulting from the variation of each parameter (Figures 5.4 - 5.10). Each graph shows the results arising from the neutral landscapes, shown with a solid trace with error bars giving one standard deviation and the results arising from the centralised landscape, shown with a dashed trace.

The results for the specific case (the centralised landscape) effectively fitted the general case (the neutral landscapes) within  $\pm 1$  standard deviation in all cases, except for the lower range ( $< 2$  ha) of the territory size tests (Figure 5.4) and the matrix dispersal mortality tests (Figure 5.9). As the specific case landscape represented a possible instance of the set of neutral test landscapes, an exact match between results would not be expected.

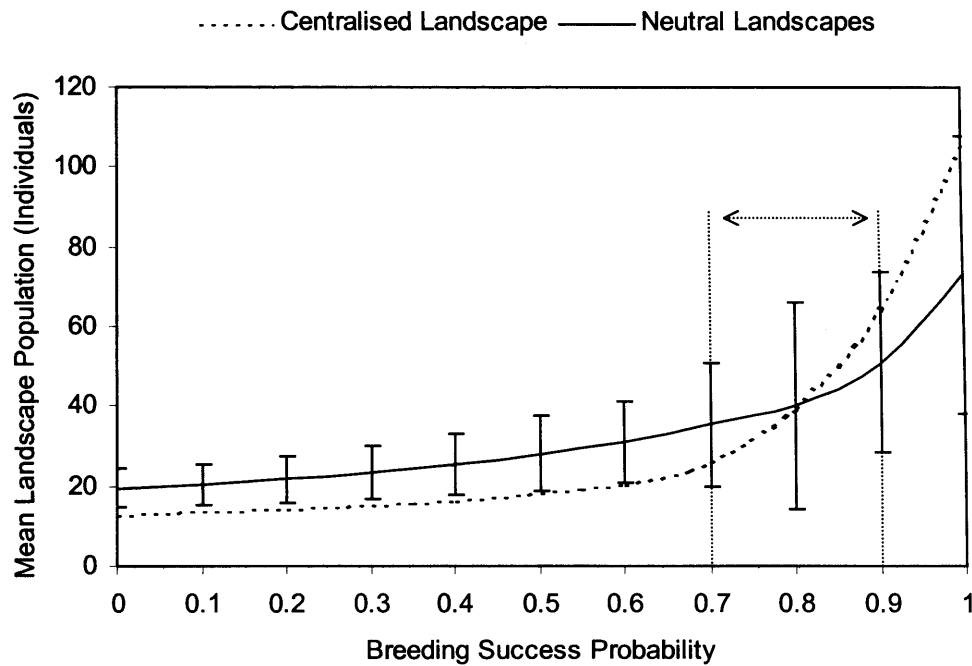
The territory size tests measured the response of the model to changes in the maximum areal density of nuthatches and it is to be expected that the lower the carrying capacity of a given area, the lower will be the maximum possible population. These expectations were borne out by the response graphs (Figure 5.4). The drop in population size at the smaller territory size for the centralised landscape is discussed further in Section 5.4.2. The lack of a population for the 0-cell territory size is to be expected and suggests that the model coding is valid.



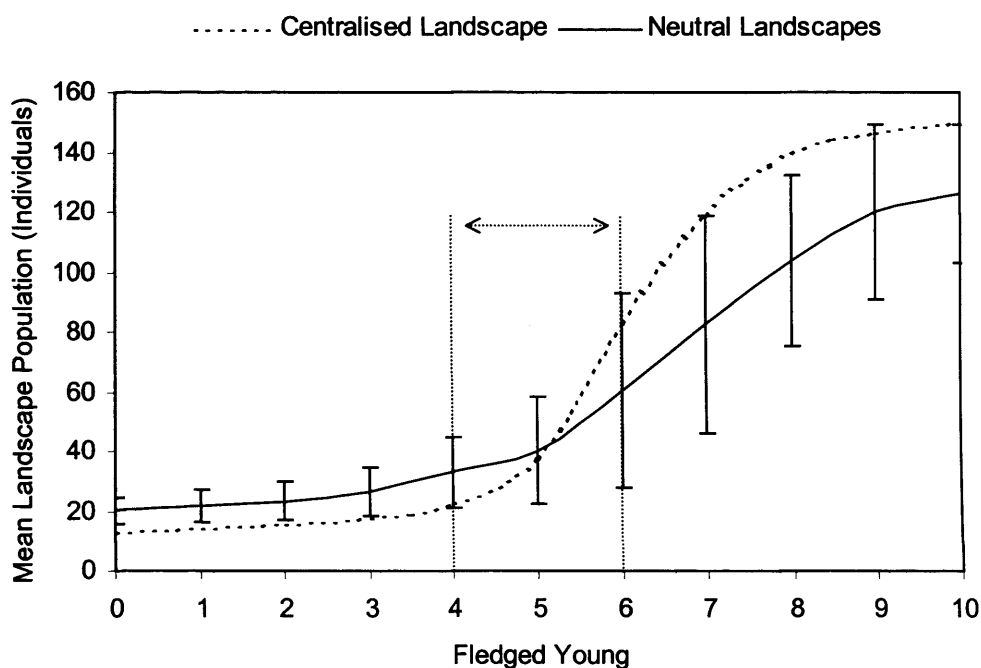
**Figure 5.4:** Response to variations in territory size. The dashed line gives the territory size used for the nuthatch model tests described in Chapter 4. The error bars give  $\pm 1$  standard deviation.

The breeding success, fledged young, winter and summer survival mortality probability tests gave similar results in that lower thresholds were evident, where there were not enough surviving birds to overcome (landscape) emigration and mortality rates (Figures 5.5 through 5.8). Upper thresholds were also evident in the fledged young (Figure 5.6) and the winter survival (Figure 5.7) tests, where the population increase was limited by the availability of territorial vacancies. A ranking of the effects of varying the nuthatch demographic parameters over their realistic ranges is given and discussed in Section 5.4.1.

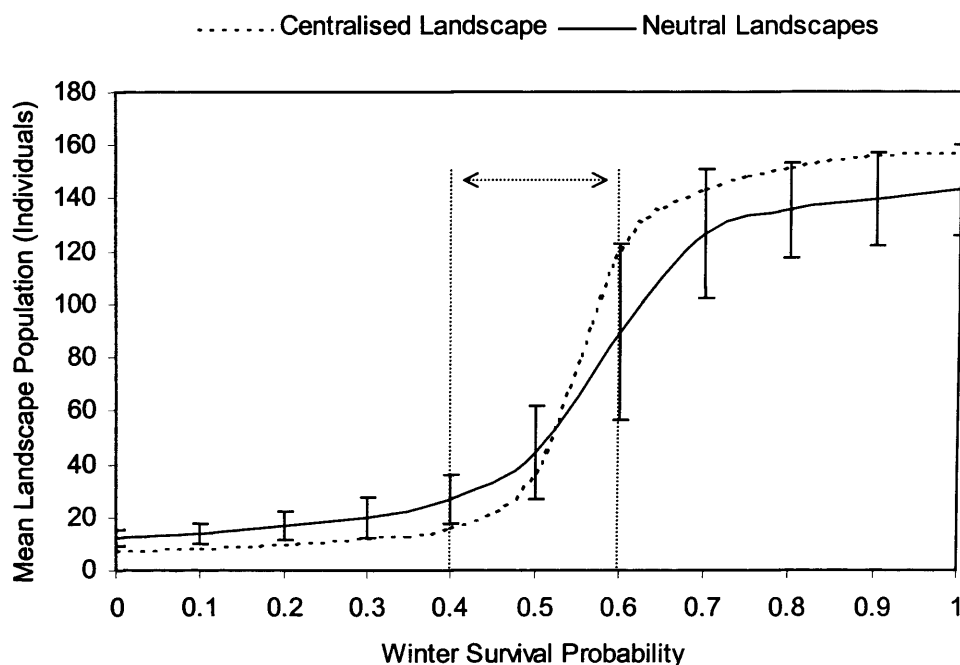
No distinct thresholds were evident with the matrix and habitat dispersal mortality tests, which showed an expected decrease in population size with increase in mortality probability over the tested range (Figures 5.9 and 5.10).



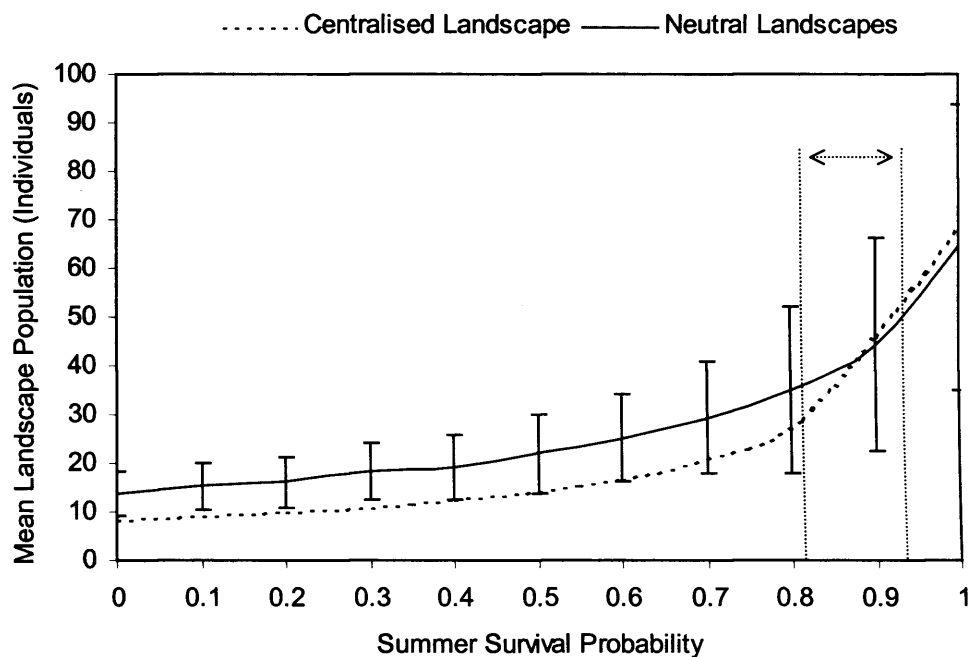
**Figure 5.5:** Response to variations in breeding success probability. The dashed lines give the range of breeding success probability used for the nuthatch model tests described in Chapter 4. The error bars give  $\pm 1$  standard deviation.



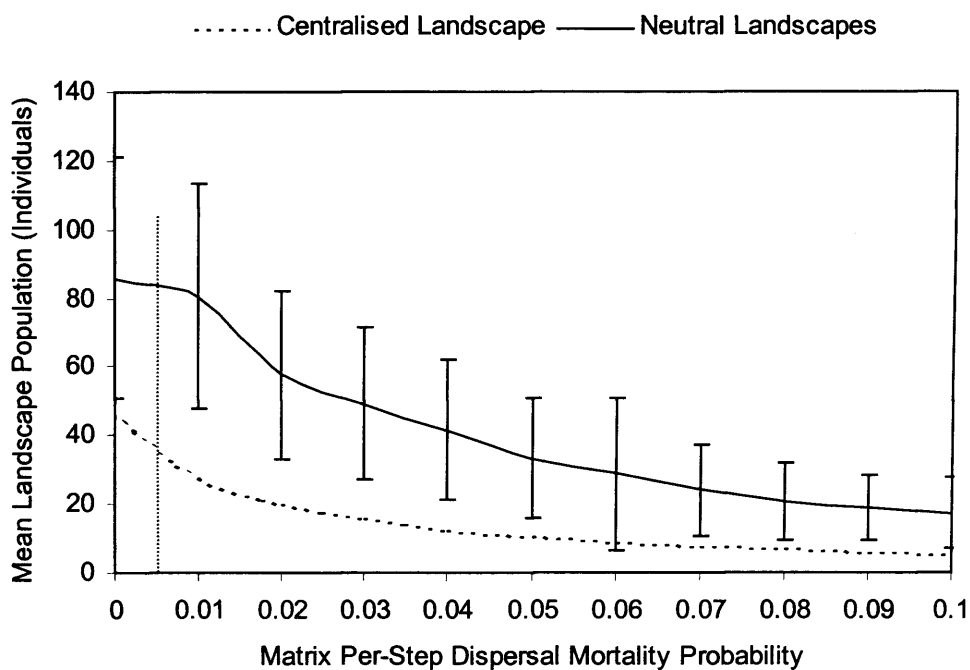
**Figure 5.6:** Response to variations in fledged young. The dashed lines give the range of fledged young used for the nuthatch model tests described in Chapter 4. The error bars give  $\pm 1$  standard deviation.



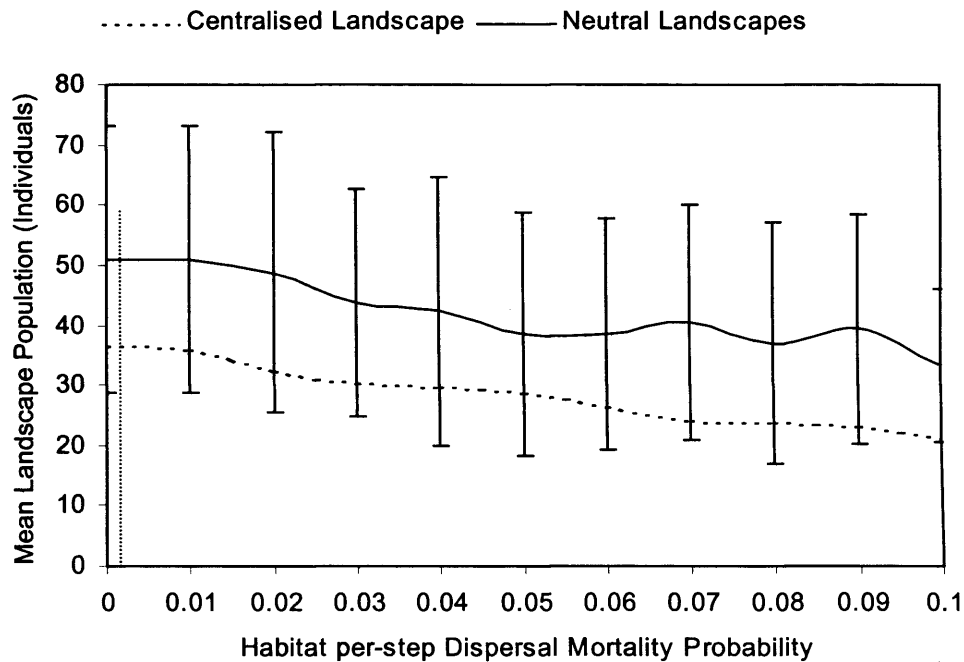
**Figure 5.7:** Response to variations in winter survival probability. The dashed lines give the range of winter survival probability used for the nuthatch model tests described in Chapter 4. The error bars give  $\pm 1$  standard deviation.



**Figure 5.8:** Response to variations in summer survival probability. The dashed lines give the range of summer survival probability used for the nuthatch model tests described in Chapter 4. The error bars give  $\pm 1$  standard deviation.



**Figure 5.9:** Response to variations in matrix per-step dispersal mortality probability. The dashed line gives the matrix per-step dispersal mortality probability used for the nuthatch model tests described in Chapter 4. The error bars give  $\pm 1$  standard deviation.



**Figure 5.10:** Response to variations in habitat per-step mortality probability. The dashed line gives the habitat per-step dispersal mortality probability used for the nuthatch model tests described in Chapter 4. The error bars give  $\pm 1$  standard deviation.

### 5.3.2 Immigration Direction

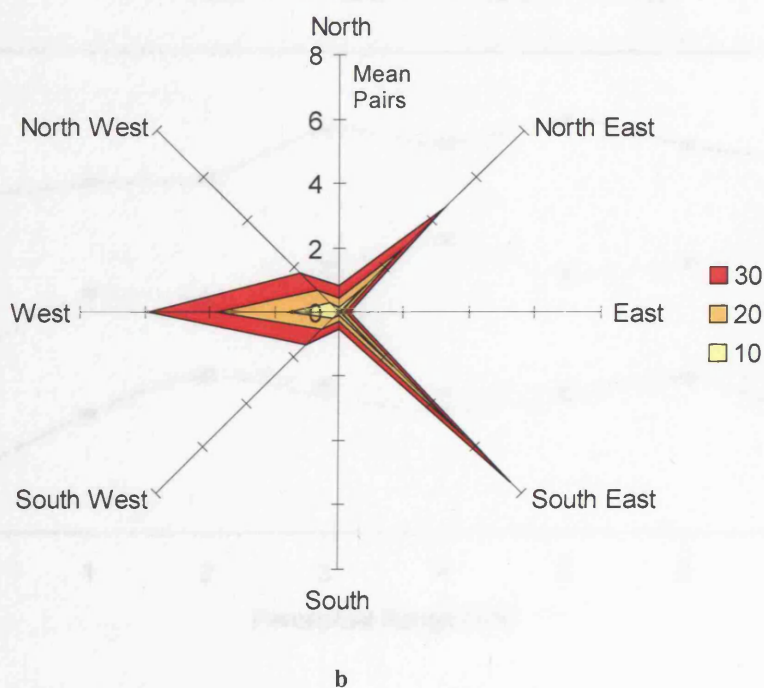
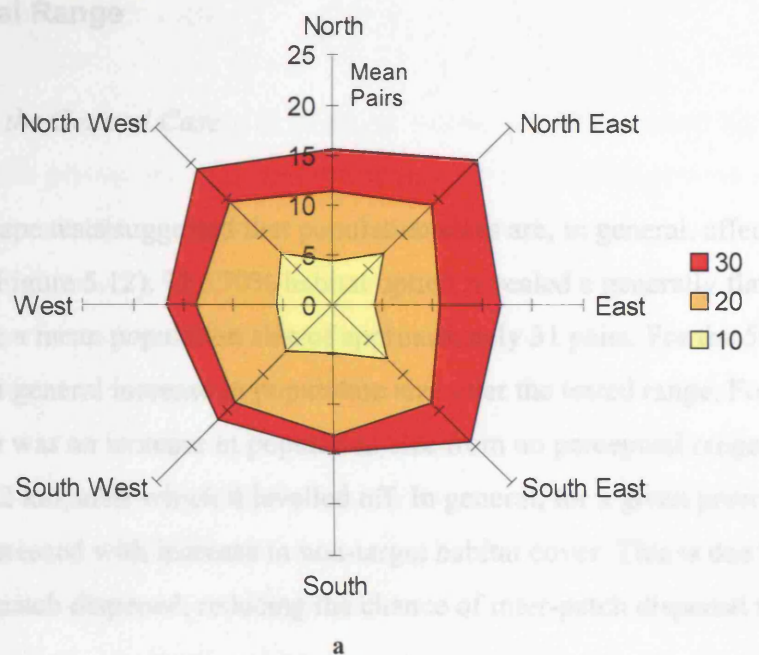
As expected, the neutral landscape immigration direction tests indicated no overall directional bias (Figure 5.11a). The centralised landscape test produced significant directional biases, with the size of the population in Monks Wood found to be most sensitive to immigration from the south-east, north-east and westerly directions (Figure 5.11b).

The response to immigration from the quadrantal directions was greater than that from the cardinal directions. On investigation, including direct testing, this was revealed as being due to the diagonals presenting a greater apparent area (in the quadrantal directions) than the sides (in the cardinal directions). The smaller inter-cardinal and inter-quadrantal biases were due to the limited sample size (100 landscapes per immigration rate per direction).

### 5.3.3. Perceptual Range

#### 5.3.3.1. Results for Central Habitat Patch

The neutral landscape analysis suggests that population size, in general, is affected by perceptual range (Figure 5.12). For the central habitat patch, at the neutral range, with a mean population size of 31 pairs, the population size was 31 pairs. For the 4 and 10% options, there was a general increase in population size at the tested range. For the 4 and 10% options, there was an increase in population size at the tested range, up to approximately 1.5 times the neutral range. In general, the population size at the tested range, population size increased with increase in the range of habitat cover. This is due to a reduction in inter-patch dispersal, reducing the chance of inter-patch dispersal mortality.

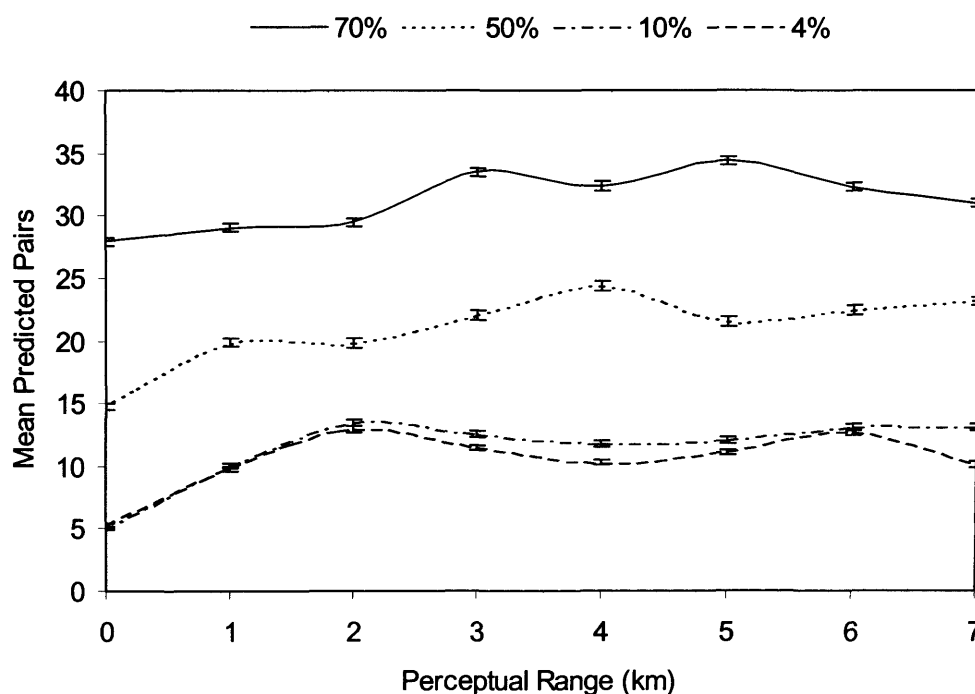


**Figure 5.11:** The sensitivity of population size to immigration direction. Figure 5.11a shows the results for the central habitat patch in the set of neutral landscapes (Figure 5.1). Figure 5.11b shows the results for Monks Wood in the centralised landscape (Figure 4.8). Results are shown for annual immigration rates of 10, 20 and 30 individuals into the study area (as per the keys). Perceptual range was set to 2 km and the field-of-view to 90°.

### 5.3.3 Perceptual Range

#### 5.3.3.1 Results for the General Case

The neutral landscape tests suggested that population sizes are, in general, affected by perceptual range (Figure 5.12). The 70% habitat option revealed a generally flat result over the test range, with a mean population size of approximately 31 pairs. For the 50% habitat option, there was a general increase in population size over the tested range. For the 4 and 10% options, there was an increase in population size from no perceptual range, up to approximately 1 - 2 km, after which it levelled off. In general, for a given perceptual range, population size increased with increase in non-target habitat cover. This is due to a reduction in inter-patch dispersal, reducing the chance of inter-patch dispersal mortality.



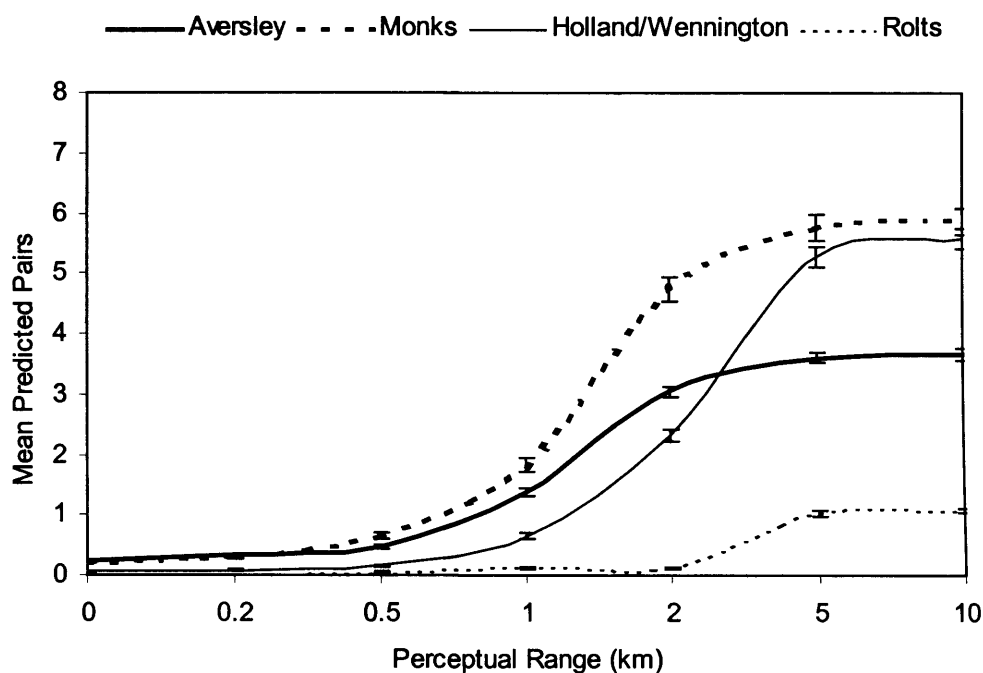
**Figure 5.12:** The mean number of pairs recorded in the target habitat patch, for the general case neutral landscapes (Figure 5.2) with 4, 10, 50 and 70 percent total habitat area (as per the key), as a function of perceptual range. All tests used a westerly immigration rate of 30 birds per annum, with a 90° field-of-view. The error bars give 95% confidence intervals.



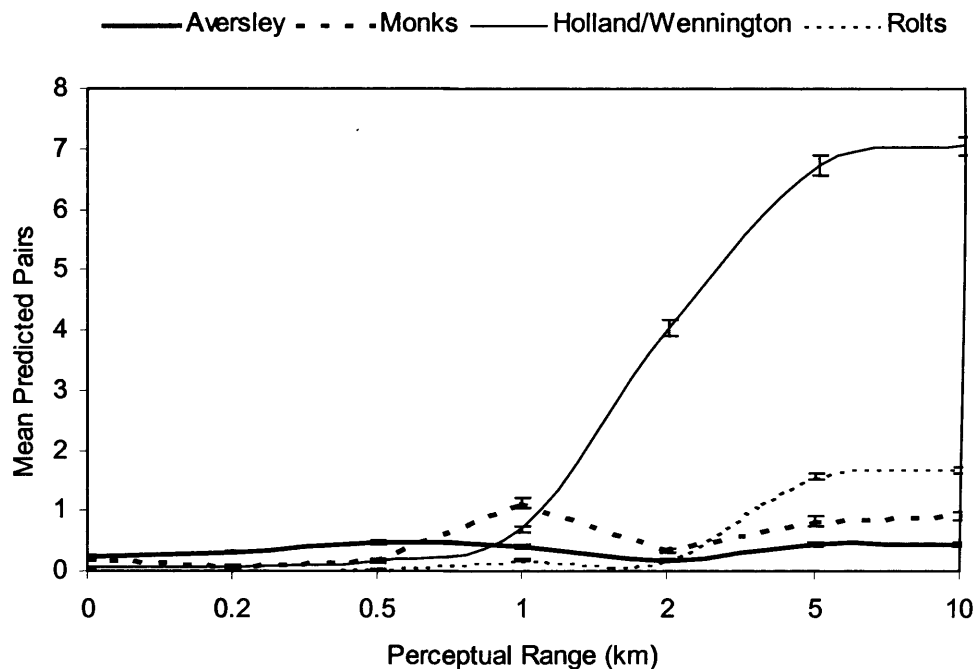
### 5.3.3.2 Results for the Specific Case

As expected, the mean population size in all target woods in the centralised landscape increased in line with perceptual range (Figure 5.13a). Lower thresholds were evident, where there were not enough immigrants into the target woods to overcome emigration and mortality rates. Upper thresholds were also evident, above which populations in the target woods could not increase, due to all territories being taken or the immigration rate balancing the combined emigration and mortality rates.

With the adjusted landscape, the population size in Holland/Wennington and Rolts Woods increased over that for the centralised landscape (Figure 5.13b). The population in Aversley Wood effectively remained constant. The population size in Monks Wood responded in a similar fashion to that of the centralised landscape up to a range of 1 km, but then dropped to a lower level for the remainder of the tested perceptual ranges. Lower and upper thresholds similar to those for the centralised landscape were evident. The effective failure of the population size in Aversley and Monks Woods to increase over the tested perceptual ranges is noteworthy and is discussed further in Section 5.4.4.



a



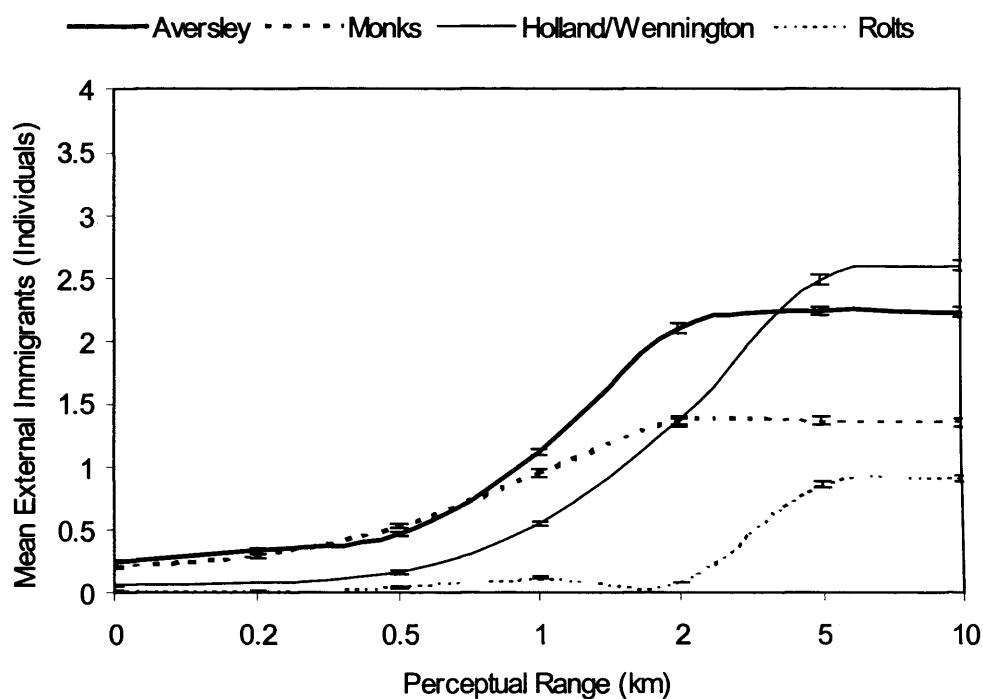
b

**Figure 5.13:** The mean number of pairs in Aversley, Monks, Holland/Wennington and Rolts Woods as a function of perceptual range, as per the legends. Figure 5.13a shows the results for the centralised landscape (Figure 4.8). Figure 5.13b shows the results for the adjusted landscape (Figure 5.3b). The error bars give 95% confidence intervals.

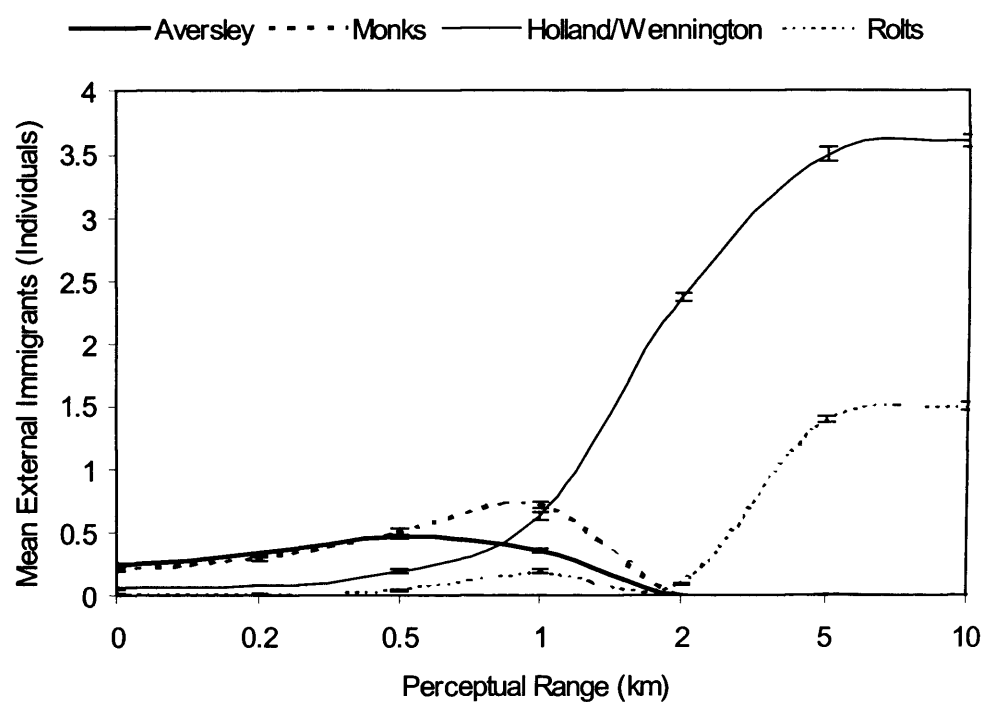
The mean number of immigrants entering the landscape and successfully settling in the target woods in the centralised landscape increased in line with perceptual range (Figure 5.14a). This is to be expected. Lower thresholds were evident, below which immigrants did not have enough perceptual range to locate potential habitat patches. The longer the distance required to travel to reach a vacant territory, the greater the chance of dispersal mortality, which (in this model) can only be (partially) overcome with a higher perceptual range. This is reflected in the lower thresholds occurring at increasingly higher perceptual ranges, the further the woods were from the immigration source (the westerly edge of the landscape). Upper thresholds were evident, where there were no more immigrants available to settle in the target woods, no vacant territories existed or the immigration rate balanced the emigration and mortality rates.

For the adjusted landscape, the results for Holland/Wennington and Rolts Woods were similar to those for the centralised landscape, except that the maximum number of successfully settling external immigrants was greater (Figure 5.14b). For Aversley and Monks Woods, the number of settling immigrants peaked at approximately 1 km perceptual range and then decreased to zero at approximately 2 km and remained so for the remainder of the tested perceptual ranges. The drop in immigrants for these two woods corresponded to a drop in their population sizes (Figure 5.13b), suggesting that the population in the target woods is reliant on immigration (Alderman *et al.* 2004, reproduced in Appendix B.1). Reasons behind this drop are further discussed in Section 5.4.4.

The graphs for the number of immigrants from woods within the study area successfully settling in the target woods showed broadly similar response curves for both landscapes (Figure 5.15). The lower maximum values in the target woods for the adjusted landscape (Figure 5.15b) were ascribed to the generally lower population size in the target woods for that landscape (Figure 5.13b), compared with the centralised landscape (Figure 5.13a), being expected to produce fewer emigrants.

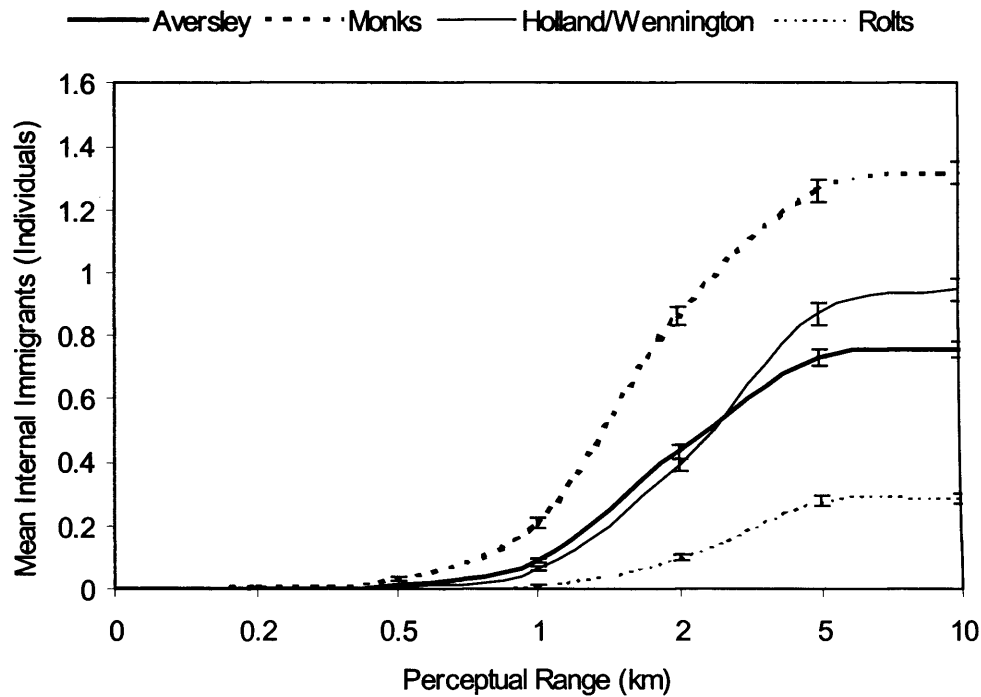


a

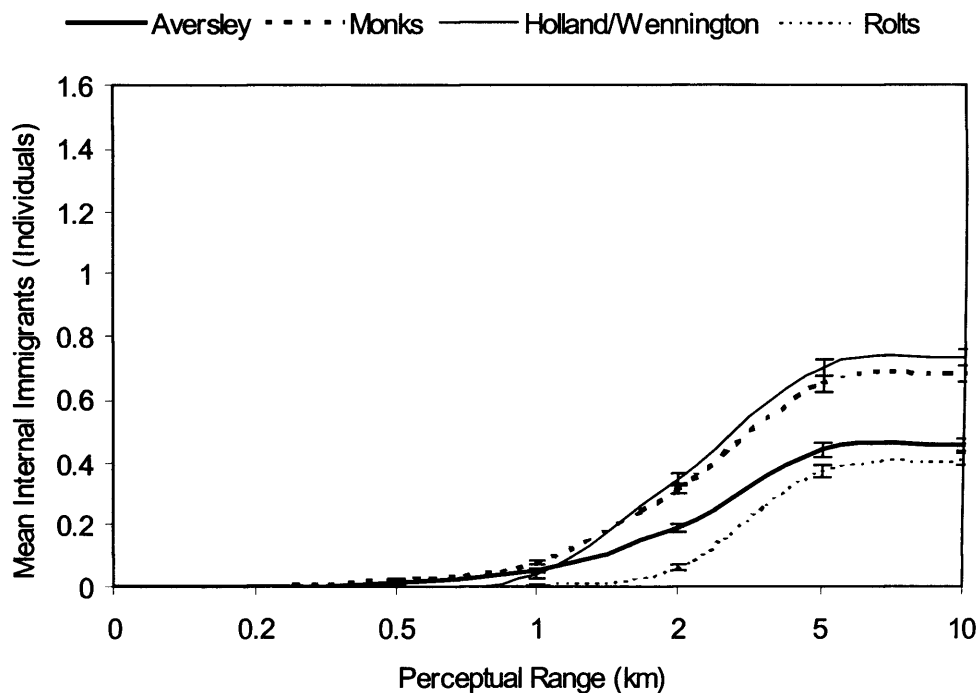


b

**Figure 5.14:** The mean number of individual immigrants entering the landscape, successfully occupying territories in Aversley, Monks, Holland/Wennington and Rolts Woods as a function of perceptual range, as per the legends. Figure 5.14a shows the results for the centralised landscape (Figure 4.8). Figure 5.14b shows the results for the adjusted landscape (Figure 5.3b). The error bars give 95% confidence intervals.



a

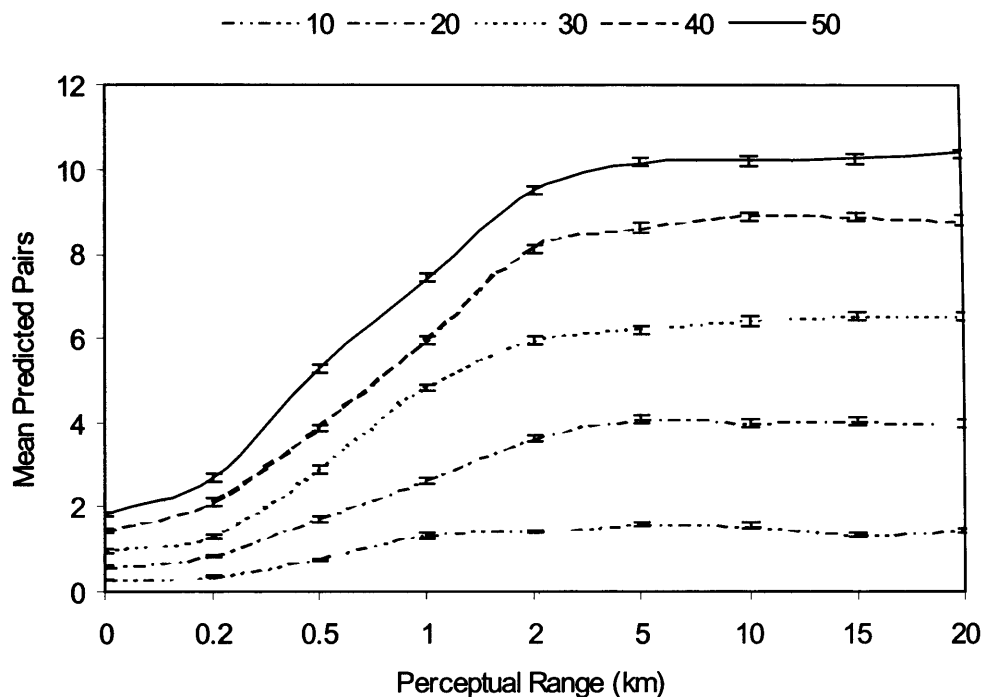


b

**Figure 5.15:** The mean number of individual immigrants originating from woods within the landscape, successfully occupying territories in Aversley, Monks, Holland/Wennington and Rolts Woods as a function of perceptual range, as per the legends. Figure 5.15a shows the results for the centralised landscape (Figure 4.8). Figure 5.15b shows the results for the adjusted landscape (Figure 5.3b). The error bars give 95% confidence intervals.

### 5.3.3.3 Immigration and Perceptual Range

The immigration and perceptual range tests showed that the population size in Monks Wood (Figure 5.16) was a function of both immigration rate and perceptual range. The mean number of predicted pairs in Monks Wood increased with perceptual range, levelling off at thresholds between 1 to 5 km.



**Figure 5.16:** The mean number of pairs in Monks Wood using the centralised landscape (Figure 4.8), as a function of perceptual range, for annual immigration rates of 10, 20, 30, 40 and 50 individuals into the study area (as per the key). Direction of immigration was set to the west and field-of-view to 90°. The error bars give 95% confidence intervals.

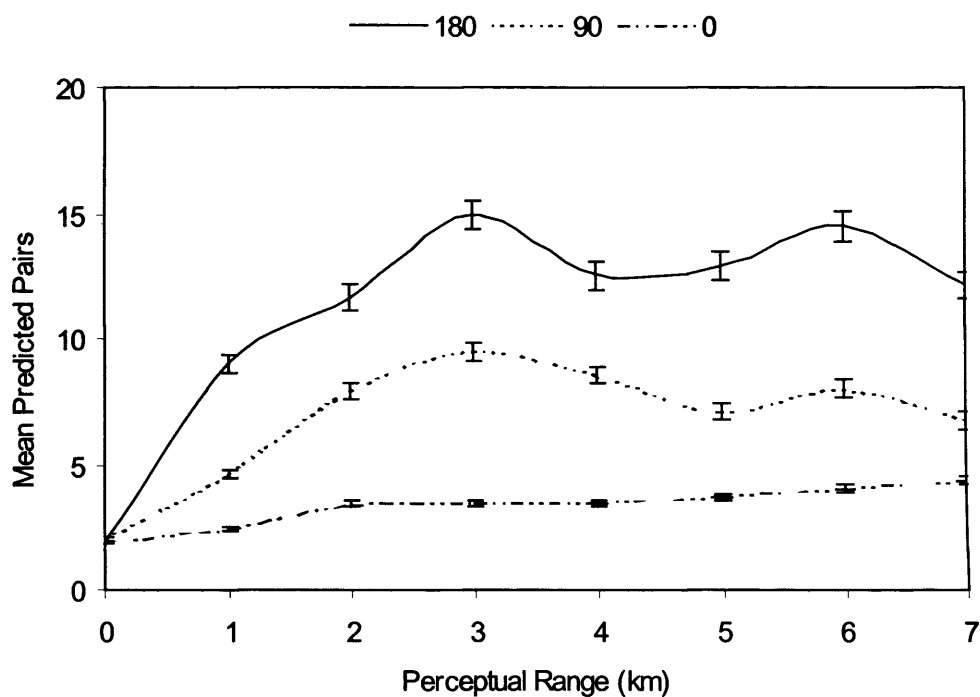
### 5.3.4 Field-of-View

The neutral landscape field-of-view tests revealed that the population size in the target patch increased in line with a widening field-of-view for a given perceptual range (Figure 5.17a). The narrow straight-ahead field-of-view produced only a slight increase in population size over the tested 0 - 7 km perceptual range. The wider fields of 90° and 180° increased population size up to a threshold at approximately 3 km perceptual range, beyond which a general decrease occurred.

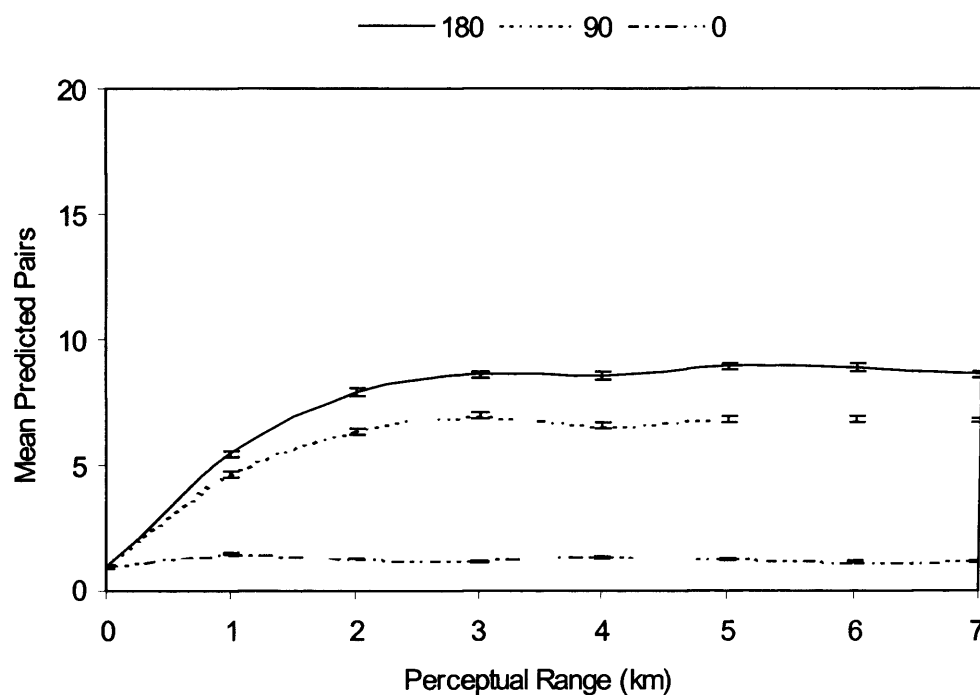
As with the neutral landscape tests, the centralised landscape field-of-view tests also revealed that the predicted population size in Monks Wood increased in line with a widening in field-of-view for a given perceptual range (Figure 5.17b). The narrow straight-ahead field-of-view again produced no real increase in population size. The 90° and 180° fields of view both resulted in an upper threshold in population size at a perceptual range of approximately 3 km.

As expected, the neutral landscape directional field-of-view tests indicated no overall directional bias (Figure 5.18a). The centralised landscape tests, however, revealed significant directional biasing (Figure 5.18b). In general, the 180° field-of-view increased dispersal compared to the straight-ahead and 90° options, which gave similar results, except when immigration was westerly or south-easterly. All three options gave the same result when immigration was south-westerly.

As with the immigration direction tests (Figure 5.11), immigration from the quadrantal directions produced a greater response to that from the cardinal directions. The reasons behind this are given in Section 5.3.2.



a



b

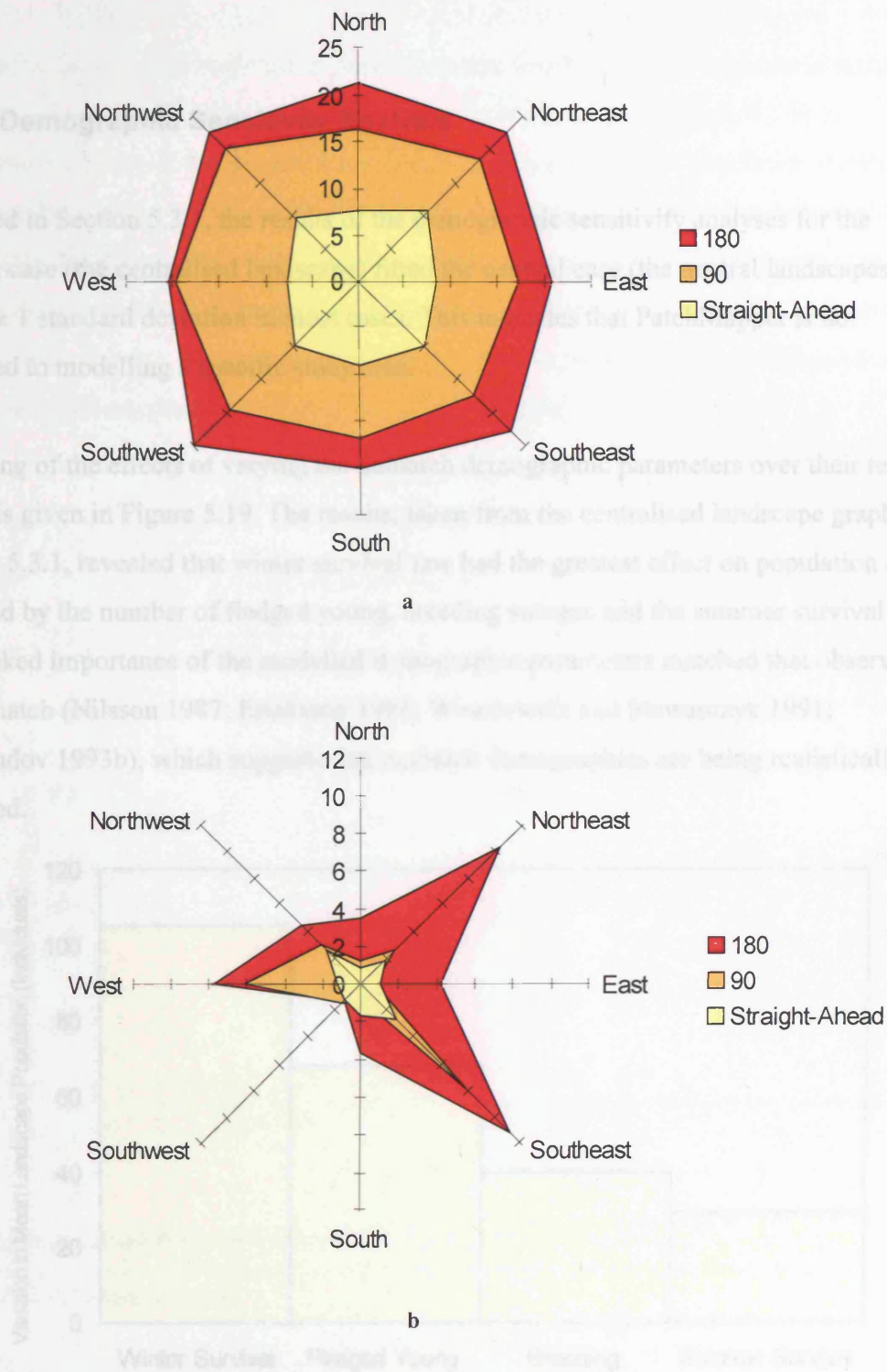
**Figure 5.17:** Predicted mean pairs in the target habitat patch within the neutral landscapes (Figure 5.17a) and in Monks Wood using the centralised landscape (Figure 5.17b), for the straight-ahead, 90° and 180° fields of view (as per the legends) as a function of perceptual range. Immigration was westerly at a rate of 30 birds per annum. Plot 5.17b is, in essence, a specific example of the general case. The error bars give 95% confidence intervals.



## 5.4 Nuthatch Model Sensitivity Analysis Discussion

### 5.4.1 Demography

As stated in Section 5.3.1, the sensitivity analyses for the specific values of the demographic parameters (within a 1 standard deviation range) revealed that the number of fledged young had the greatest effect on population size, followed by the number of fledged young surviving winter and the summer survival rate. The ranked importances of the modelled demographic parameters matched that observed for the nuthatch (Nilsson 1987; Eason *et al.* 1997; Woodroffe and Potts 1997; Pravosudov 1993b), which suggests that the demographic parameters are being realistically modelled.



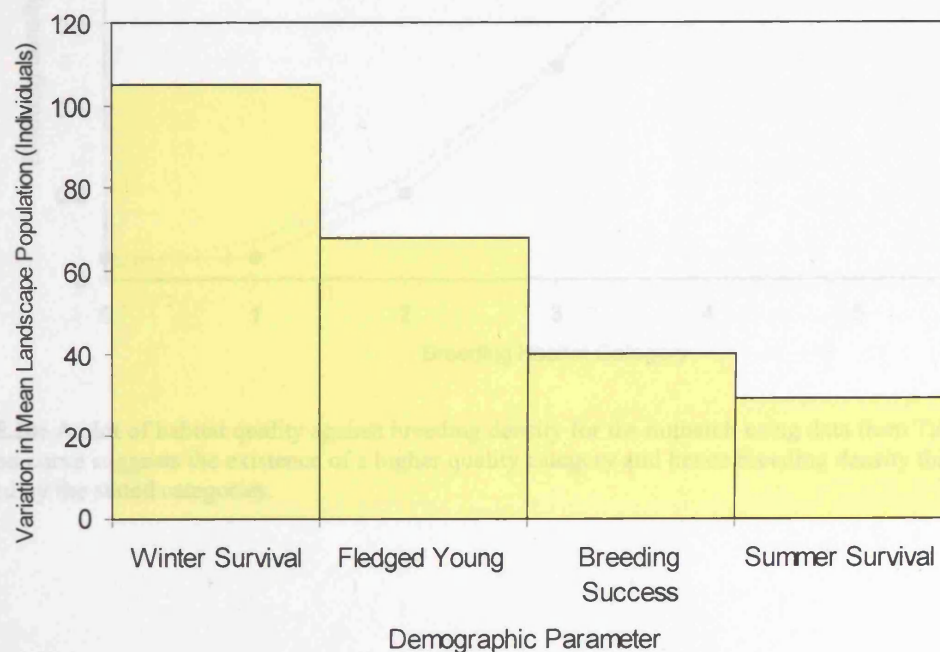
**Figure 5.18:** The sensitivity of population size to immigration direction and field-of-view. Figure 5.18a shows the results for the central habitat patch in the set of neutral landscapes (Figure 5.1). Figure 5.18b shows the results for Monks Wood, in the centralised landscape (Figure 4.8). Immigration rate was 20 birds per annum, with fields of view of straight-ahead, 90° and 180°, as per the keys.

## 5.4 Nuthatch Model Sensitivity Analysis Discussion

### 5.4.1 Demographic Sensitivity Analysis

As stated in Section 5.3.1, the results of the demographic sensitivity analyses for the specific case (the centralised landscape) fitted the general case (the neutral landscapes) within  $\pm 1$  standard deviation in most cases. This indicates that PatchMapper is not restricted to modelling a specific study area.

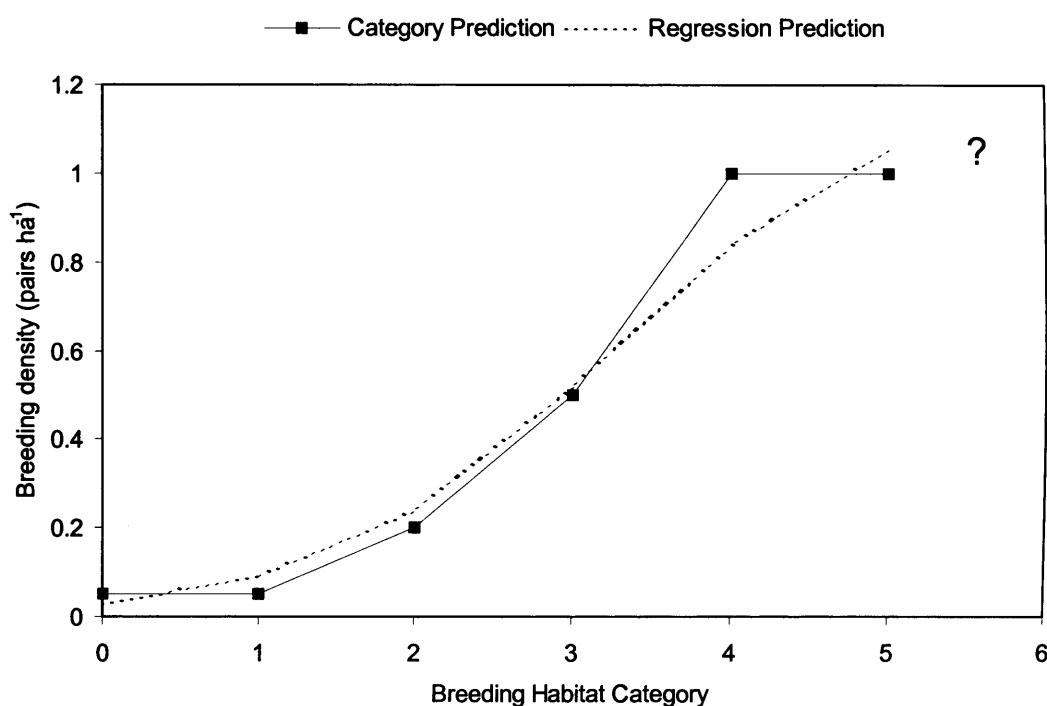
A ranking of the effects of varying the nuthatch demographic parameters over their realistic ranges is given in Figure 5.19. The results, taken from the centralised landscape graphs in Section 5.3.1, revealed that winter survival rate had the greatest effect on population size, followed by the number of fledged young, breeding success and the summer survival rate. The ranked importance of the modelled demographic parameters matched that observed for the nuthatch (Nilsson 1987; Enoksson 1988; Wesolowski and Stawarczyk 1991; Pravosudov 1993b), which suggests that nuthatch demographics are being realistically modelled.



**Figure 5.19:** Ranked minimum to maximum variations in mean landscape population arising from varying the stochastic demographic parameters over their realistic ranges.

### 5.4.2 Habitat Surveys

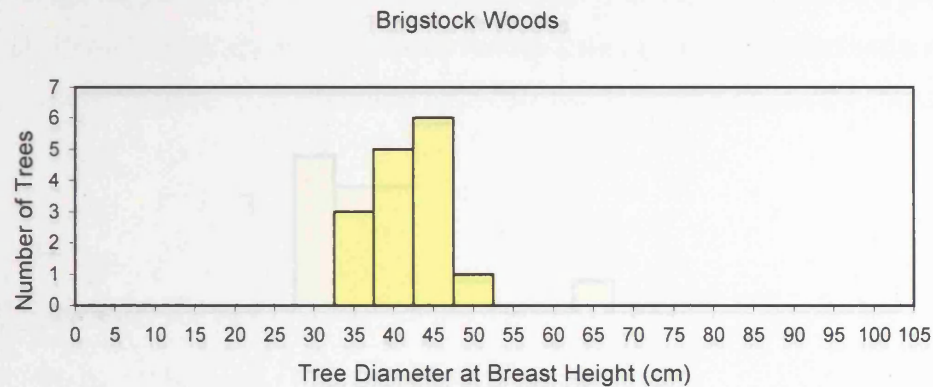
The graphs showing the response in population size resulting from variations in territory size for the nuthatch (Figure 5.4) and the white-footed mouse (Figure 5.33), both demonstrated a drop at the smaller sizes. These results suggest that population density may not increase beyond a certain level of habitat quality. Nuthatch habitat has been divided into five categories, giving a maximum breeding density according to the diameter of the (mainly deciduous) trees at breast height (Table 4.2). Plotting the five categories against breeding density suggests that a further category may exist, resulting in a higher breeding density than the suggested maximum of  $0.5 \text{ ha}^{-1}$  (Figure 5.20).



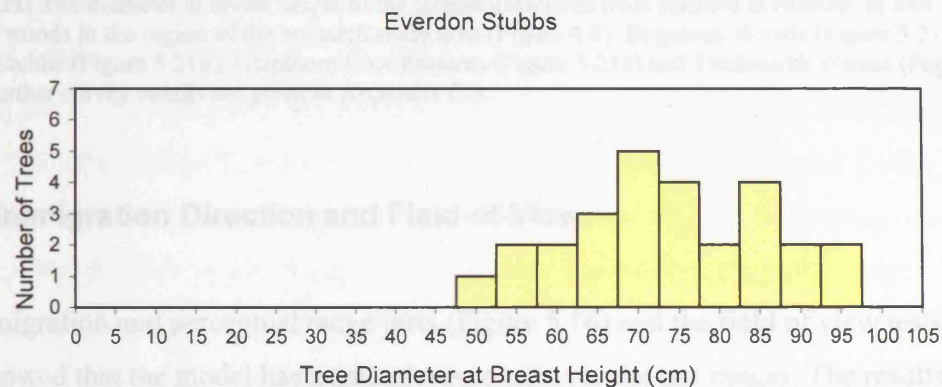
**Figure 5.20:** A plot of habitat quality against breeding density for the nuthatch using data from Table 4.2. The regression curve suggests the existence of a higher quality category and hence breeding density than that suggested by the stated categories.

To investigate the possibility of a higher nuthatch habitat quality category, field trips to four mature broadleaf woodlands in the region of the study area were undertaken. Where present, trees larger than 40 cm were selected at random and their diameter at breast height recorded. The results for each surveyed wood are given in Figure 5.21, with further details in Appendix C.4 and show the existence of a range of larger sized trees. The highest habitat quality category (number 5) groups trees greater than 40 cm diameter at breast height, but does not give a higher limit. One subject for further research is an investigation into the existence of a higher level of habitat quality and whether or not a higher breeding density occurs therein. This could be followed by a re-survey and re-modelling of the Monks Wood study area, and a comparison with the results given in this thesis.

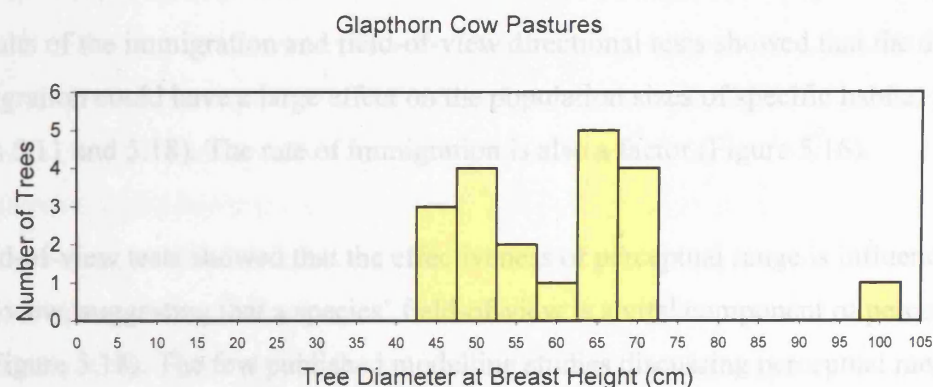




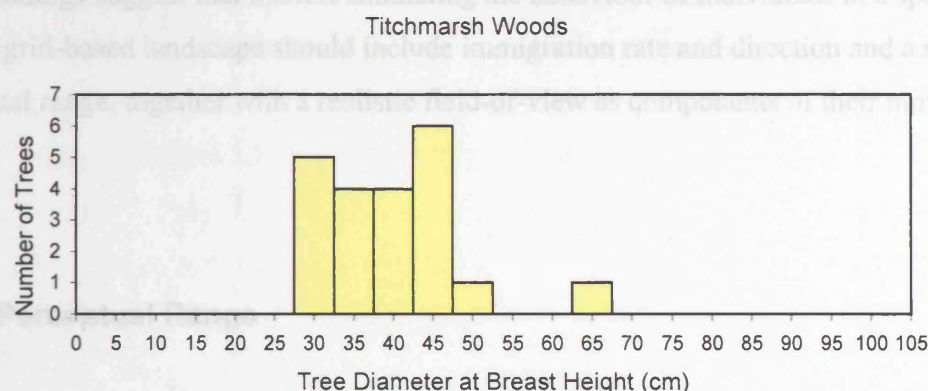
**Figure 5.21a:** The diameter at breast height of the largest deciduous trees selected at random in Brigstock Woods.



**Figure 5.21b:** The diameter at breast height of the largest deciduous trees selected at random in Everdon Stubbs.



**Figure 5.21c:** The diameter at breast height of the largest deciduous trees selected at random in Glaphorn Cow Pastures.



**Figure 5.21d:** The diameter at breast height of the largest deciduous trees selected at random in Titchmarsh Wood.

**Figure 5.21:** The diameter at breast height of the largest deciduous trees selected at random, in four mature broadleaf woods in the region of the nuthatch study area (Figure 4.6): Brigstock Woods (Figure 5.21a), Everdon Stubbs (Figure 5.21b), Glapthorn Cow Pastures (Figure 5.21c) and Titchmarsh Woods (Figure 5.21d). Further survey details are given in Appendix C.4.

### 5.4.3 Immigration Direction and Field-of-View

The immigration and perceptual range tests (Figure 5.16) and the field of view tests (Figure 5.17) showed that the model has a smooth response over the test ranges. The results of these tests did reveal thresholds, but they were not abrupt (i.e. not a step function), indicating that PatchMapper's movement and searching algorithms are valid and that spatial distribution governed the results.

The results of the immigration and field-of-view directional tests showed that the direction of immigration could have a large effect on the population sizes of specific habitat patches (Figures 5.11 and 5.18). The rate of immigration is also a factor (Figure 5.16).

The field-of-view tests showed that the effectiveness of perceptual range is influenced by field-of-view, suggesting that a species' field-of-view is a vital component of perceptual range (Figure 5.18). The few published modelling studies discussing perceptual range used a 360° field-of-view (Cain 1985; Fahrig 1988) or looked directly ahead (Zollner and Lima 1999a). Field-of-view was not varied in these studies, which meant that performance comparisons with PatchMapper in this respect were not possible.

These findings suggest that models simulating the behaviour of individuals in a spatially explicit grid-based landscape should include immigration rate and direction and a realistic perceptual range, together with a realistic field-of-view as components of their movement rules.

#### 5.4.4 Perceptual Range

As stated in Section 5.2.4.2, it may be supposed that increasing perceptual range would always increase the population size in target woods. The perceptual range test results for the general case (Figure 5.12) did indeed show an overall, although not dramatic, increase in predicted population size in line with perceptual range. The thresholds revealed by the tests using the centralised landscape (Figure 5.13a), by the immigration and perceptual range tests (Figure 5.16), along with the published results described in Section 2.4.7, certainly support this supposition. The thresholds for the adjusted landscape (Figure 5.13b), however, revealed that increasing perceptual range had no effect on the population size in Aversley Wood. With Monks Wood, the population size peaked at approximately 1 km. In this case, making small adjustments in the landscape, by removing four 1 ha patches and adding seven 1 ha patches of non-quality breeding habitat produced unexpected results, revealing that intuition is not a reliable guide to a (modelled) species' response to fragmentation.

The thresholds for the centralised landscape suggested that habitat perceptual range would enable a dispersing species to overcome the effects of fragmentation to some extent. Above a particular perceptual range, a habitat patch will always be detected from another patch. This would limit the advantage of increasing perceptual range beyond some optimal value for particular species in particular landscapes. The perceptual range tests for the specific case using the adjusted landscape, suggested that this optimal range may not be constant over a particular landscape (Figures 5.13b, 5.14b and 5.15b). The optimal perceptual range for populating Holland, Wennington and Rolts Woods in this landscape was approximately

5 km and approximately 1 km for Monks Wood. There was no optimal perceptual range for Aversley Wood (within the test limits). As a contrast, the optimal perceptual range for populating all target woods in the centralised landscapes was approximately 2 - 5 km (Figures 5.13a, 5.14a and 5.15a).

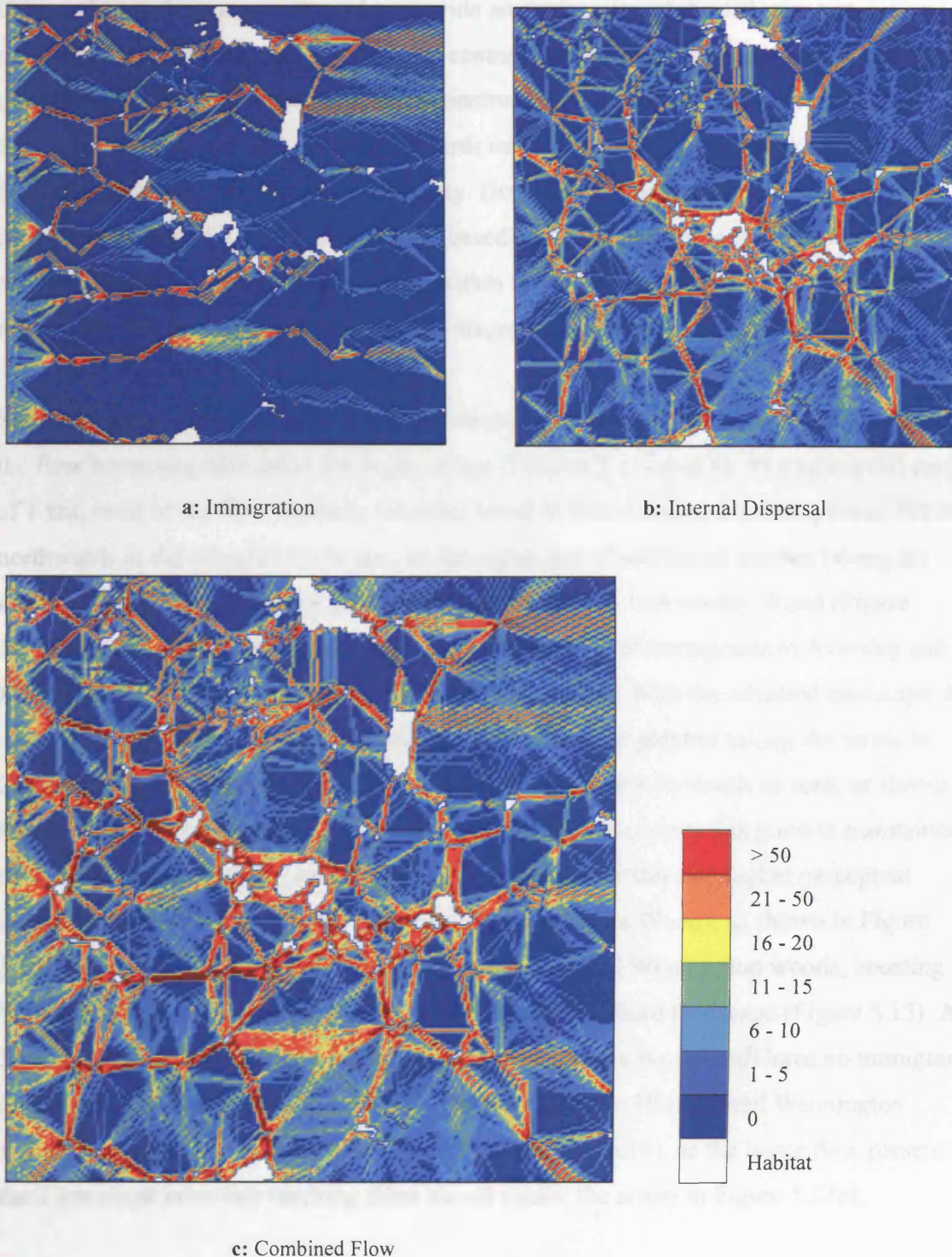
#### *5.4.4.1 The Case for Dispersal Flow Diagrams*

The immigration graphs for the specific case tests (Figures 5.14 and 5.15) go some way to explaining what is happening. The external immigration graphs show that successful immigration from outside the study area increased in line with increase in perceptual range, as expected, for the centralised landscape (Figure 5.14a). For the adjusted landscape, this remained true for Holland/Wellington and Rolts Woods, but dropped off after approximately 1 km for Monks and Aversley Woods, reducing to zero at 2 km (Figure 5.14b). This, together with the similar 'shapes' of the internal immigration graphs (Figure 5.15), suggested that immigrants entering the landscape were unable to discover, or experienced difficulties in discovering, Monks and Aversley Woods. This is not a complete explanation and demonstrates the problems with relying solely on graphs when analysing the results of individual-based SEPMs.

A better, and far more interesting, explanation can be provided with dispersal flow diagrams, one of the possible outputs of PatchMapper (Section 3.8.5). Dispersers can either originate from patches outside (immigration) or from patches inside (internal dispersal) the landscape. The flow patterns generated by the two types of dispersal combine to form an overall dispersal flow pattern for a particular landscape. To reveal their contributions towards the overall pattern, separate flow diagrams were constructed for the immigrating and the internal dispersers, together with a single flow diagram combining the immigration and internal dispersal paths (Figure 5.22). This was accomplished by recording the dispersal paths of 5,000 immigrating birds until they found good quality territory, left the landscape or suffered dispersal mortality. These examples used the centralised habitat and quality landscapes (Figure 4.8), westerly immigration, a perceptual range of 2 km and a 90° field-of-view.



The combined immigration and internal dispersal flow diagram (Figure 5.22c) showed that dispersal of the nuthatches was governed by the spatial arrangement of target and non-target habitat patches. Several dispersal paths linking habitat and non-habitat patches, creating a dispersal network, were revealed. Dead spots were also revealed, through which nuthatches were unlikely to disperse. The two elements of the combined flow diagram showed that a greater level of dispersal was generated by internal (originating from a natal patch within the landscape) dispersal (Figure 5.22b) than by the immigrating nuthatches (Figure 5.22a). The immigration rate was low, but has been found necessary to maintain the nuthatch population in this particular landscape (Alderman *et al.* 2004, reproduced in Appendix B.1), and results in an overall west to east flow bias.



**Figure 5.22:** The dispersal flow diagrams for the centralised landscape, showing the accumulated immigration and internal dispersal paths for a total of 5,000 nuthatches. The combined flow (Figure 5.22c) results from the constituent elements of flow due to immigration (Figure 5.22a) and internal dispersal from good quality habitat (Figure 5.22b). Perceptual range was set to 2 km and the field-of-view to 90°. The key shows the number of dispersers.

Dispersal flow diagrams were used to provide an explanation of the difference in population sizes in the target woods in the centralised and adjusted landscapes (Figures 4.8 and 5.3b). Dispersal flow diagrams were constructed using both landscapes, by recording the dispersal paths of 3,000 immigrating birds until they found good quality territory, left the landscape or suffered dispersal mortality. Dispersal flow diagrams were created for perceptual ranges of 0, 0.5, 1, 2, and 5 km based on westerly immigration and a 90° field-of-view. For clarity, internal (originating within the landscape) dispersal paths were not recorded for these examples. The resultant diagrams are given in Figure 5.23.

Similar diagrams resulted from perceptual ranges of 0 and 0.5 km for both landscapes, with the flow becoming directed at the higher range (Figures 5.21a and b). At a perceptual range of 1 km, most of the flow reaching Aversley wood in the centralised landscape was directed northwards in the adjusted landscape, by the upper line of additional patches (along the arrow in Figure 5.23c), reducing the size of the population in Aversley Wood (Figure 5.13b). At 2 km perceptual range, there was a strong flow of immigrants to Aversley and Monks Woods in the centralised landscape (Figure 5.23d). With the adjusted landscape, the same flow was redirected along the lower line of additional patches (along the arrow in Figure 5.23d), reducing the external immigration into these two woods to zero, as shown in Figure 5.14b. As the population in Monks and Aversley Woods at this point is maintained by internal dispersal, their population does not increase for this and higher perceptual ranges (Aversley Wood), or only increases slightly (Monks Wood), as shown in Figure 5.13b. The redirected flow joins that reaching Holland and Wennington woods, boosting their population size in comparison with that in the centralised landscape (Figure 5.13). At 5 km perceptual range (Figure 5.23e), Aversley and Monks Woods still have no immigrants in the adjusted landscape (Figure 5.14b). The population in Holland and Wennington Woods is boosted still further in both landscapes (Figure 5.14), as the lower flow present at the 2 km range joins that reaching these woods (along the arrow in Figure 5.23e).



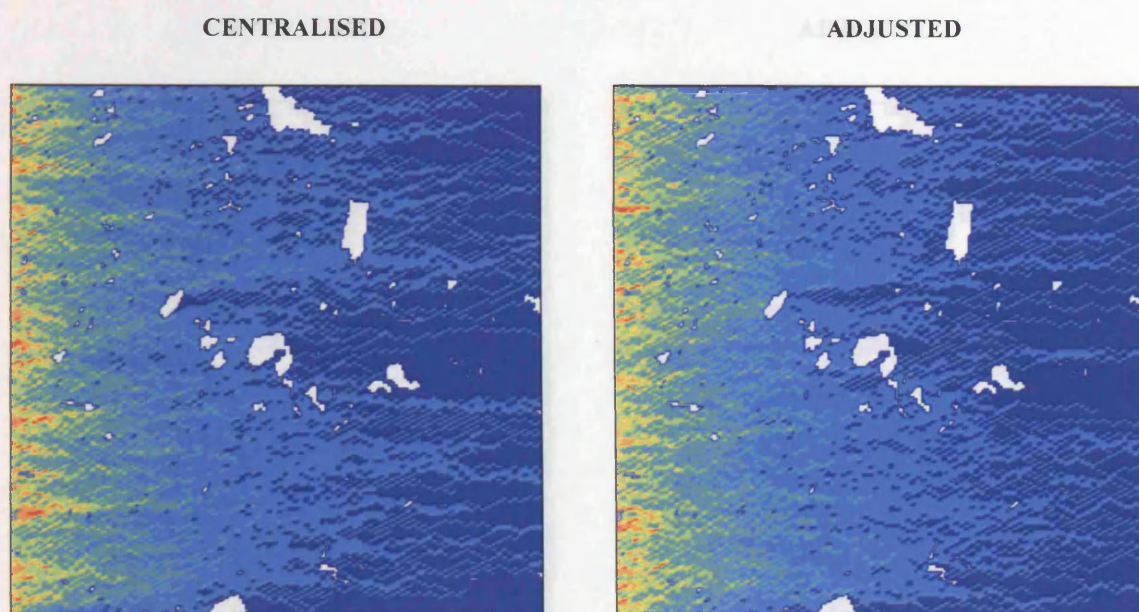


Figure 5.23a. 0km

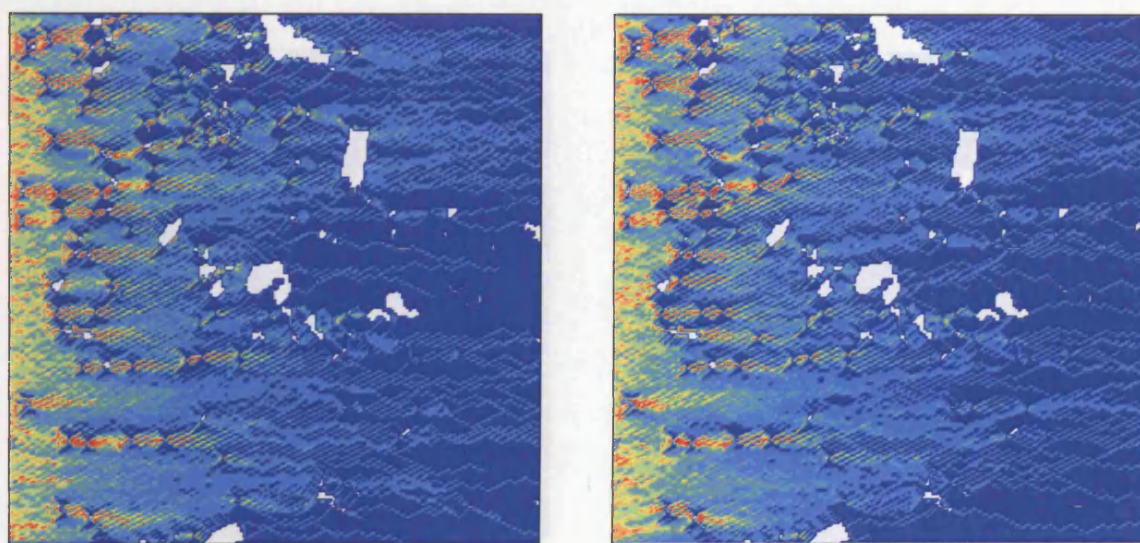


Figure 5.23b. 0.5km

**Figure 5.23:** The dispersal flow diagrams for the centralised (left hand column) and adjusted (right hand column) landscapes, showing the accumulated dispersal paths for a total of 3,000 immigrating nuthatches for 0 (Figure 5.23a) and 0.5 (Figure 5.23b) km habitat perceptual ranges with a 90° field-of-view. The key in Figure 5.22 shows the number of dispersers.



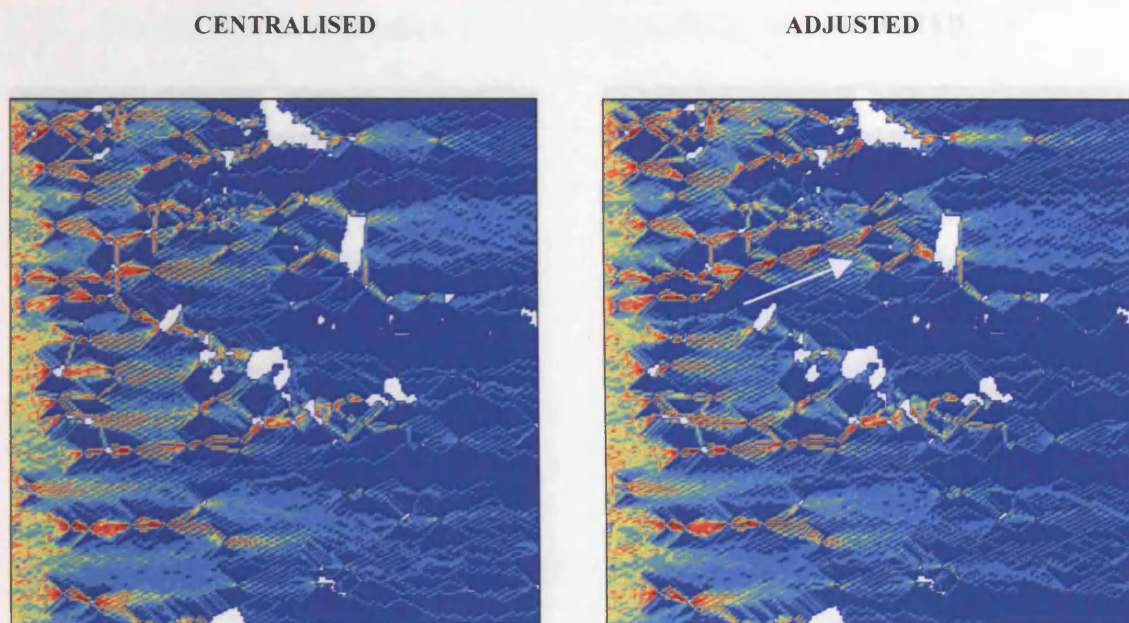


Figure 5.23c. 1km

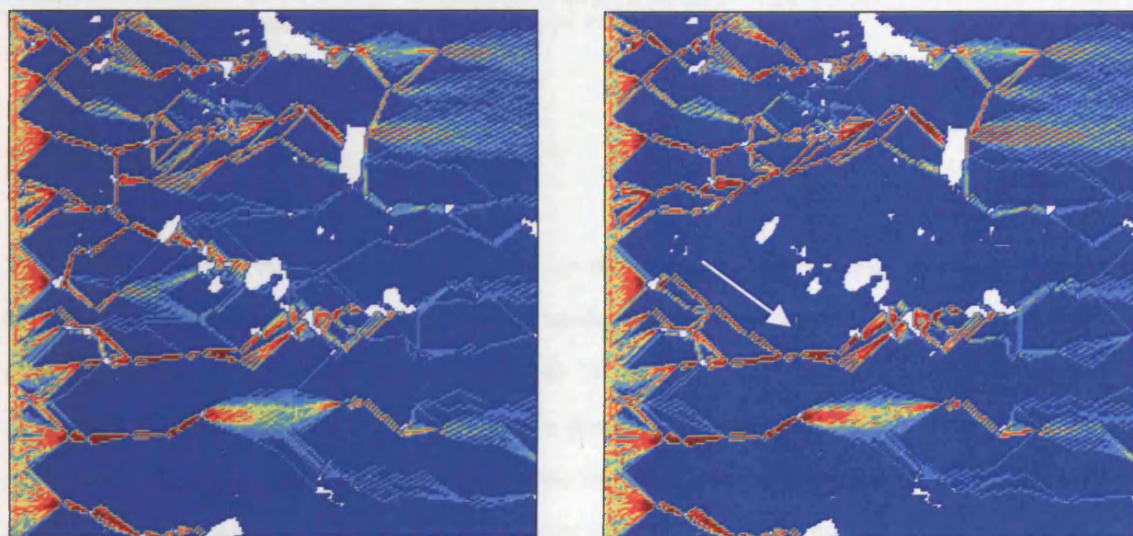


Figure 5.23d. 2km

**Figure 5.23 (cont.):** The dispersal flow diagrams for the centralised (left hand column) and adjusted (right hand column) landscapes, showing the accumulated dispersal paths for a total of 3,000 immigrating nuthatches for 1 (Figure 5.23c) and 2 (Figure 5.23d) km habitat perceptual ranges with a 90° field-of-view. The arrows are explained in the text. The key in Figure 5.22 shows the number of dispersers.



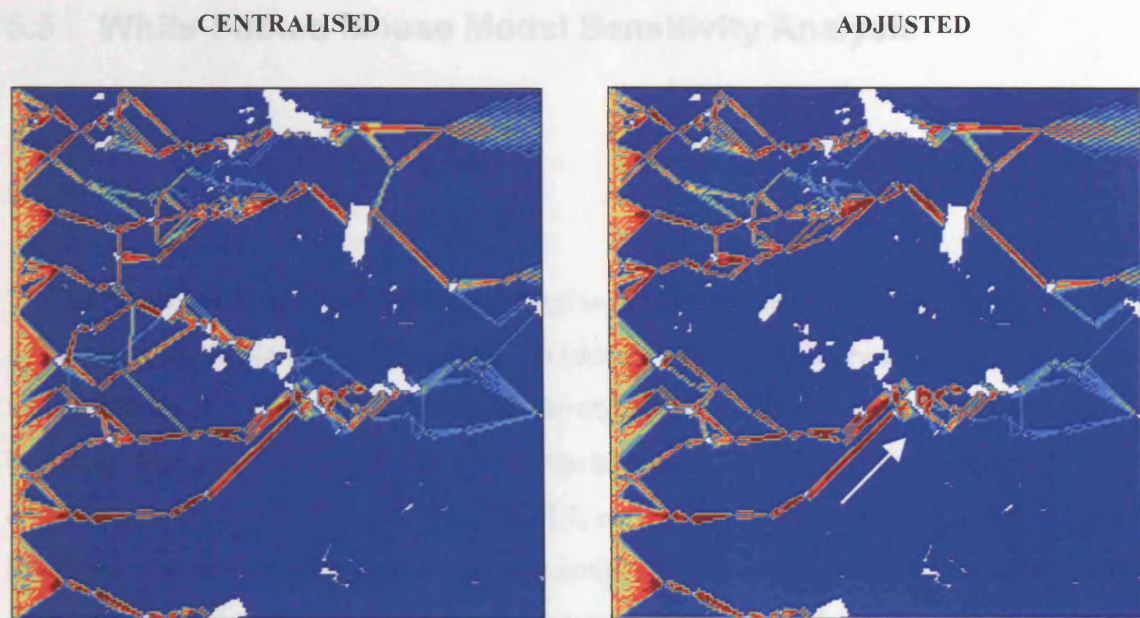


Figure 5.23e. 5km

**Figure 5.23 (cont.):** The dispersal flow diagrams for the centralised (left hand column) and adjusted (right hand column) landscapes, showing the accumulated dispersal paths for a total of 3,000 immigrating nuthatches for 5 km (Figure 5.23e) habitat perceptual ranges with a 90° field-of-view. The arrow is explained in the text. The key in Figure 5.22 shows the number of dispersers.

#### 5.4.4.2 Dispersal Flow Diagram Summary

The results given in this section were based on the nuthatch, a territorial, resident woodland bird, which has to disperse in a fragmented landscape in order to seek suitable territory (Matthysen *et al.* 1995; Matthysen and Currie 1996). The specific-case perceptual range tests showed that flow patterns became more directed as perceptual range increased (Figure 5.23). It therefore seems reasonable to assume that dispersal flow patterns are both species and landscape dependent. These findings point towards the usefulness of dispersal flow diagrams for ‘seeing’ what is happening with dispersal in a landscape. Such diagrams would be difficult to construct with spatially implicit models, such as those by Lamberson *et al.* (1994), Ruxton *et al.* (1997) and Carter and Finn (1999). The diagrams do not, however, provide a complete explanation and are seen as a useful feature, to be used in conjunction with the more traditional graphed and numerical outputs.

## 5.5 White-Footed Mouse Model Sensitivity Analysis

### 5.5.1 Introduction

The white-footed mouse test sequence started with an analysis of the response of the model to variations in the demographic parameters (*demographic sensitivity analysis*), followed by an analysis of the parameters affecting the ability of the mouse to locate and settle in breeding habitat (*landscape related sensitivity analysis*). The parameters were set to the default values given in Tables 4.5, 4.6 and 4.7, except for the only stochastic parameter, litter size, which was set to four. As per the nuthatch tests, each tested parameter was varied in turn (Section 5.2.2). Table 5.4 lists the tested parameters and their range of variation. The model response was measured by recording the mean landscape population over 1,000 breeding cycles, for each test. All tests used the ‘all good’ habitat and quality landscapes, which consisted of four habitat patches, linked by good quality corridors (Figure 4.15b), with no immigration.

Parameter	Tested range
Breeding probability for Low, Moderate and High rates	0 - 1
Number of young	0 - 10
Nestling survival probability	0 - 1
Juvenile survival probability	0 - 1
Sub-adult survival probability	0 - 1
Adult survival probability	0 - 1
Winter survival probability	0 - 1
Dispersal mortality probability for Q1 (Habitat), Q2 (Corridor), Q3 (Unused) and Q4 (Matrix) (per 10m step)	0 - 0.01
Perceptual range (m)	0 - 200 (0 - 20 cells)
Territory size (ha)	0 - 0.2 (0 - 20 cells)

**Table 5.4:** The tested white-footed mouse parameters and their range of variation. In some cases, such as winter survival, the range spanned the maximum possible, in other cases, such as number of young and perceptual range, the range was limited to show a relevant response spanning the default values (Tables 4.5, 4.6 and 4.7). The Q1 - Q4 labels refer to modelled habitat quality (Section 4.4.5.2).

## 5.5.2 The Analyses

### 5.5.2.1 Demographic Sensitivity Analyses

The demographic test sequence started by varying the probability of breeding success and the number of young, followed by the survival probability for the nestling, juvenile, sub-adult and adult life-stages, and the probability of winter survival. These tests were designed to investigate the model's response to variations in modelled demographic parameters, without the influence of any changes in landscape related factors.

### 5.5.2.2 Landscape Related Sensitivity Analyses

The dispersal mortality rates, perceptual range and territory size tests were designed to measure the model's response to changes in landscape quality. These factors were those thought most likely to vary between different landscapes, as opposed to the demographic characteristics of the mouse, which appear to vary little across its range (Timm and Howard 1994).

In the model, dispersal mortality is quality related, with three different rates used for the habitat, corridor and matrix quality levels (Table 4.7). This left one of the quality levels unused. Dispersal mortality in all four levels was varied. If the model coding is valid, then varying the unused level should not affect the results.

The perceptual range variation was chosen to span the 30 to 120 m perceptual range of the white-footed mouse (Section 4.4.2).

Ignoring the 0 cell size, the territory size test varied the maximum density from 200 individuals  $\text{ha}^{-1}$  (1 cell territories) down to 10 individuals  $\text{ha}^{-1}$  (20 cell territories) (Section 4.4.3), spanning the maximum population density of 37 individuals  $\text{ha}^{-1}$  (Section 4.4.2). If the model coding is valid, then the 0 cell territory size should result a population size of zero.

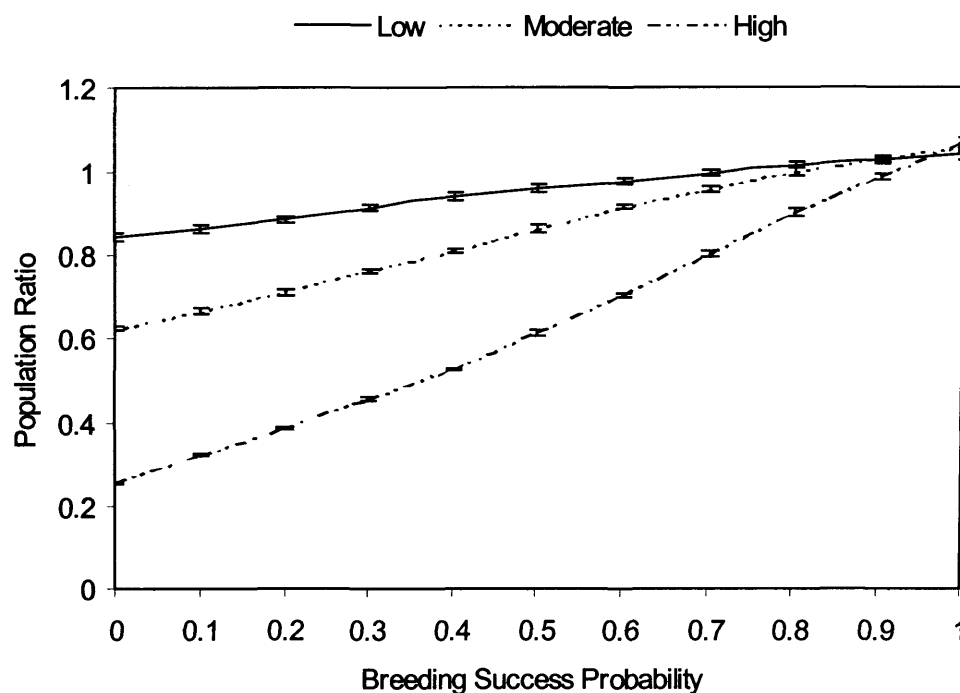


### 5.5.3 Results

As the sensitive analyses used an artificial landscape, relative results were thought more important than absolute values. The results are therefore presented as a set of mean landscape population sizes, relative to the mean population size generated by the default values, (1 on the y-axis represents the default value mean landscape population).

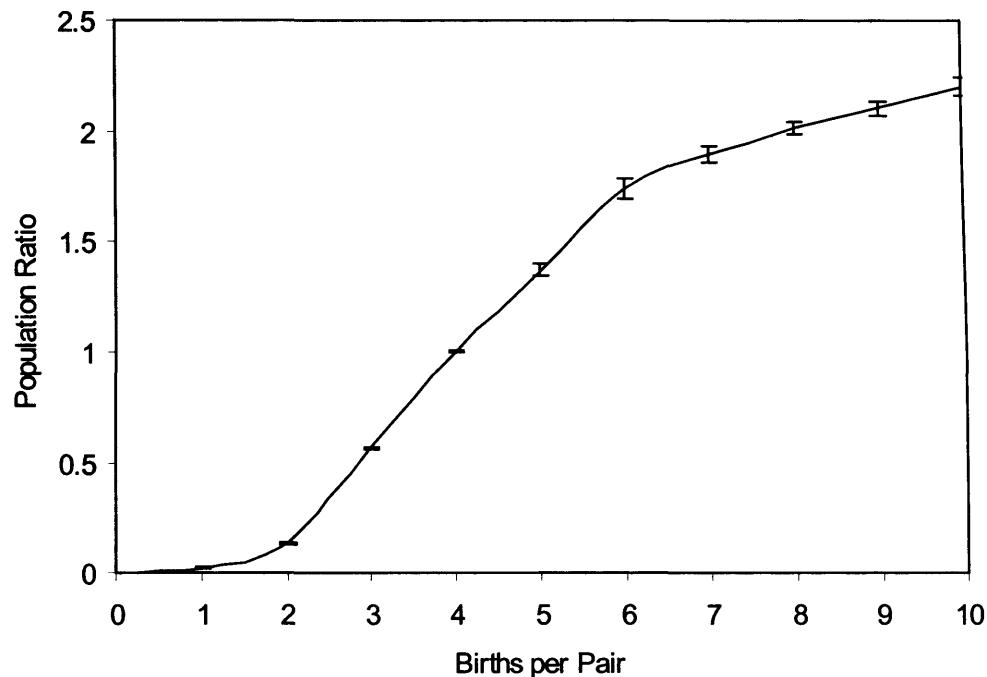
#### 5.5.3.1 Demographic Sensitivity Analyses

The responses to variations in the low, moderate and high breeding success rates are given in Figure 5.24. Due to its annual (once per 33 weeks) application (Section 4.4.2), the low rate would be expected to have the least effect on population size. Breeding success is bimodal (Section 4.4.2), and the high rate was the first of the applied breeding probabilities, coming in week 1, after the application of the winter survival probability (Tables 4.5 and 4.6). For a given probability, the high rate would therefore be expected to have the greatest effect on population size. These expectations were borne out by the response graph (Figure 5.24).



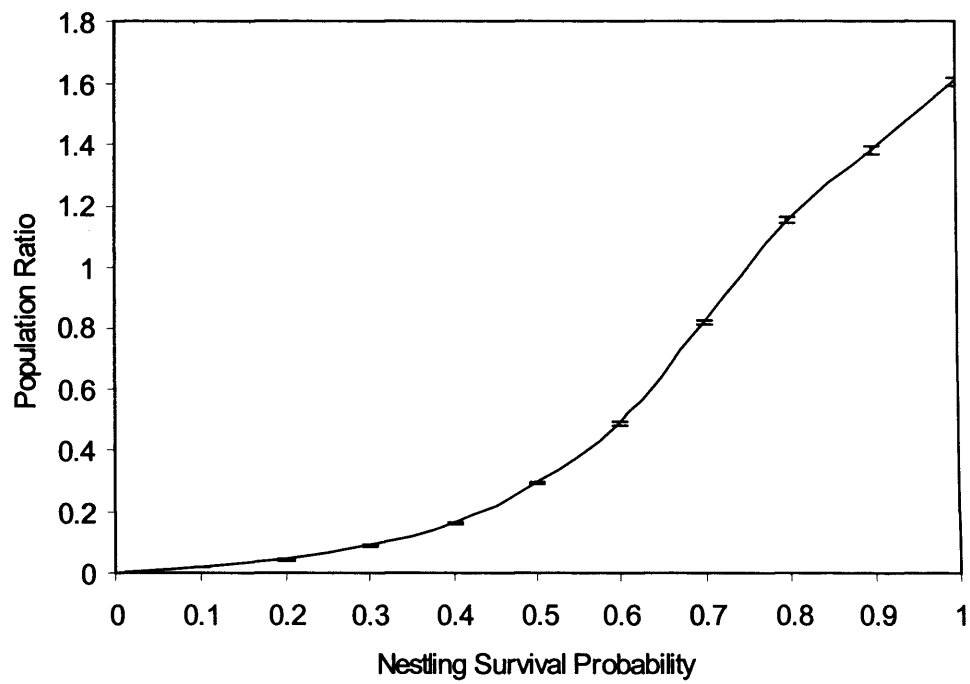
**Figure 5.24:** Response to variations in probability of breeding success. The error bars give 95% confidence intervals.

The response to variations in number of young is given in Figure 5.25. Although the actual number depends on the bimodal breeding success rates (Section 4.4.2), increasing the number of young should increase population size. This expectation was borne out by the response graph (Figure 5.25).

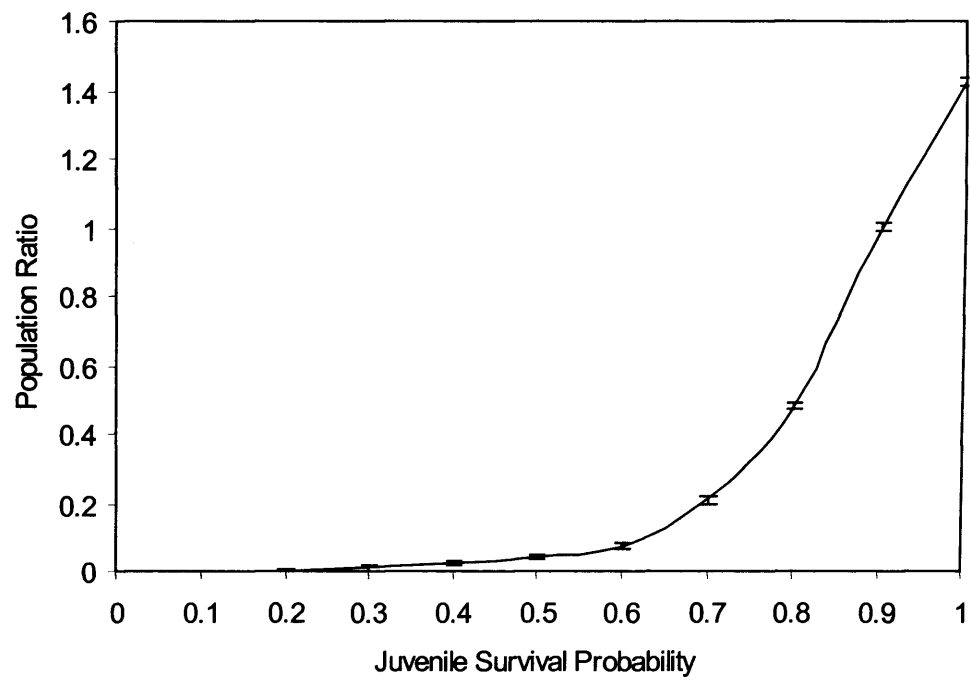


**Figure 5.25:** Response to variations in number of young. The error bars give 95% confidence intervals.

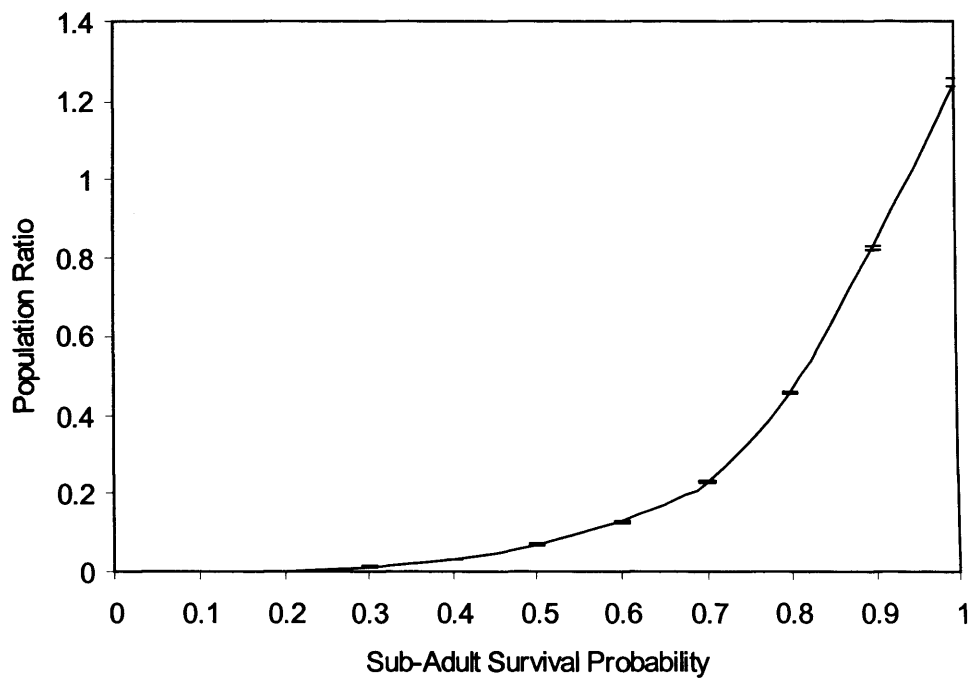
The landscape population would be expected to rise in line with an increase in any of the nestling, juvenile, sub-adult and adult life-stage and winter survival probabilities. For a given variation, the weekly applied juvenile, sub-adult and adult survival rates would be expected to have a greater effect on population size than the nestling survival rate, which is only applied once every eight weeks (Figure 4.13; Table 4.6). As only the adults can breed, the adult survival rate should be the most sensitive of the survival rates. It is to be expected that population size would rise in line with an increase in the winter survival rate. These expectations were borne out by the response graphs (Figures 5.26 through 5.30).



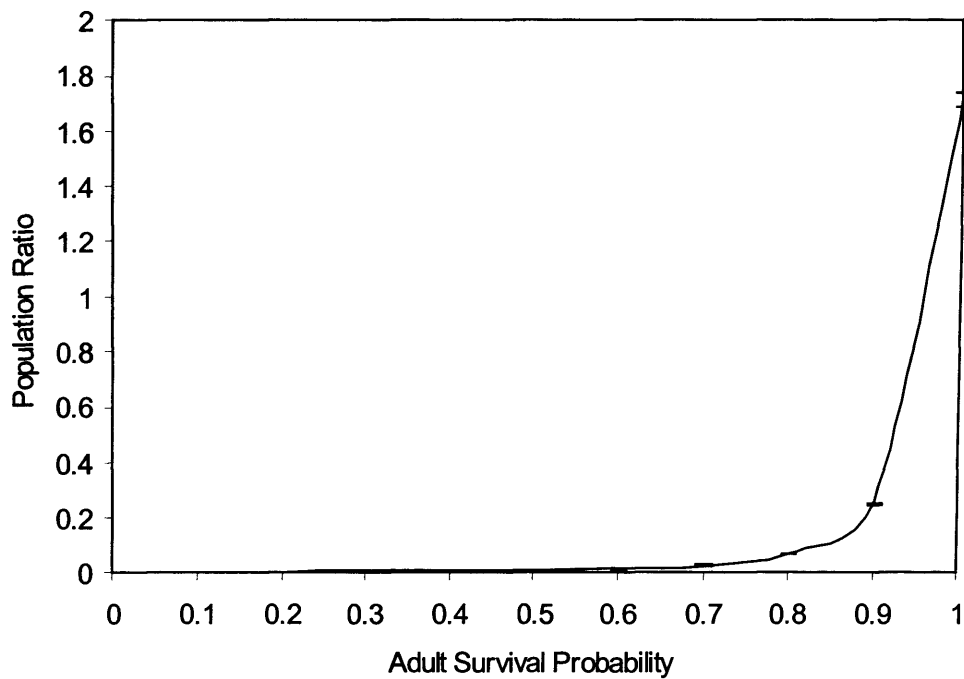
**Figure 5.26:** Response to variations in nestling survival probability. The error bars give 95% confidence intervals.



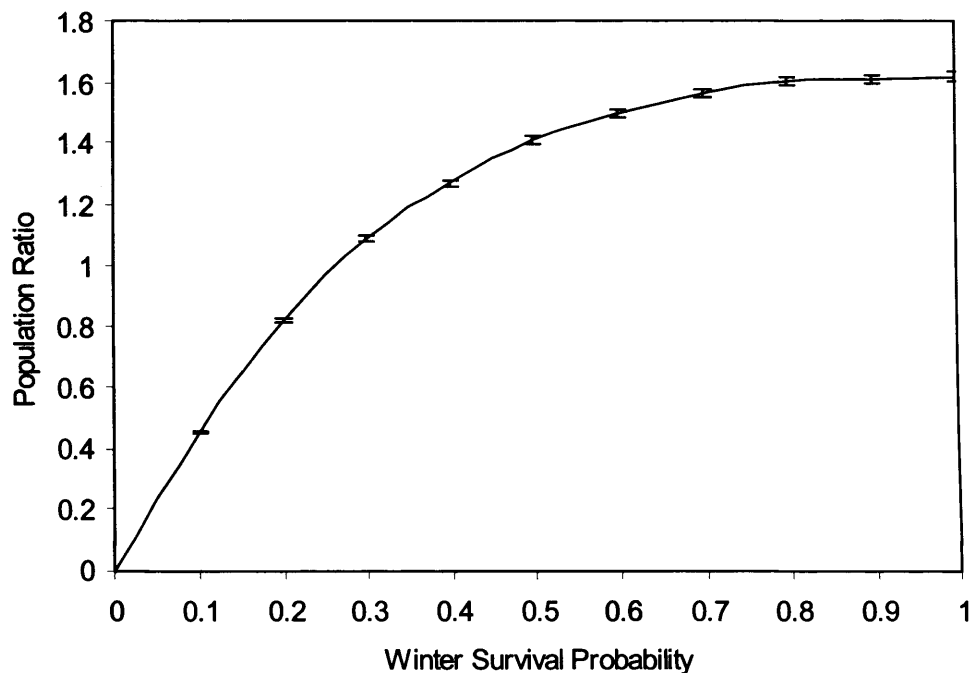
**Figure 5.27:** Response to variations in juvenile survival probability. The error bars give 95% confidence intervals.



**Figure 5.28:** Response to variations in sub-adult survival probability. The error bars give 95% confidence intervals.



**Figure 5.29:** Response to variations in adult survival probability. The error bars give 95% confidence intervals.

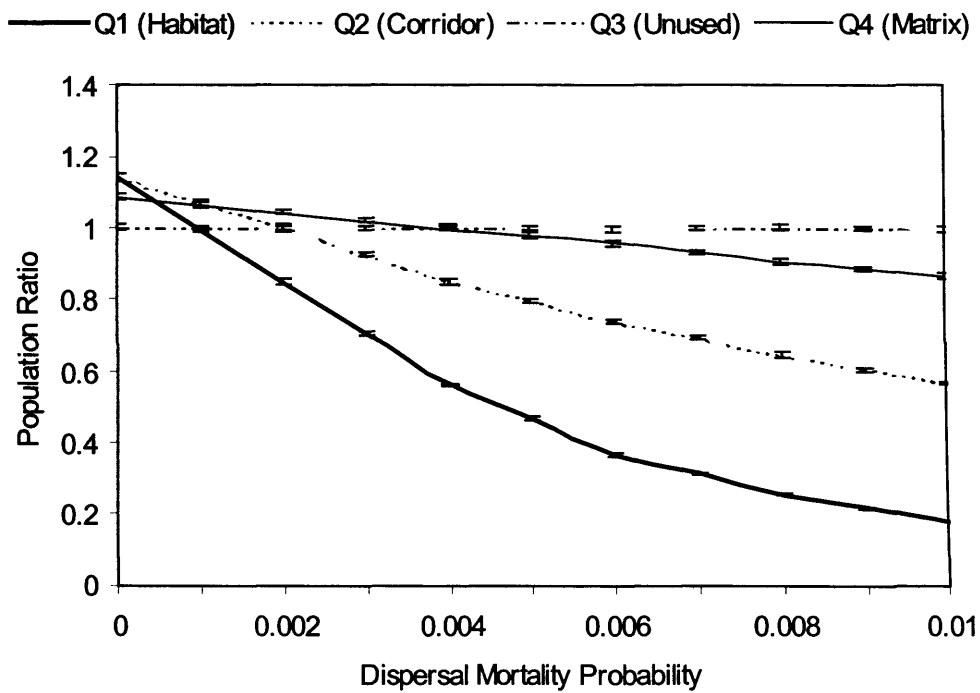


**Figure 5.30:** Response to variations in winter survival probability. The error bars give 95% confidence intervals.

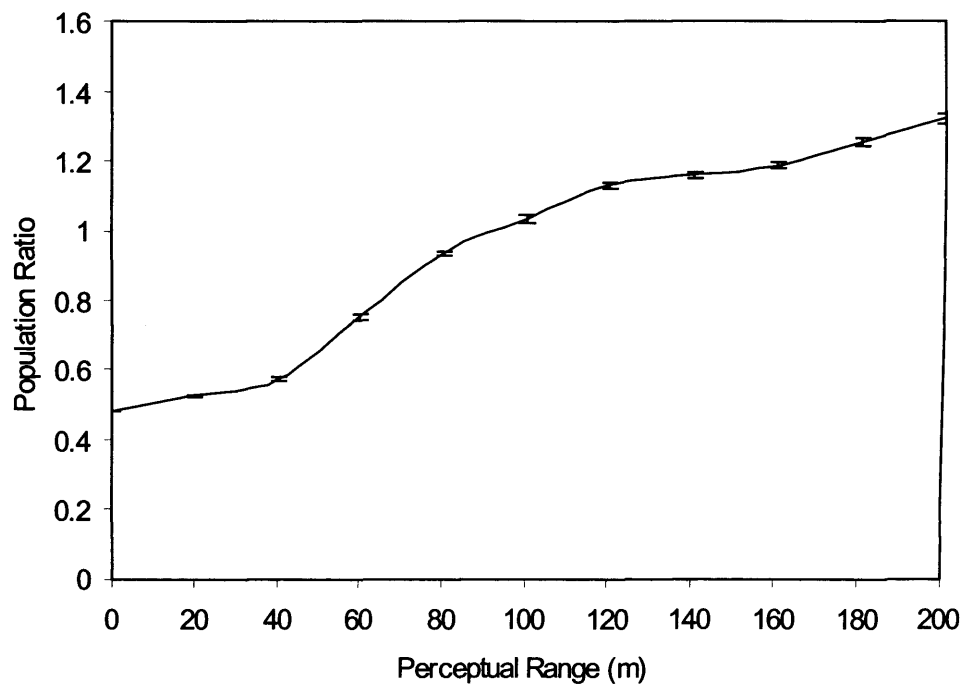
#### 5.5.3.2 Landscape Related Sensitivity Analyses

In the test landscape, perceptual range was used to locate the best quality habitat, reducing time spent in the matrix. Movement would be expected to be greater within the habitat patches and inter-connecting corridors. It is to be expected, therefore, that varying the movement resistance in the matrix, in the form of per-step dispersal mortality, would have a lesser effect on population size than varying that in the corridors or habitat patches. The dispersal mortality results (Figure 5.31) revealed that this was the case, with variations in habitat movement resistance having the greatest effect.

As with the dispersal mortality tests, the perceptual range tests measured the response of the model to different levels of inter-patch movement ‘resistance’. It is to be expected that increasing movement ‘resistance’ in this manner would increase the time spent outside the habitat patches, increasing inter-patch dispersal mortality and thereby decreasing population size. This expectation was born out by the response graph (Figure 5.32). The perceptual range findings are also in agreement with the published literature on this subject (Section 2.4.7).

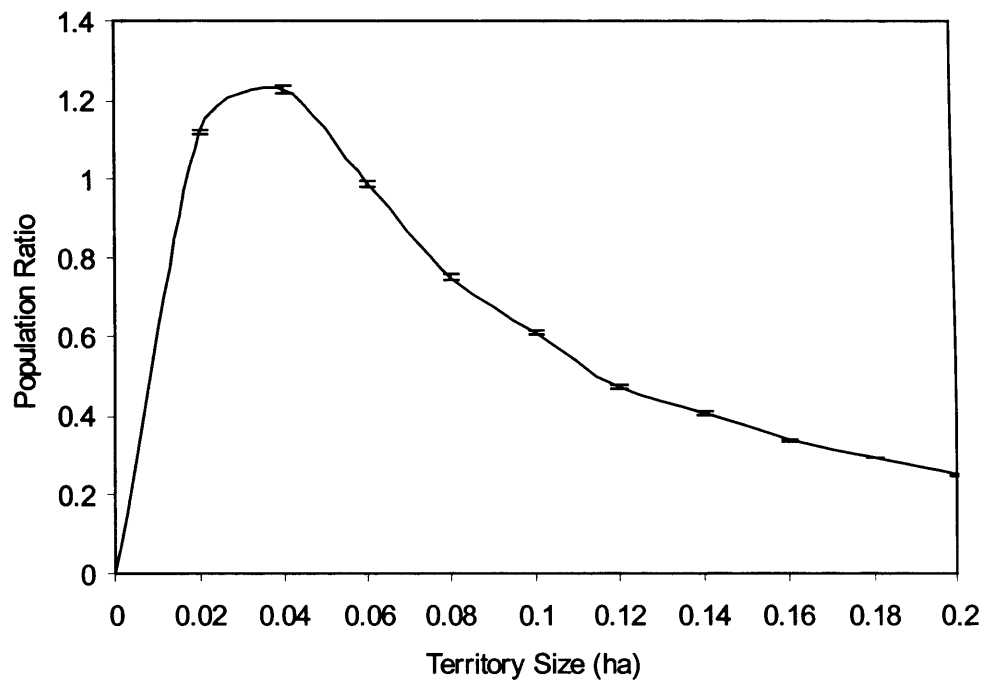


**Figure 5.31:** Response to variations in dispersal mortality. The error bars give 95% confidence intervals.



**Figure 5.32:** Response to variations in perceptual range. The error bars give 95% confidence intervals.

The territory size tests measured the response of the model to changes in the maximum areal density of white-footed mice, with population size dropping with increase in territory size (Figure 5.33). The drop in population size at the smaller territory size is similar to that obtained from the nuthatch model (Figure 5.4) and is discussed further in Section 5.4.2.



**Figure 5.33:** Response to variations in territory size. The error bars give 95% confidence intervals.

#### **5.5.4 White-Footed Mouse Model Sensitivity Analysis Discussion**

The white-footed mouse sensitivity analyses demonstrated an even response to variations in the modelled inputs, with no abrupt changes (i.e. not a step function). The responses were as expected in all cases, such as the population size being more sensitive to changes in high breeding success probability than the lower rate (Figure 5.24) and being more sensitive to changes in habitat than matrix dispersal mortality (Figure 5.31). This suggests that the modelling algorithms are valid.

Lower and upper thresholds were evident in some cases, such as the number of young (Figure 5.25) and winter survival probability (Figure 5.30). The lower thresholds signify the points at which mortality begins to be overcome and the upper thresholds signify points at which the landscape starts to become saturated. The perceptual range response also had upper and lower thresholds (Figure 5.32), which although not so pronounced as that for the nuthatch (Figure 5.13), do point towards an optimal perceptual range for a particular landscape.



## **5.6 Black Hairstreak Model Sensitivity Analysis**

### **5.6.1 Introduction**

To investigate the sensitivity of the black hairstreak model, three tests on the habitat management model and one on the species model were devised. The mean habitat patch population size over 10,000 yearly cycles per run was recorded for each scenario. To simulate the effects of abandoning the management schemes, habitat replacement arbitrarily ceased at the end of year 96.

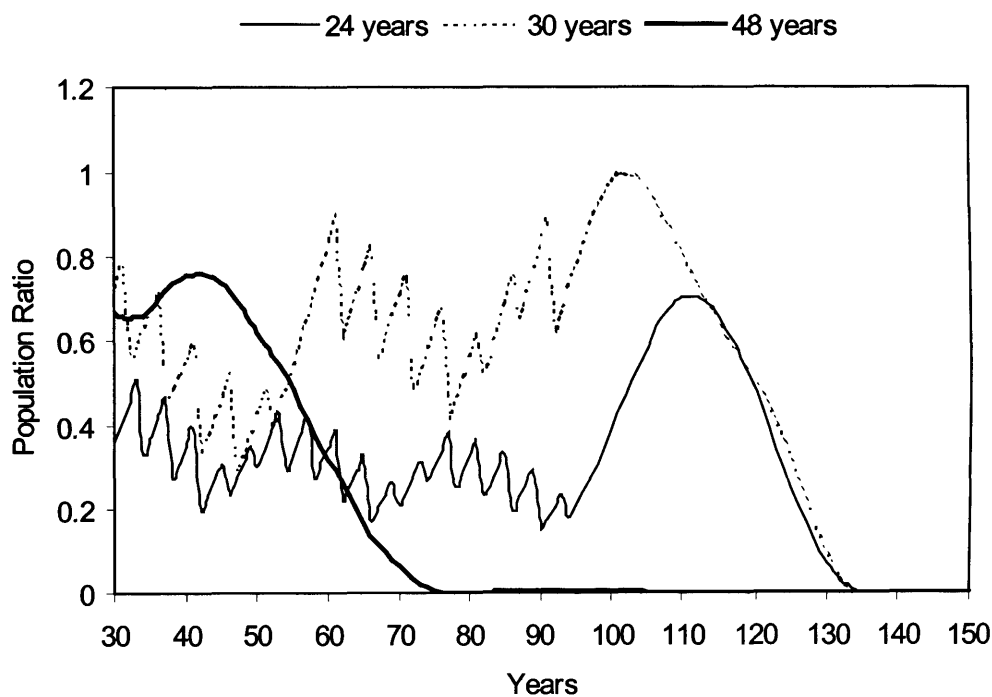
The first habitat management test modelled replacement cycles of 24, 30 and 48 years, using the basic rectangular habitat strip (Figure 4.20a). The second test modelled the effect of varying the basic rectangular strip width for 24 and 48-year replacement cycles. Three strip widths were used: half, unchanged and twice the basic rectangular strip width. The third habitat management test varied the age at which the blackthorn started to become moribund, from 20 to 40 years. The dynamic habitat model is an essential part of the black hairstreak model; the first two tests were designed to explore the response of the model to various habitat management schemes and the last test was designed to explore the response of the model to variations in habitat characteristics.

The species model test varied the probability of dispersal from 0.05 to 0.25. This input varies the probability that individuals leave their immediate location and move to other parts of the habitat patch. If the black hairstreak were being modelled at the landscape scale, then this input would govern the species' propensity to leave the natal patch. The parameters given in Table 4.8 were used for all the sensitivity analyses, except for the variation of the dispersal probability input.

### 5.6.2 Results

As with the white-footed mouse tests (Section 5.5.2), the black hairstreak sensitivity analyses also used an artificial landscape and relative results were thought more important than absolute numbers. The results are therefore presented as a set of mean landscape population sizes, relative to the peak mean population size generated by each set of tests, (1 on the y-axes represents the peak mean landscape population).

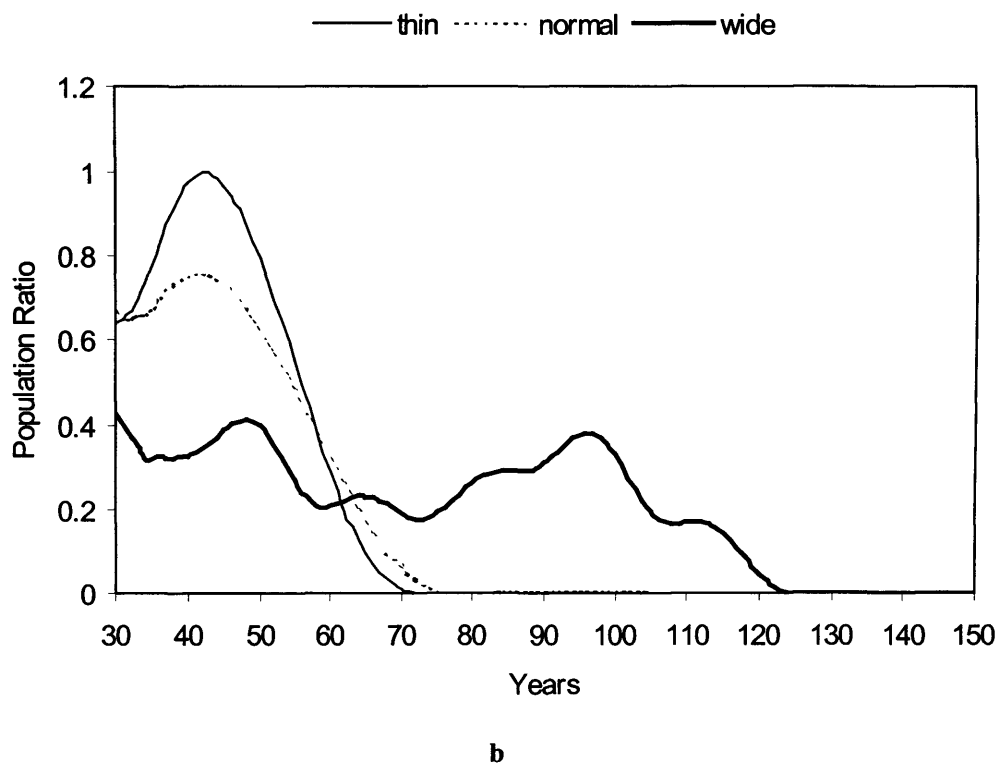
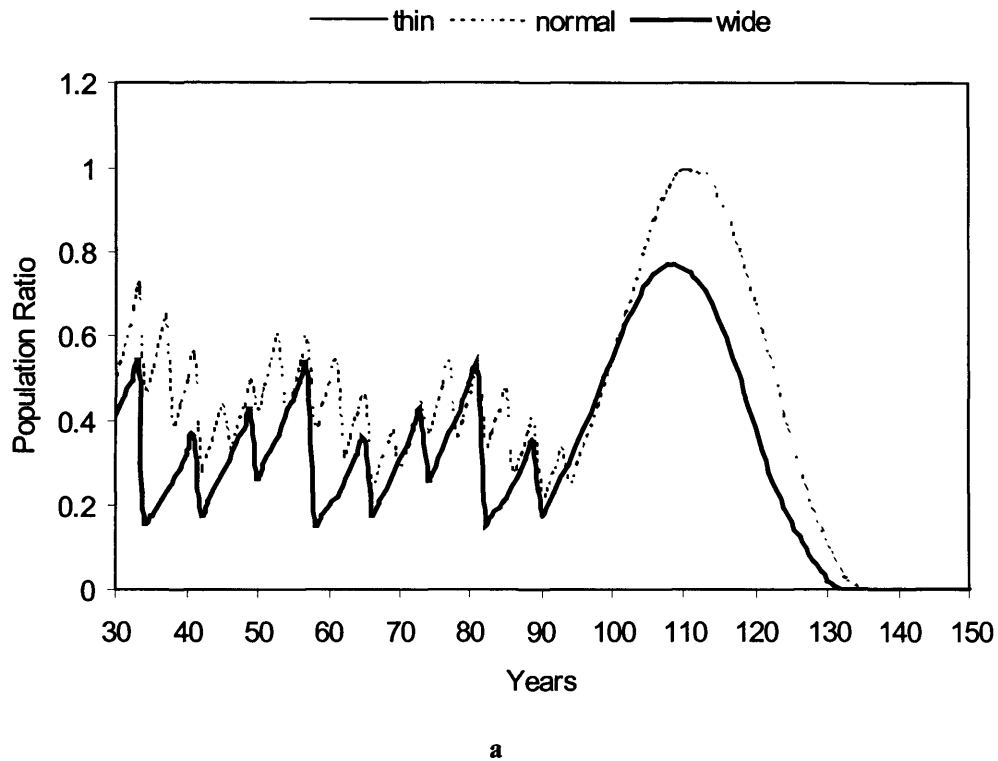
The results of varying the basic habitat strip replacement cycle revealed that increasing the cycle from 24 to 30 years increased the population size, but increasing the cycle still further to 48 years caused the population to become essentially extinct after approximately 75 years (Figure 5.34).



**Figure 5.34:** The relative population sizes resulting from strip replacement cycles of 24, 30 and 48 years, using the basic rectangular strip (Figure 4.20a). The settling down period (years 1 to 29) is not shown for clarity.

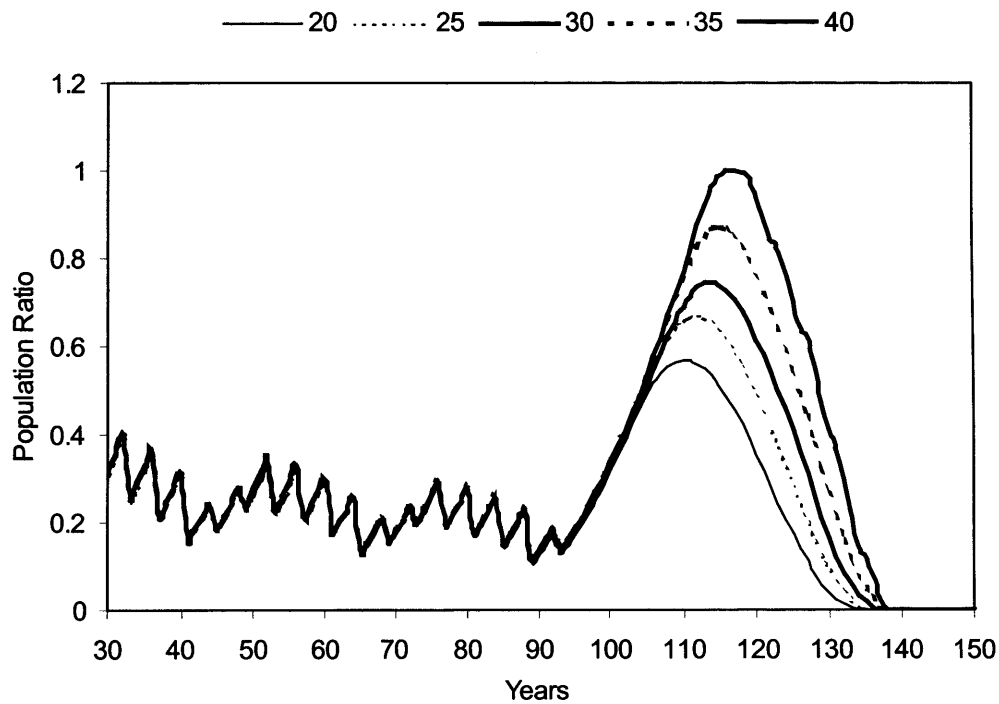
Using various width habitat strips over a 24-year replacement cycle produced little change in population size for the normal (basic strip width) and wide (twice basic strip width) options (Figure 5.35a). The population was unable to exist when using the thin option (half the basic strip width).

Using the same strips over a 48-year replacement cycle (Figure 5.35b) caused the population to become extinct between 70 to 80 years for both the thin and normal options. The wide option produced a gradual decline of the population until the management scheme ceased at year 96.



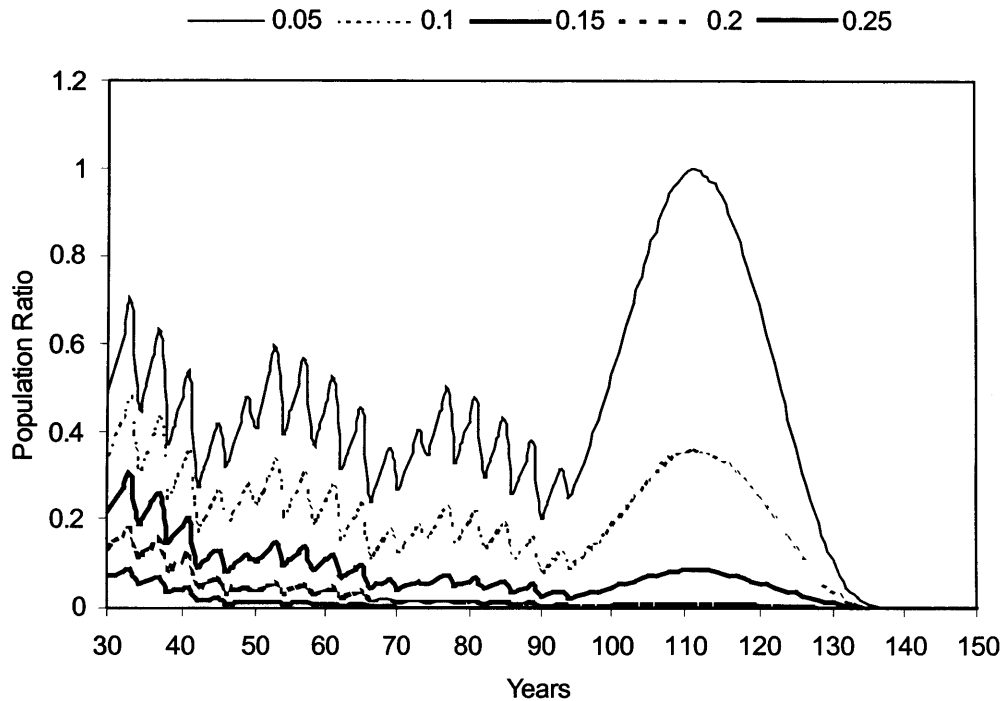
**Figure 5.35:** The relative population sizes resulting from strip widths of half (thin), unchanged (normal) and twice (wide) the basic habitat strip width, for a 24 year (Figure 5.35a) and a 48 year (Figure 5.35b) replacement cycle. The absence of a trace for the thin option in Figure 5.35a is explained in the text. The settling down period (years 1 to 29) is not shown for clarity.

Varying the age at which the blackthorn started to become moribund from 20 to 40 years produced little variation in population size until the habitat management scheme ceased (at year 96). After this point, increasing the die-off age increased the peak population (Figure 5.36).



**Figure 5.36:** The relative population sizes resulting from varying the age at which the blackthorn started to die off, using a 24-year replacement cycle. The settling down period (years 1 to 29) is not shown for clarity.

Increasing the dispersal probability decreased the population size (Figure 5.37). This is perhaps not intuitive, but was ascribed to two causes. A global effect increasing the number of individuals leaving the habitat patch and a local effect causing individuals to traverse unsuitable (too young for settlement (Section 4.5.3.2)) replaced strips, thereby increasing dispersal mortality.



**Figure 5.37:** The relative population sizes resulting from varying the dispersal probability from 0.05 to 0.25, using a 24-year replacement cycle. The settling down period (years 1 to 29) is not shown for clarity.

### 5.6.3 Black Hairstreak Model Sensitivity Analysis Discussion

The sensitivity analysis results showed that the model responded ‘evenly’ to variations in the tested inputs, with no evidence of abrupt changes (i.e. not a step function) (Figures 5.34 through 5.37). The habitat management tests showed that optimum replacement cycles and strip widths existed and that the model was cable of identifying these (Figures 5.34 and 5.35). Adjusting the blackthorn die-off age was shown to affect the peak population following cessation of the management plan, demonstrating the sensitivity of the model to this input and suggesting the need to accurately model habitat dynamics (Figure 5.36). The

sensitivity of the model to dispersal probability revealed the requirement for accurate modelling of species demographics (Figure 5.37). The reason behind the ‘humps’ in population size after the cessation of the management schemes is described in Section 4.5.4.4. Although not reported here, the sensitivity of the model to the other inputs gave similar ‘even’ responses, but the tests described in this chapter were thought sufficient to demonstrate the overall performance of the black hairstreak model.

## 5.7 Chapter Summary

This chapter describes the sensitivity analyses of the nuthatch, white-footed mouse and black hairstreak models and presents the results. All three models were shown to respond in a predictable manner to variations in their inputs and any thresholds were explained. This suggests that the model coding is valid. Where appropriate, the models were shown to be sensitive to perceptual range, field-of-view and immigration direction and rate, indicating that these inputs should be included as elements of individual-based SEPMs.

The ranking of the modelled nuthatch demographic parameters was shown to match that for the real species, as reported in the literature (Section 5.4.1). The usefulness of dispersal flow diagrams in providing a visual explanation of numerical results (both predicted and observed) was also demonstrated (Section 5.4.3.1). The responses of the nuthatch and white-footed mouse models suggested that landscape structure affects population size (Sections 5.3, 5.4 and 5.5). The black hairstreak model was shown to be sensitive to habitat dynamics, revealing the requirement to incorporate a realistic model of habitat dynamics when modelling habitat management schemes (Section 5.6.2).

The next and final chapter presents the thesis summary and conclusions.

## 6. SUMMARY AND CONCLUSIONS

### 6.1 Introduction

The overall aim of this thesis was to develop, test and apply an individual-based SEPM to the analysis of population viability in fragmented landscapes (Section 1.3). In meeting this aim, the objectives listed in Section 1.3 all had to be met. A review of the relevant areas of population ecology modelling was first undertaken (Chapter 2), meeting the first objective. The results of the review determined the characteristics of the model which would be required to meet the overall aim of the thesis (Section 2.7). These features were not found in any single published model (Section 2.6), so a new model was designed and constructed. The model, called PatchMapper, was coded in Java to allow for as wide a user-base as possible (Section 3.2; Appendix F). A real-time (computer) visual display of the simulation results was provided, meeting part of the second objective. Importing digitised landscapes from a variety of sources, such as a GIS, enables specific study areas to be modelled (Section 3.6.3). An internal neutral landscape generator enables modelling for general results (Section 3.6.2). The ability to model digitised real and neutral landscapes met objective 2a. Three species with differing ecological requirements were modelled: the nuthatch (*Sitta europaea*), the white-footed mouse (*Peromyscus leucopus*) and the black hairstreak (*Satyrrium pruni*) (Section 3.7.3; Chapter 4). The ability to model representatives of different taxonomic groups met objective 2b. Objectives 2c and d were met by providing two dynamic landscape modelling options (Section 3.6.5) and the ability to model habitat quality (Section 3.6.4). To meet the third objective, the nuthatch and white-footed mouse models were validated against published studies and, for the nuthatch, against observed numbers in a landscape of regional interest (Chapter 4). The results of this thesis have general importance for the field of landscape ecology, in particular assisting those organisations involved in conservation and land-use planning in studying the effects of habitat fragmentation on population viability. This chapter summarises the main results and findings of the thesis and discusses some potential applications and possible directions for future research, meeting the fourth objective.



## 6.2 Summary and Discussions of the Main Findings

### 6.2.1 General Findings

The flow diagrams presented in Section 5.4.4.1 demonstrated that the distribution of a population within a landscape (as modelled by PatchMapper) is a function of both behavioural characteristics and landscape structure. The linking of habitat patches and the ability of a particular species to reach them has been defined as the ‘functional connectivity’ of the landscape (Tischendorf and Fahrig 2000b). In the case of PatchMapper, the simulation of the movement of individuals in a spatially explicit landscape incorporates immigration direction, rate, perceptual range (including field-of-view) and distance-related dispersal mortality, all of which play a part in modelling functional connectivity (Sections 4.2, 4.3, 5.2 and 5.3; Tischendorf and Fahrig 2000b). In a poorly wooded landscape, nuthatch populations may not be viable without external immigration, thus the size of any extant nuthatch population in a particular patch is a function of perceptual range (including field-of-view) and immigration rate (Section 5.3; Appendix B.2). It is also a function of immigration direction and spatial structure (Figure 5.11; Alderman *et al.* 2004, reproduced in Appendix B.1). It is recommended that these inputs, which should be both separate and controllable, are included in individual-based SEPMs. The values chosen for these inputs must be verifiable, both for the species being modelled and for the landscape in question and should result in realistic effects.

The model of the multivoltine white-footed mouse had to be simplified by modelling home ranges as territories and by synchronising lifecycle stages (Sections 4.4.2 and 4.4.3), but even with this level of simplification, the model code was complex. Nevertheless, useable results were achieved which demonstrated that the overall size of a metapopulation was affected by the quality of the inter-patch connecting corridors (Section 4.4.5.4). These results agreed with those of two published studies that modelled the white-footed mouse, using the same habitat configuration, but employing individual-based spatially implicit analytical techniques (Section 4.4.5.5) and reinforced the ability of PatchMapper to model functional connectivity.

Belonging to a different taxon than the nuthatch and white-footed mouse, the black hairstreak model is population-based, with dispersing females (Section 4.5). The model was tested with several habitat management plans (Section 4.5.3), which used the dynamic landscape capability of PatchMapper and showed that the most effective habitat management plan was closest to the recommended method of providing irregular indentations into the blackthorn (Sections 3.6.5.2 and 4.5.4.4). A sensitivity analysis was also undertaken, with the results demonstrating that the model performed as expected. The sensitivity of the black hairstreak model to the various habitat management schemes, dispersal mortality and blackthorn ageing, demonstrated the model's reliance on habitat modelling (Section 5.6). These results suggested that individual-based SEPMs should model habitat dynamics, particularly if habitat management schemes and/or long-term predictions are of concern.

As discussed in Section 2.3.2, fractal-based algorithms are commonly employed to generate neutral landscapes. As stated in Section 3.6.2, the MRC-based algorithm was employed to investigate its suitability as an alternative method of neutral landscape generation. The results of the neutral landscape-based tests presented in Chapters 4 and 5 demonstrated the applicability of the MRC algorithm as a practical method of neutral landscape generation.

### **6.2.2 Specific Findings from the Nuthatch Model**

The model of the univoltine, territorial nuthatch gave a good match to observed population sizes in specific woods within a landscape consisting of fragmented habitat patches and gave better predictions than an analytical model applied to the same area (Section 4.3.4.1; Appendix B1). The sensitivity analyses demonstrated expected responses to the modelled inputs (Section 5.3), suggesting that the coding was valid. This observation was reinforced by the ranked importance of the demographic parameters matching that observed for the real species (Section 5.4.1).

The comparison analytical model was originally developed for use in the Netherlands (Section 4.3.1), but despite being modified, when it was applied to a different, although superficially similar, landscape it gave misleading results (Section 4.3.4.1). Such models take the effects of landscape structure, immigration and habitat perceptual range into account by default and therefore may be prone to error if any of these parameters change, as they are likely to do when landscape configuration changes. These models may also fail to track changes in landscape structure, and other characteristics, and thus may have a limited 'shelf-life'. Caution should therefore be applied when using models outside their target landscapes (Section 2.5.1).

The importance of immigration into the study area was established (Section 4.3.4.2). The nuthatch model was tested with three habitat management plans which had the aim of reducing the reliance of the resident nuthatch population on immigration, by increasing the amount of breeding quality habitat in existing woods, without increasing the overall wood area (Section 4.3.3.3). The largest suitable wood in the area (Monks Wood) was found to be a key feature and that, for this study area, improving the quality of core woods would be more effective than improving that of the smaller, dispersed ones (Section 4.3.4.2). Thus, improving the quality of existing woodland could increase population viability of the nuthatch, without incurring the costs of buying land in this intensively farmed area (Section 4.3.5; Appendix B.2). In landscapes with fragmented habitat, the results of this study showed that large core habitat blocks can be important for maintaining the population within the landscape, and that improving the quality of existing habitat can be as important as creating new habitat for population survival. Furthermore, the importance of immigration in supporting populations and the effects of neighbouring populations on those within a study area both need to be taken into account when planning and implementing habitat management schemes.

With about 40 ha of existing breeding quality habitat and a total area of 157 ha, this target for Monks Wood could be achieved with appropriate management, without having to extend the wood. Restoration of an adjoining conifer plantation would also be a possibility (Hinsley pers. comm.). This approach of increasing quality would be suitable for other landscapes where sympathetic management was a more realistic prospect than land purchase. The observed pattern of occupation of Monks Wood by nuthatches is indicative of increasing habitat quality. A pair was present in 1992, followed by sporadic records of single birds until breeding (by a single pair) was confirmed in 1998. Breeding, by one, or possibly two, pairs has since been confirmed in 2001, 2003 and 2004 (Hinsley *et al.* 2004). Persistence of the species in the study area may also have improved if recent increases in the UK national nuthatch population (Gibbons *et al.* 1993) have increased immigration into the area. Breeding has not been confirmed in Wennington and Holland Woods, but nuthatches have been regularly recorded in both woods since 2000, which is consistent with a possible increase in immigration (Hinsley pers. comm.).

The results of the perceptual range tests for the general case (Section 5.3.3.1) suggest that possession of an ability to perceive habitat at a distance is of greater value to survival of the nuthatch in a fragmented landscape and is of less value within homogeneous woodland. As fragmentation decreases, an ability to detect target habitat within non-target habitat would be more useful and non-visual traits may play a greater part in territorial establishment and settlement (Section 4.2.5). If the level of fragmentation gets too high, perceptual range is not so effective, but it is always an advantage as a disperser can still use its perceptual ability to reduce time spent in the matrix by moving directly to a patch when detected. The perceptual range tests for the specific case (Section 5.3.3.2), suggest the existence of an optimal range for particular species in particular landscapes, but that this optimal range may not be constant over a particular landscape.

The perceptual range tests for the specific case (Section 5.3.3.2), revealed that the effects of adding habitat may not be the desired ones and local population reductions could well occur. Small (1 ha in this case) adjustments had distant effects, which may not be apparent to the local observer. The nearest 'adjusted' 1 ha patch to Holland/Wennington Woods, for example, lay approximately 8 km to the west (Figure 5.3). Conversely, increases in population size may be due to distant changes and not to local conservation efforts. Modelling the effects of habitat additions and quality changes with an individual-based SEPM such as PatchMapper, with its ability to generate dispersal flow diagrams (Section 5.4.4.1), could be used to analyse the effects of habitat management plans at the landscape scale. The specific case tests also revealed, despite the limited published research on this subject (Section 2.4.7) and the results of the white-footed mouse sensitivity analyses (Section 5.5.3.2) suggesting otherwise, that increasing perceptual range does not always result in an increase in population size.

The perceptual range test results for the adjusted landscape (Section 5.3.3.2), were for a net gain of 3 ha (four 1 ha patches removed, seven 1 ha patches added (Figure 5.3b)) over the centralised landscape. This produced a drop in population size in target woods at the higher perceptual ranges, compared with that in the centralised landscape (Figure 5.13). This suggests that adding habitat may not always be beneficial.

General solutions are useful (Section 2.3.2; Section 2.6.2.4), but care must be taken when applying them as they often do not apply to specific cases (Kirby 2004). The centralised and adjusted landscape comparison emphasised the need to model the specific case (Section 5.3.3.2). PatchMapper was shown to meet this need by being able to model both for the general (the neutral landscapes) and specific cases (the centralised and adjusted landscapes) (Section 5.3.3).

### 6.2.3 Species Modelling

PatchMapper simulates the dispersal of individuals from their natal site, through to pair formation and territorial establishment. The nuthatch has a yearly breeding cycle, with young nuthatches leaving the natal territory and occupying the first found suitable territorial vacancy (Section 4.2.2). This leads to each individual's dispersion being modelled once per model cycle. The white-footed mouse has five breeding cycles per year, spread over a 33-week cycle (Section 4.4.2), with more than one life-stage between leaving the natal site and pair formation. Each individual 'moves' from the nest as a juvenile, is aged at each (weekly) model cycle, through the sub-adult and on to the adult stage and then 'moves' a second time, to occupy the first found suitable territorial vacancy. The situation is exacerbated with the multiple breeding cycles creating a new 'set' of juvenile mice every seven weeks. The repeated checking (for ageing and mortality) and the double movement of each individual, along with the multiple breeding cycles, over-complicated the white-footed mouse model, making it difficult to debug, with relatively high run times. As an example, using a 2.66 GHz Intel P4 CPU with 256 MB memory and Windows XP, a test length of 10,000 breeding cycles, took approximately 30 hours. As a comparison, the same test length with both the nuthatch and black hairstreak models took approximately 35 minutes.

These findings suggest that the individual-based SEPM approach of PatchMapper is best suited to modelling univoltine species which have no intermediate life-stages between leaving the natal site and pair formation, and which form pairs for at least one breeding season. The species should ideally have one dispersal phase, such as the nuthatch's single movement between natal site and settlement in the breeding site (Figure 4.2) and the black hairstreak, with its single egg-laying phase (Figure 4.18). The black hairstreak model presents a successful method of modelling a univoltine species which falls between the nuthatch and the white-footed mouse in that it has intermediate life-stages, but only one movement phase (Section 4.5.2). That said, the white-footed mouse model results matched those of the two comparison studies (Section 4.4.5), which suggests that multivoltine species, such as rodents and (some) invertebrates, could be modelled if longer run-times, or a greater level of simplification can be tolerated. A (necessary) pre-modelling scoping should provide some guidance on this matter (Jeffers 1982).

### 6.2.4 The Visual Aspect

As stated in Section 3.8.2, one of the advantages of individual-based SEPMs is the possibility of constructing them to produce a visual feedback of the simulation results, although the literature is short on examples (Section 2.6.2). PatchMapper meets this challenge by providing a real-time (computer) display of the positions of the individuals in the landscape, enabling a visual judgement of the effects of various habitat structure and quality scenarios on the viability and distribution of the population in question. An option is also provided to enable dispersal trails to be displayed (Section 5.4.4.1). During the presentations of the model (the major ones are listed in Appendix A), the visual features generated a great deal of interest and feedback, supporting the observation by Turner *et al.* 1995, that ‘a picture may be worth a 1,000 graphs in explaining a model simulation to a land manager’. Of particular interest was the ability to aggregate the dispersal trails to generate dispersal flow diagrams (Figure 5.22). The real-time (computer) visual output of the simulation was also found to be a key element in the debugging of the model, increasing confidence in the final product (Section 3.8.2). These findings validated the decision to provide the various visual outputs (Section 1.3).

### 6.2.5 Potential Model Artefacts

Model artefacts may give lead to misleading results and should be identified in any modelling study (Section 2.5.1). Some of the sensitivity analyses presented in chapter 5 revealed responses that may suggest that model artefacts are playing a part in the results. This is in particular evidence in Figures 5.12 and 5.17a and possibly also in Figures 5.10 and 5.32. The model outputs in these cases arose either as a result of limited sample sizes or, more importantly, as a combination of landscape structure and species behavioural characteristics. As an example, the ‘dips’ in Figures 5.13 and 5.14 were shown to result from a combination of landscape structure and nuthatch perceptual range (Section 5.4.4.1). The ripples in the black hairstreak responses, prior to the cessation of the management plans (Figures 5.34 and 5.35), give another example. The dips result from the removal of a strip of habitat and the subsequent demise of its occupants, followed by an increase in

numbers as the remaining population recovers and the existing habitat matures. Despite the small difference between the spatial structure of the centralised and adjusted landscapes (Figure 5.3), the results were different and provide a warning of the errors that can arise from the digitisation process. It is advisable to carefully check digitised landscapes, to avoid potentially misleading results. Scale can also affect results, in that smaller, flow-altering woods may not be present in the landscapes if the modelling is undertaken at an inappropriate resolution (Section 2.5.2).

### 6.3 Potential Applications

Potential applications for PatchMapper include investigations into the effects of different habitat types and spatial arrangements on ecological flow. This has conservation implications, allowing, for example, best site allocations to be suggested and determining the positive and negative effects of habitat siting.

One example application is presented by the Rockingham Forest Trust, who are charged with the conservation of Rockingham Forest in north-east Northamptonshire, U.K. The trust, with its long-term aim of creating a mature woodland, has recently planted Weldon Woodland Park (52°30'N, 0°36'W), a 20 ha site, with 14,000 young trees. Modelling the effect of adding the wood as initial non-target habitat and then target habitat on maturity could identify any landscape-wide effects on dispersal flow and population sizes of the various species likely to be affected.

To be realistic as a habitat management tool, the black hairstreak model had to include a dynamic model of blackthorn, its main larval food plant (Section 5.6.3). Habitat management for black hairstreak conservation is possible, but care is needed to avoid interrupting its life-cycle. Species action plans for regional counties call for the linking of existing black hairstreak sites, adding more habitat and encouraging effective management of blackthorn (Bourn and Warren 1998). The challenge is to identify optimum spatial arrangements of interconnected existing and new sites, along with any adverse



consequences of the various options. Computer modelling provides an ideal way of meeting challenges of this nature, by allowing investigations into the effects of various spatial arrangements on species recovery times and extinction thresholds, in computer rather than real time. PatchMapper could enable optimum solutions for the relevant species' action plans to be identified and habitat conservation guidelines to be developed.

## **6.4 Conclusions and Future Research Directions**

### **6.4.1 Conclusions**

One of the advantages of PatchMapper is that it can be used for different species in different landscapes as required, making the model more general. The simulation method automatically copes with the spatial structure of suitable and non-suitable habitat. Provided that up-to-date maps are available, changes in landscape structure and quality can be compared without re-formulating the model. Another major advantage of PatchMapper is the visual feedback of the simulation results.

PatchMapper, in simulating dispersal and incorporating immigration direction, immigration rate, perceptual range and variable habitat quality, can play a useful part in the selection of suitable habitat sites. Different patch positions and configurations can be compared in a short time, playing a useful role in predicting any undesirable consequences of habitat placement and could be used to good effect by conservation bodies charged with increasing biodiversity. Habitat quality improvements could be achieved at minimal cost, through judicious management or through the targeting of appropriate grant schemes. Minimum habitat areas could also be identified, reducing land acquisition and management costs.

PatchMapper is a generalised, easy-to-use, individual-based SEPM that can be used to check the effectiveness of various conservation and management approaches and is offered as a step forward in realising the potential of individual-based spatially explicit population modelling.

### 6.4.2 Future Research Directions

The ability of dispersing woodland birds, such as the nuthatch, to perceive separate habitat patches should be separated from their ability to locate good quality habitat within poor quality habitat. In the study area, the landscape consists largely of isolated woodlands, separated by low-lying arable farmland (Section 4.3.2). It is assumed that dispersing birds would find it relatively easy to spot woodlands in such an environment. Within a wood, it will not in general be possible to look ahead a great distance. Predatory pressure should also be much lower in woodlands than in open farmland and resource depletion less of a risk. It therefore seems reasonable to assume that the search mechanisms employed when searching woods for good quality habitat will be different than those employed when traversing the matrix (Wiens *et al.* 1997). This thesis only covered the ability to detect habitat patches at a distance and not other aspects of inter and intra-patch movement, which could be incorporated into future models.

The perceptual range algorithm used in the nuthatch module forms a useful starting point for further modelling with perceptual range. Future work could involve extending the perceptual range algorithm to encompass wider fields of view and investigating further the effects of perceptual range on ecological flow. The larger the patch, the easier it will be for a dispersing nuthatch to locate, thus it is suspected that the effect on flow patterns will be greater. The more habitat a patch contains, the more nuthatches will be 'caught', reducing the numbers for dispersal to other patches and the more likely the patch would itself act as a source of dispersers.

One subject for further research is further investigation into the existence of a higher level of habitat quality and whether or not a higher breeding density occurs therein, the possibility of which is visited in Section 5.4.2. This could be followed by a re-survey and re-modelling of the Monks Wood study area and a comparison with the results given in this thesis.

Although an easy-to-use method of loading different landscapes and incorporating dynamics was devised, an equally easy method of adding different species to the model was not provided. In its current state of development, adding extra species to PatchMapper requires access to the source code, knowledge of the program structure and the ability to program in Java. The user-addition of species was not one of the objectives of this thesis (Section 1.3), but the provision of such a facility presents a possible future development objective.

No studies were found that investigated the relationship between pattern metrics (other than habitat area and connectivity) and population parameters (Section 2.5.1; Appendix E). Although not discussed herein, the model development work carried out for this thesis failed to reveal any useful connections between commonly used spatial pattern metrics and population viability. The commonly used metrics (Appendix E.3) failed to take account of metapopulation dynamics such as asymmetrical dispersal flow and immigration rate and direction into the study area. This raises the question as to whether landscape metrics have any application to the field of conservation biology and offers another area for future research.

Other subjects for future research include modelling the effects of multiple additional patches, the effects of different sized patches and the effects of anthropogenic landscape elements such as urban areas and roads. Another area not explored in this thesis is the effect on population viability of habitat removal and quality reduction that may occur during replanting, such as replacing a deciduous wood with a coniferous one. The model could also be further developed to decrease its simplification by including more realistic features such as the reduction of fertility due to inbreeding in isolated patches and the effects of resource depletion.

## APPENDICES

## Appendix A: Major Milestones

Date	Event title	Event details	Presentation details	Location
July 2002	Research Conference	University College Northampton annual conference	Presentation of general results to date	University College Northampton
September 2002	Extinction Thresholds: Insights from ecology, genetics, epidemiology and behaviour	University of Helsinki, Spatial Ecology conference	Poster presentation and demonstration of PatchMapper	Unitas Congress Centre, Helsinki
November 2002		Invited presentation	Demonstration of nuthatch modelling	Centre for Ecology and Hydrology, Monks Wood
February 2003		Thesis transfer stage	Transfer Presentation	University College Northampton

**Table A.1:** The major milestones passed whilst undertaking the work for this thesis.

Date	Event title	Event details	Presentation details	Location
July 2003	Research Conference	University College Northampton annual conference	Presentation of general results to date	University College Northampton
December 2003	Applications of Computing in Entomology	Royal Entomological Society: Entomological Computing and Technology Special Interest Group annual conference. (Reported in January 2004 RES bulletin: Antenna Vol.28(1): 39)	Conference presentation	Royal Entomological Society, London
June 2004	Landscape Ecology of Trees and Forests	International Association of Landscape Ecologists (UK chapter) annual conference	Paper presentation, reproduced in Appendix B.1	Royal Agricultural College, Cirencester
March 2005		Paper accepted for publication by the journal Landscape Ecology	Publication of a paper in a refereed journal	

**Table A.1 (cont.):** The major milestones passed whilst undertaking the work for this thesis.

## **Appendix B: Papers**

This appendix reproduces four papers prepared from the research carried out for this thesis:

**B.1 Simulating Population Viability**

**B.2 Modelling the effects of dispersal and landscape configuration**

## Appendix B.1:

### **Simulating population viability in fragmented woodland: nuthatch (*Sitta europaea* L.) population survival in a poorly wooded landscape in eastern England**

This appendix reproduces a paper presented to the conference entitled: International Association of Landscape Ecologists (UK): Landscape ecology of trees and forests held on June 2004 at the Royal Agricultural College, Cirencester (UK).

#### **Reference:**

Alderman, J., McCollin, D., Hinsley, S., Bellamy, P., Picton, P. and Crockett, R. 2004. Simulating population viability in fragmented woodland: nuthatch (*Sitta europaea* L.) population survival in a poorly wooded landscape in eastern England. In: Smithers, R. (ed) *Landscape ecology of trees and forests: Proceedings 12th Annual IALE(UK) Conference, Royal Agricultural College, Cirencester*. pp. 76-83.



---

**Simulating population viability in fragmented woodland: nuthatch (*Sitta europaea* L.) population survival in a poorly wooded landscape in eastern England****J. Alderman <sup>1</sup>, D. McCollin <sup>1</sup>, S. Hinsley <sup>2</sup>, P. Bellamy <sup>2</sup>, P. Picton <sup>3</sup> and R. Crockett <sup>3</sup>**

<sup>1</sup> School of Environmental Science, University College Northampton, Park Campus, Northampton, NN2 7AL, UK. E-mail: jolyon.alderman@btinternet.com, duncan.mccollin@northampton.ac.uk

<sup>2</sup> Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, PE28 2LS, UK. E-mail: sahi@ceh.ac.uk, pbe@ceh.ac.uk

<sup>3</sup> School of Technology and Design, University College Northampton, Avenue Campus, Northampton, NN2 6JD, UK. E-mail: phil.picton@northampton.ac.uk, robin.crockett@northampton.ac.uk

---

**Abstract**

An individual-based spatially explicit population model of the nuthatch was developed and used to explore reasons behind the scarcity of nuthatches in apparently suitable woodland habitat in an area of eastern England. Predictions were compared with observed population sizes in the study area and with the previously published results of an analytical model applied to the same problem. Within our model, based on individual behaviour, nuthatch life cycle and immigration (direction and rate) parameters were user selectable. A novel aspect is user-selection of habitat perceptual range, which was found to influence the study area population size. The number of breeding pairs predicted by the model gave a closer match to observed levels than those achieved by the analytical model. According to model simulations, the main cause of nuthatch scarcity in the study area was the inability of patches to support viable populations. Predicted population sizes were found to be a function of immigration direction, immigration rate and habitat perceptual range and it is recommended that these essential elements be considered in population viability studies, especially when habitat is fragmented and patchily distributed.

---

**Introduction**

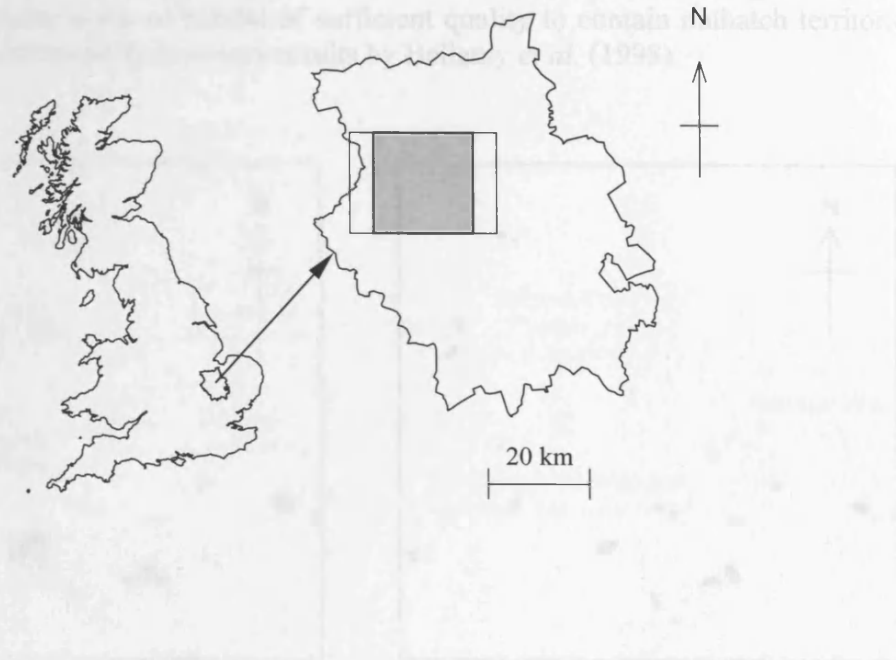
The nuthatch, *Sitta europaea* L., is a small (c.22-26g) cavity-nesting woodland passerine (Nilsson, 1976) resident in the UK, whose scarcity from an area in eastern England, centred on Monks Wood (52°24'N, 0°14'W) in Cambridgeshire, has been the subject of several studies (Hinsley *et al.*, 1995; Bellamy *et al.*, 1998).

Bellamy *et al.* (1998) compared observed numbers of breeding pairs in woods in the Monks Wood study area with the results from an analytical model developed in the Netherlands to predict nuthatch abundance in fragmented woodland (Schotman and Meeuwsen, 1994). Bellamy *et al.* (1998) found that the numbers of breeding pairs predicted by the Dutch model were lower than that expected from habitat area alone and that observed numbers were even lower than the model predictions. The nuthatch is noted as being sensitive to isolation (e.g., Enoksson *et al.*, 1995; Matthysen *et al.*, 1995), but despite taking this into account, the analytical model still predicted too high an occupancy level. To investigate whether an alternative modelling technique could more closely match the observed occupancy and abundance values, an individual-based spatially explicit population model (SEPM), named PatchMapper, was developed. This paper describes the model structure, followed by its application to the problem of nuthatch scarcity in the Monks Wood area. The aims of this study were to investigate whether an individual-based SEPM could produce more realistic predictions than the analytical model (Schotman and Meeuwsen, 1994) and whether factors other than habitat isolation influenced the numbers of breeding nuthatches in the study area.

## Study Area

The main study in Cambridgeshire, in eastern England (Figure 1), was based on that used by Bellamy *et al.* (1998), but was trimmed to 20 x 20 km (40,000 ha) to match the model input requirements (Figure 2). This 'main' map was used for comparison with the analytical model results of Bellamy *et al.* (1998). Approximately 4% (1570 ha) of this reduced area was wooded and 28 woods (totalling 512 ha) were deemed suitable for nuthatch occupancy. The total area of good quality nuthatch territory was approximately 261 ha (0.65% of the total landscape area) (Bellamy *et al.*, 1998). To avoid any directional bias in the results, the main map was adjusted approximately 1 km westwards and 5 km southwards to place Monks Wood at the centre. This second 'centralised' map (also 20 x 20 km), was used for the initial tests and had similar woodland cover (*c.* 4%) and number of woods (35) to the main study area. South Rockingham Forest, about 12 km west of the main study area, was the most suitable area within reasonable dispersal distance capable of acting as a source of immigrant nuthatches.

**Figure 1.** Location of the 20 x 20 km main study area (darker shading) in relation to the 20 x 25 km study area used by Bellamy *et al.* (1998), within the county of Cambridgeshire in eastern England, UK (redrawn from Bellamy *et al.*, 1998).



## Methods

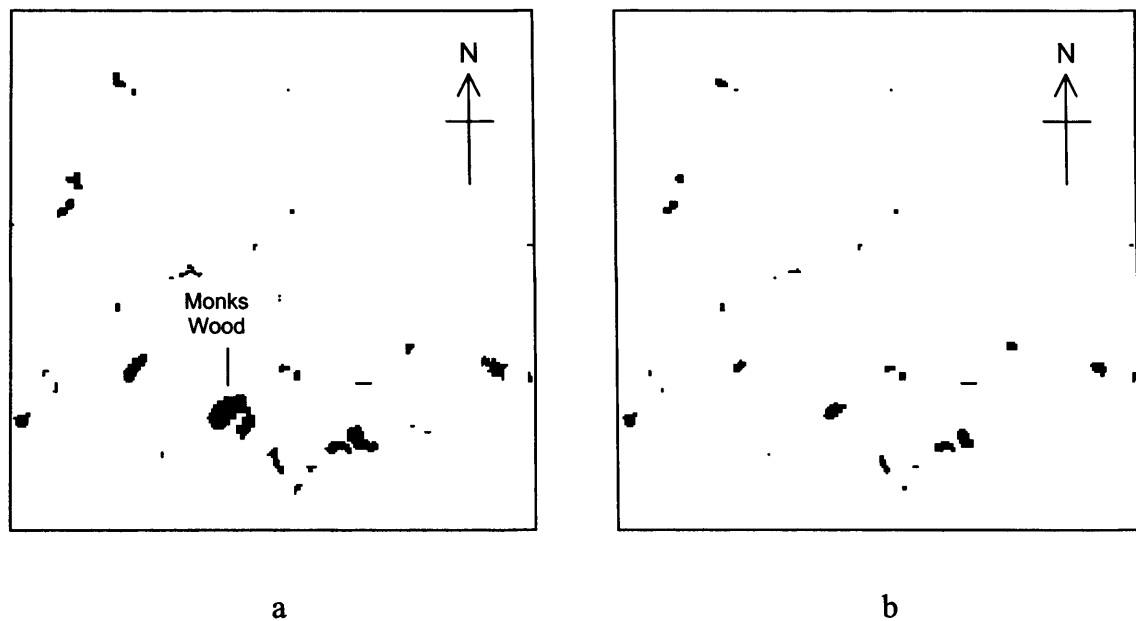
### Model description

PatchMapper combines a nuthatch population simulator with a grid-based representation of the landscape. Nuthatch life history, dispersal and territorial parameters are user selectable, as are initial population sizes and immigration rates into the study area. Different habitat configurations and landscape management scenarios can be tested with a choice of landscapes, either input from a GIS or user generated. During a run, nuthatch locations are superimposed on the landscape, providing a real-time visual output.

### Landscape

The landscape was modelled with three elements: target habitat, non-target habitat and matrix. Non-target habitat is a wooded area likely to be perceived by a dispersing nuthatch as containing good quality habitat, but which in fact does not. Target habitat represents good quality habitat and the matrix represents non-wooded areas. Two maps were used to accommodate this idea. The first map (the habitat map) was a cartographic view, representing all woods in the study area. A second map (the quality map) represented habitat quality, which determines nuthatch territory size (Wesolowski and Stawarczyk, 1991) (Figure 2). Maps were represented using a grid of square cells. For this study, the grid size was 200 x 200, which for the study area of 20 x 20 km gives a cell area of 1ha. Nuthatch territory size for the area was taken as 2 ha (Bellamy *et al.*, 1998).

**Figure 2.** The two main maps used in PatchMapper. The first map is a binary representation of the landscape comprising wooded areas (potential habitat) and matrix. For illustration, woods containing suitable habitat are shown in black, with all other woods shaded light grey. Monks Wood, the focal wood for this study is labelled (Figure 2a). The second map represents areas of habitat of sufficient quality to contain nuthatch territories (Figure 2b). Data extracted from survey results by Bellamy *et al.* (1998).

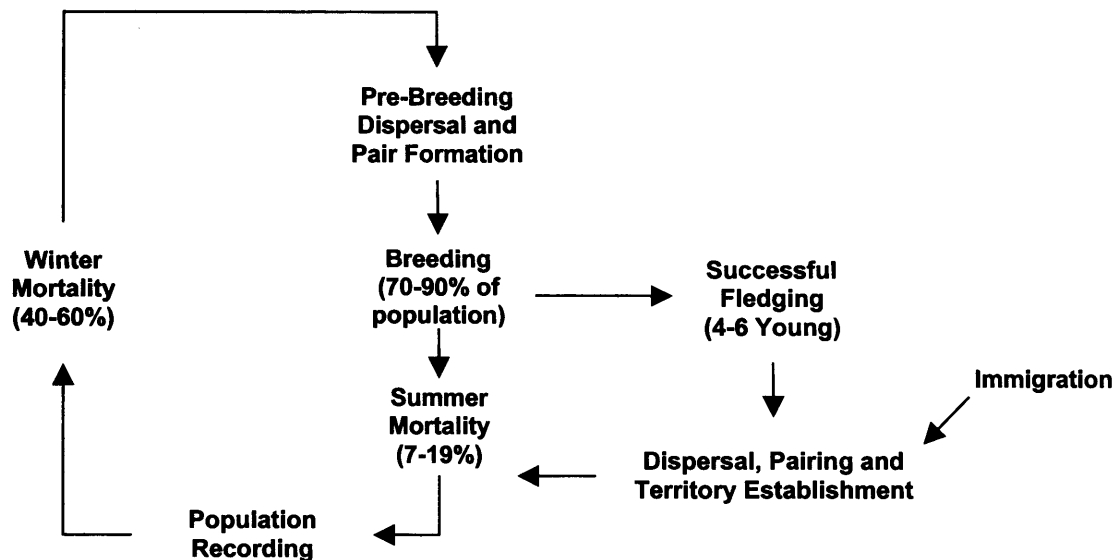


### Nuthatch simulator

Nuthatches were modelled by applying behavioural rules to each individual bird, with reference to the structure of the habitat and quality maps, an approach in which both landscape structure and species' characteristics govern population sizes and distribution.

Figure 3 shows the nuthatch modelling cycle. Life cycle parameters and territorial establishment behaviour for this study were taken from the literature (Nilsson, 1987; Wesolowski and Stawarczyk, 1991; Pravosudov, 1993; Matthysen *et al.*, 1995; Bellamy *et al.*, 1998; Matthysen and Adriaensen, 1998) and implemented as a set of rules applied to each individual. Population size, dispersal mortality, average age and other demographic statistics are recorded after each cycle of the model.

**Figure 3.** Nuthatch lifecycle modelled by PatchMapper. The immigration input allows individuals to disperse from distant sources into the study area. The parameters are taken from the literature, as cited in the text.



Dispersing nuthatches search for habitat, traversing the matrix with a correlated random walk. When a habitat patch is encountered, it is searched for good quality habitat. If none is found, the search for a new patch is resumed. If good quality habitat is found, then depending on its occupancy status, a new territory is established, a pair formed or if no vacancies exist, the disperser is forced to search for further suitable habitat within the wood or to search the matrix for another wood. A dispersal mortality probability is applied at each step.

To incorporate the possible effects of landscape structure on dispersal patterns, a habitat perceptual range mechanism was added to the basic dispersal rules, allowing the disperser to move directly to the nearest wood. The distance at which the disperser perceives a wood should represent the actual habitat perceptual range, but such data is not known for the nuthatch (or for many other species). A visual landscape survey was carried out to determine at what distance a wood could be clearly identified. The resulting mean distance of 2 km was used for this study.

### Tests

To test the self-supporting ability of the main landscape, the model was populated and run without immigration. With immigration into the centralised map, the effects of immigration direction, immigration rate and habitat perceptual range of dispersers were tested for their effects on population size in Monks Wood. To test the effects of variations in immigration rate and direction on the nuthatch population size in the study area, the

model was run with immigration into the area from an external source located at each of the cardinal and quadrantal points. If habitat perceptual range is a factor in guiding dispersers towards distant woods and reducing dispersal mortality, then varying the awareness distance should have an effect on population size. To test this, a series of runs with a perceptual range of 0 to 10 km and westerly immigration levels of 10, 20 and 30 individuals were undertaken. The results were used with the main map to judge PatchMapper's performance against the analytical model and study observations (Bellamy *et al.*, 1998). Each run was repeated for 10, 20 and 30 immigrating individuals. All tests used 100 runs of 100 years per run.

## Results

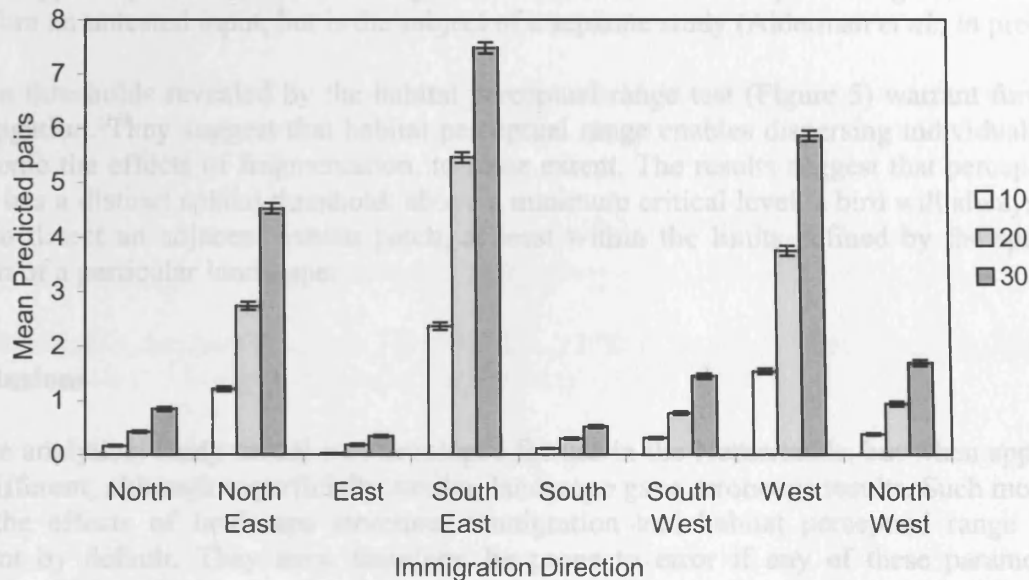
The self-supporting test revealed that without immigration, the main study area population reduced to zero after a mean of 8 years  $\pm$  0.5 years (95% C.I. over 100 runs). Immigration was therefore included in the model.

Figure 4 shows that both the direction and the numbers of immigrants were potential factors governing the population size in Monks Wood. Annual immigration into the centralised study area of between 10 and 20 birds, from the north east and westerly directions matched the observed level of 2 pairs in Monks Wood (Bellamy *et al.*, 1998), as did immigration from the south east at approximately 10 individuals per annum. Rockingham Forest, some 12 km to the west, is the most likely source of nuthatches, so a westerly immigration rate into the study area of 10 – 20 individuals per annum seemed the most realistic. The habitat perceptual range tests (Figure 5) showed that the distance at which a dispersing nuthatch can perceive habitat influenced the population size in Monks Wood, suggesting that perceptual range should also be modelled.

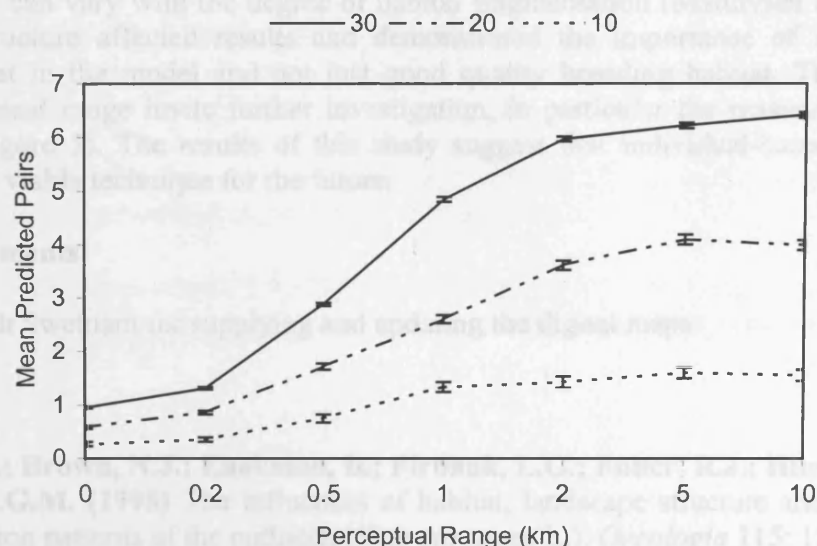
## Discussion

The fragmented structure of suitable habitat in the study area was found to be incapable of supporting a nuthatch population without immigration. This was seen as the main reason for the scarcity of nuthatches in the study area. When using viable, but unvalidated parameters, PatchMapper's predictions gave a closer match to the observed population size in Monks Wood than the analytical model's prediction of 63 pairs (Bellamy *et al.*, 1998). Individual-based SEPMs have been criticised for their reliance on unverified parameters, particularly with respect to dispersal and movement rules (Conroy *et al.*, 1995; Wennergren *et al.*, 1995). Nevertheless, the results from this study suggest that the technique of modelling population viability by simulating the behaviour of individuals in a spatially explicit grid-based landscape has the potential for higher accuracy than analytical models, with the added advantage of increased generality. Immigration direction and rate can have a large influence on population sizes (Figure 4), indicating that these inputs should be separate and controllable instead of using wrap-around or reflective immigration models such as BACHMAP (Pulliam *et al.*, 1992).

**Figure 4.** The effects of immigration direction on the mean number of pairs of nuthatches in Monks Wood using the centralised study area (error bars give 95% C.I.). Results are given for 10, 20 and 30 immigrating individuals per annum, shaded as per the key. Habitat perceptual range was set to 2 km.



**Figure 5.** The effect on population size in Monks Wood of habitat perceptual range from 0 to 10 km, with westerly annual immigration rates into the centralised study area of 10, 20 and 30 individuals, as per the key. Error bars give 95% confidence levels.



South Rockingham Forest is thought to be the main source of immigrating nuthatches into the study area, but another possible source is a wood near Peterborough, which lies to the northwest of the study area (Enoksson, 1993). With immigration direction and rate affecting predicted population sizes within the study area (Figures 4 and 5), identification of these sources and their likely emigration rate are necessary to increase the accuracy of PatchMapper's predictions. The immigration level from the nearby Rockingham forest is therefore an untested input, but is the subject of a separate study (Alderman *et al.*, in prep).

The thresholds revealed by the habitat perceptual range test (Figure 5) warrant further investigation. They suggest that habitat perceptual range enables dispersing individuals to overcome the effects of fragmentation, to some extent. The results suggest that perceptual range has a distinct spatial threshold: above a minimum critical level, a bird will always be able to detect an adjacent habitat patch, at least within the limits defined by the spatial pattern of a particular landscape.

## Conclusions

The analytical study model was developed for use in the Netherlands, but when applied to a different, although superficially similar, landscape gave erroneous results. Such models take the effects of landscape structure, immigration and habitat perceptual range into account by default. They may, therefore, be prone to error if any of these parameters change, which is likely when landscape configuration changes. Caution should therefore be applied when using models outside their target landscapes.

Immigration direction, immigration rate and habitat perceptual range were all found to have an important effect on population size. It is recommended that these inputs are included in population viability models, but the values chosen must be verifiable within the landscape in question and should result in realistic effects. For example, dispersal characteristics can vary with the degree of habitat fragmentation (Matthysen *et al.*, 1995). Landscape structure affected results and demonstrated the importance of including all suitable habitat in the model and not just good quality breeding habitat. The effects of habitat perceptual range invite further investigation, in particular the reasons behind any thresholds (Figure 5). The results of this study suggest that individual-based simulation modelling is a viable technique for the future.

## Acknowledgements

Thanks to Ruth Swetnam for supplying and updating the digital maps.

## References

- Bellamy, P.E.; Brown, N.J.; Enoksson, B.; Firbank, L.G.; Fuller, R.J.; Hinsley, S.A. & Schotman, A.G.M. (1998) The influences of habitat, landscape structure and climate on local distribution patterns of the nuthatch (*Sitta europaea* L.). *Oecologia* 115: 127-136.
- Conroy, M.; Cohen, Y.; James, F.; Matsinos, Y. & Maurer, B. (1995) Parameter estimation, reliability and model improvement for spatially explicit models of animal populations. *Ecological Applications* 5: 17-19.



- Enoksson, B. (1993)** Nuthatch. D.W. Gibbons; J.B. Reid & R.A. Chapman (Eds.) *The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991*. British Trust for Ornithology, Thetford, 376-377.
- Enoksson, B.; Angelstam, P. & Larsson, K. (1995)** Deciduous forest and resident birds: the problem of fragmentation in a coniferous forest landscape. *Landscape Ecology* **10**: 267-275.
- Hinsley, S.A.; Bellamy, P.E.; Newton, I. & Sparks, T.H. (1995)** Habitat and landscape factors influencing the presence of individual bird species in woodland fragments. *Journal of Avian Biology* **26**: 94-104.
- Matthysen, E. & Adriaensen, F. (1998)** Forest size and isolation have no effect on reproductive success of eurasian nuthatches (*Sitta europaea*). *The Auk* **115**: 955-963.
- Matthysen, E.; Adriaensen, F. & Dhondt, A.A. (1995)** Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* **72**: 375-381.
- Nilsson, S.G. (1976)** Habitat, territory size and reproductive success in the nuthatch *Sitta europaea*. *Ornis Scandinavica* **7**: 179-184.
- Nilsson, S.G. (1987)** Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *Journal of Animal Ecology* **56**: 921-937.
- Pravosudov, V.V. (1993)** Breeding biology of the eurasian nuthatch in northeastern Siberia. *Wilson Bulletin* **105**: 475-482.
- Pulliam, H.; Dunning, J. & Liu, J. (1992)** Population dynamics in complex landscapes: a case study. *Ecological Applications* **2**: 165-177.
- Schotman, A.G.M. & Meeruwsen, H.A.M. (1994)** *Predicting the effects of defragmentation measures in the Rolde/Gieten area*. (In Dutch). IBN report 118, Instituut voor Bos en Natuuronderzoek (IBN-DLO), Wageningen, Netherlands.
- Wennergren, U.; Ruckelshaus, M. & Kareiva, P. (1995)** The promise and limitations of spatial models in conservation biology. *Oikos* **74**: 349-356.
- Wesolowski, T. & Stawarczyk, T. (1991)** Survival and population dynamics of nuthatches *Sitta europaea* breeding in natural cavities in a primeval temperate forest. *Ornis Scandinavica* **22**: 143-154.

## **Appendix B.2:**

### **Modelling the effects of dispersal and landscape configuration on population distribution and viability in fragmented habitat**

This appendix reproduces a paper for which notification of acceptance for publication in the journal *Landscape Ecology* was received in March 2005.

# Modelling the effects of dispersal and landscape configuration on population distribution and viability in fragmented habitat

Jolyon Alderman <sup>1</sup>, Duncan McCollin <sup>1</sup>, Shelley A. Hinsley <sup>2</sup>, Paul E. Bellamy <sup>2</sup>, Phil Picton <sup>1</sup> & Robin Crockett <sup>1</sup>

<sup>1</sup> School of Applied Sciences, University College Northampton, Park Campus, Northampton, NN2 7AL, UK.  
email: [jolyon.alderman@btinternet.com](mailto:jolyon.alderman@btinternet.com), [duncan.mccollin@northampton.ac.uk](mailto:duncan.mccollin@northampton.ac.uk),  
[phil.picton@northampton.ac.uk](mailto:phil.picton@northampton.ac.uk), [robin.crockett@northampton.ac.uk](mailto:robin.crockett@northampton.ac.uk)

<sup>2</sup> Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire, PE28 2LS, UK.  
email: [sahi@ceh.ac.uk](mailto:sahi@ceh.ac.uk), [pbe@ceh.ac.uk](mailto:pbe@ceh.ac.uk)

---

**Keywords:** bird dispersal, habitat fragmentation, isolation, metapopulation, PatchMapper, perceptual range, woodland, *Sitta europaea*, habitat threshold

## Abstract

Landscape configuration and dispersal characteristics are major determinants of population distribution and persistence in fragmented habitat. An individual-based spatially explicit population model was developed to investigate these factors using the distribution of nuthatches in an area of eastern England as an example. The effects of immigration and increasing the area of breeding quality habitat were explored. Predictions were compared with observed population sizes in the study area. Our model combined a nuthatch population simulator based on individual behaviour with a grid-based representation of the landscape; nuthatch life cycle and immigration parameters were user selectable. A novel aspect of the model is user-selection of habitat perceptual range. Using a realistic set of parameters, the number of breeding pairs predicted by the model matched observed numbers. According to model simulations, the main cause of nuthatch scarcity in the study area was the inability of patches to support viable populations without immigration from elsewhere. Modelled habitat management, which increased breeding quality habitat in existing woods, lowered the threshold above which the study area population became self-sustaining. The existence of a large core habitat area was critical in producing a self-sustaining population in this landscape, the same area in dispersed small woods failed to sustain populations.

## Introduction

In many species, habitat loss and subsequent fragmentation, in association with changing land-use and urbanisation, are major causes of population decline (Saunders et al. 1991; Andr  n 1994; Simberloff 1995). Surviving populations may have a scattered distribution, inhabiting discrete habitat patches (With 1997). Extinction in individual patches is a feature of such landscapes and patch re-colonisation via inter-patch dispersal is essential to maintain the population as a whole (Hanski 1998). In order to reach suitable habitat, individuals are forced to traverse unsuitable and possibly hostile matrix habitat (Zollner and Lima 1999; Ricketts 2001). With dispersal being a key process linking isolated habitat patches (Schippers et al. 1996; Lande et al. 1999), habitat configuration, as well as extent, is important for conservation strategies (Villard et al. 1999; With and King 1999). Configuration here is defined as ‘the particular spatial arrangement of habitat at a given point in time’ (Villard et al. 1999).

In addition to habitat loss, the process of fragmentation also changes habitat configuration (Wiens 1994), which has been shown to influence the movement patterns of organisms across a range of scales e.g. tenebrionid beetles *Eleodes obsoleta* Say (Wiens et al. 1997), ringlet butterflies *Aphantopus hyperantus* L. (Sutcliffe and Thomas 1996) and the european badger *Meles meles* L. (Schippers et al. 1996). Movement patterns can influence habitat occupancy within patch networks such that the spatial distribution of a population may not be predictable from the distribution of suitable habitat alone (Wiens et al. 1997). Other factors may also result in absence from apparently suitable habitat patches. For example, fragmentation may reduce patch size below a critical persistence threshold e.g. for the hemipteran *Neophilaenus albipennis* Fabricius (Biedermann 2004), and/or may cause a loss of connectivity e.g. grey squirrels *Sciurus carolinensis* Gmelin (Lurz et al. 2001) and eastern chipmunks *Tamias striatus* L. (Henein et al. 1998). Species may be patchily distributed at the edges of their ranges e.g. Alaskan tree species (Lennon et al. 2002) and rare flowering plant species in the Netherlands (Oostermeijer et al. 2002), and as a consequence of recent range changes, e.g. the expansion into the UK of the berberis sawfly *Arge berberidis* Schrank (Halstead 2004) and the rhopalid bug *Brachycarenum tigrinus* Schilling (Jones 2004). Patch occupancy may also be affected by population size and the availability of colonists (Hinsley et al. 1996).

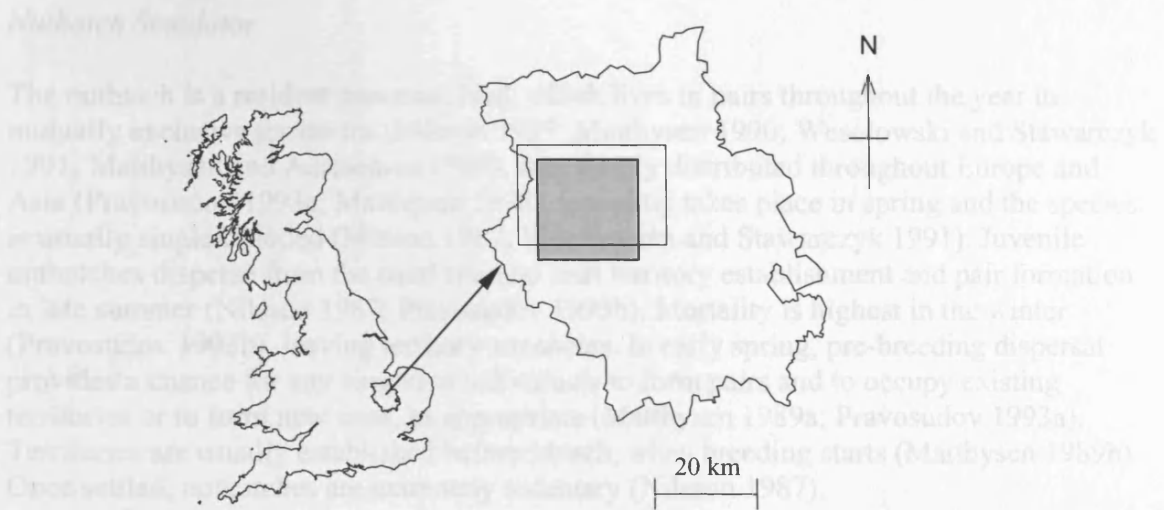
To aid the prediction of species occupancy and abundance in real landscapes, an individual-based spatially explicit population model (SEPM), named PatchMapper, was developed. A SEPM can be defined as a model that combines a detailed population simulator with an explicit representation of a landscape (Dunning et al. 1995; Ruckelshaus et al. 1996). By simulating the behaviour of individuals in fragmented habitat, individual-based SEPMs have been used to explore the effects of management strategies on population distributions and dispersal (Cain 1985; Liu et al. 1995; Zollner and Lima 1999). The aim of this paper was to use PatchMapper to explore the possible causes of species absence from apparently suitable habitat patches using the nuthatch as an example.

The nuthatch *Sitta europaea* L., a small (c. 22-26 g) cavity-nesting woodland passerine (Nilsson 1976) is thought to be sensitive to fragmentation due to its limited dispersal abilities through unsuitable habitat (Opdam et al. 1985, Enoksson et al. 1995, Matthysen et al. 1995). Here we use it as test species to examine the role of dispersal and habitat configuration in determining habitat occupation. It's scarcity from suitable habitat in an area of eastern England, centred on Monks Wood (52°24'N, 0°14'W) in Cambridgeshire, has been noted in previous studies (e.g. Hinsley et al. 1995; Bellamy et al. 1998). While expanding its range in the U.K. since the 1970s (Gibbons et al. 1993), and in other parts of Cambridgeshire since the 1980s (Bircham et al. 1994; Clark 1996), the nuthatch is still scarce in the Monks Wood area. The main reason for this absence was thought to be the fragmented nature of suitable habitat and its isolation from other nuthatch populations (Bellamy et al. 1998). This isolation suggested that immigration was a key factor in the maintenance or extinction of the existing nuthatch population within the Monks Woods area (Alderman et al. 2004). Our first objective was to evaluate the importance of immigration in maintaining the existing population and to investigate PatchMapper's ability to predict the abundance of nuthatches in target woods in the study area. The second objective was to determine how much new breeding habitat would be required to decrease a requirement for immigration and create a self-sustaining regional population.

## Methods

### Study Areas

The study area in west Cambridgeshire, in eastern England (Fig. 1) was used for nuthatch occupancy and habitat classification surveys by Bellamy et al. (1998). Breeding quality nuthatch habitat, including Monks Wood, was concentrated in the southern half of this study area. To match the model input requirement for 'square' landscapes, the test landscape was trimmed to 20 × 20 km (40,000 ha) and adjusted to place Monks Wood at the centre. About 4% (1660 ha) of this landscape was wooded. Within this area, 34 woods were deemed suitable for nuthatch occupancy (based on the original survey by Bellamy et al. (1998)), containing a total area of approximately 300 ha of breeding quality nuthatch habitat (0.75% of the total landscape area). The definition of breeding quality nuthatch habitat was taken from Bellamy et al. (1998), as mixed deciduous woodland, including oaks, with trees of greater than 30 cm diameter trunks, in which nuthatches have territories of approximately 2 ha. The matrix comprised intensive arable farmland, with large fields bounded by hedgerows (usually well trimmed) and few individual mature trees or rows of trees (Bellamy et al. 1998). The most suitable wooded area within reasonable dispersal distance capable of acting as a source of immigrant nuthatches was thought to be South Rockingham Forest, a large area of mature deciduous forest in Northamptonshire, approximately 12 km to the west of the main study area.



**Figure 1:** Location of the  $20 \times 20$  km modelled study area (darker shading) in relation to the  $20 \times 25$  km study area used by Bellamy et al. (1998), within the county of Cambridgeshire in eastern England, UK (redrawn from Bellamy et al. 1998).

### Model Description

Coded in Java for portability, PatchMapper is an individual-based SEPM. The landscape can be either dynamic or static, with its structure directly affecting the behaviour of the modelled species. Populations are not directly modelled, but form as a direct consequence of the behaviour of the individuals. Different habitat configurations and landscape management scenarios can be evaluated with a choice of landscapes, either input from a GIS or user generated. During the run, a real-time (computer) visualisation of the positions of individuals in the landscape is presented to the user. The results of the simulation, in the form of a set of landscape metrics and population demographics, are saved to disk and are also made available for direct display on the screen. The users' selections, entered via a set of interactive screens, control the overall simulation. For this study, PatchMapper combined a nuthatch population simulator with a grid-based representation of the landscape, and is described in more detail below.

### *Nuthatch Simulator*

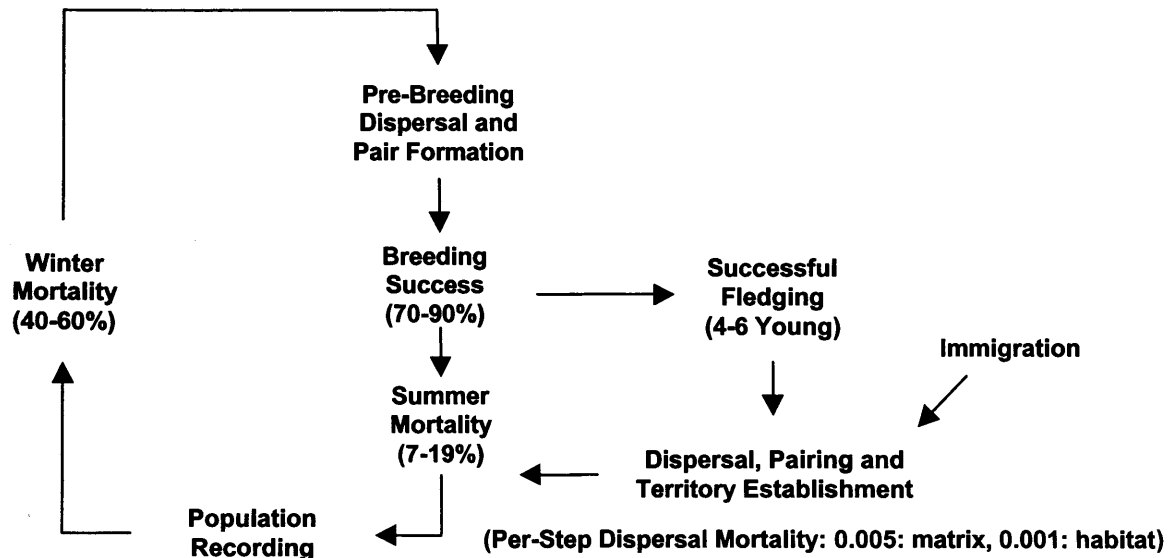
The nuthatch is a resident passerine bird, which lives in pairs throughout the year in mutually exclusive territories (Nilsson 1987; Matthysen 1990; Wesolowski and Stawarczyk 1991; Matthysen and Adriaensen 1998). It is widely distributed throughout Europe and Asia (Pravosudov 1993a; Matthysen 1998). Breeding takes place in spring and the species is usually single brooded (Nilsson 1987; Wesolowski and Stawarczyk 1991). Juvenile nuthatches disperse from the natal site and start territory establishment and pair formation in late summer (Nilsson 1987; Pravosudov 1993b). Mortality is highest in the winter (Pravosudov 1993b), leaving territory vacancies. In early spring, pre-breeding dispersal provides a chance for any singleton individuals to form pairs and to occupy existing territories or to form new ones, as appropriate (Matthysen 1989a; Pravosudov 1993a). Territories are usually established before March, when breeding starts (Matthysen 1989b). Once settled, nuthatches are extremely sedentary (Nilsson 1987).

These characteristics, based on parameters taken from the literature (Table 1), were used to model the behaviour of each individual bird, with reference to the quality of the habitat and to landscape structure (see below), an approach in which both landscape structure and species' characteristics govern population sizes and distribution. The overall model flow is given in Fig. 2, which also shows the nuthatch parameters used in this study. To model stochastic variation in the demographic and environmental parameters, the summer and winter mortality probabilities, along with the probability of successfully rearing young (breeding success) and the number of successfully fledged young, were sampled from a uniform distribution between the upper and lower limits given in Fig. 2. The simulation was based on a yearly cycle, with population size, dispersal mortality, average age and other demographic statistics recorded at the end of each 'year'.

Territory Size (ha)	Winter mortality (%)	Summer mortality (%)	Annual mortality (%)	Breeding success (%)	Mean brood size/female	Mean fledged young/female	General study area	Reference
			50				Belgium	Matthysen (1986)
	46	15	54	72% (SD=16.5)		3.72 (SD = 1.5)	Sweden	Nilsson (1987)
		9-17	58-64				Belgium	Matthysen (1989b)
	30-60		50				Belgium	Matthysen (1990)
2.08 (Breeding Habitat)			40-50	58-89 72 (Sweden) 83 (SW Germany) 91 (U.K.)	6.2		Poland	Wesolowski and Stawarczyk (1991)
				57.5 (41.9-78.2)	5.97 (4.83-7.4)	5.11 (3.6-6.33)	Siberia	Pravosudov (1993a)
30 (21-41)			32.8 (mean)				Siberia	Pravosudov (1993b)
			43			4.26	Belgium	Matthysen et al. (1995)
1-2 (Breeding Habitat)							U.K.	Bellamy et al. (1998)
					6-8		Belgium	Currie and Matthysen (1998)
1.58-1.85				75	6.5	5	Belgium	Matthysen and Adriaensen (1998)

**Table 1:** Published sources of demographic and territorial characteristics of the nuthatch (*Sitta europaea*) used to parameterise PatchMapper's nuthatch simulator. The parameters used for the simulations in this study are given in Fig. 2.





**Figure 2:** The nuthatch lifecycle as modelled by PatchMapper. The immigration input allows individuals to disperse from distant sources into the study area. The parameters are taken from the literature (see text and Table 1) and vary stochastically over their ranges during the simulation, as described in the text.

When the simulation is first run, breeding quality habitat cells are grouped into territories. Such cells are chosen at random, to provide different shaped territories, with the proviso that all cells within the territory group adjoin at least one other cell along a side (rather than a corner). The size of the territory, in number of cells, is user-selectable, with the number of territories per patch limited solely by the amount of breeding quality habitat present in the patch. This means that some cells may remain unallocated, even though of breeding quality. Each group of cells has one ‘main’ cell. All other cells in the territorial group (called territory cells) record the location of their ‘main’ cell. Once initialised, territories do not change, reflecting observations that territorial boundaries change little throughout the year (Matthysen 1986; Wesolowski and Stawarczyk 1991; Pravosudov 1993b). The ‘main’ cell is also used to store occupancy details, such as gender, age of each occupant and whether the territory is occupied by a pair or has a vacancy. During dispersal, a nuthatch locates a habitat cell. Information is gleaned from the territory’s ‘main’ cell, either directly if on the ‘main’ cell, or indirectly by obtaining its location from a ‘territory’ cell. If a suitable vacancy exists, then the territory is occupied and marked as such in the ‘main’ cell. If not, the dispersing nuthatch moves on in search of further suitable habitat. To model territorial establishment during late summer of the same year as fledging (Fig. 2), individuals do not disperse a set number of steps, but carry on moving until either a suitable territorial vacancy is found, or mortality occurs.

Dispersal in PatchMapper is governed by a set of inter and intra-patch dispersal rules. Dispersing nuthatches search for habitat, traversing the matrix with a correlated random walk in which small turns are made at intervals. On leaving the natal site, individuals are each assigned a dispersal direction, chosen at random from the set of cardinal and quadrantal directions. The disperser moves one cell in the dispersal direction and then one cell in an orthogonal direction, determined at random from a uniform distribution. On leaving the patch, dispersers ‘look’ for habitat within an arc of 180°, and up to a distance determined by a user-selectable perceptual range (see below). If a habitat patch is detected, the disperser moves directly to that patch, if not, it resumes the search, dispersing in a

random direction. During a simulation, individuals may disperse from natal patches or immigrate into the study area from the landscape boundary. In both scenarios, dispersers are searching for suitable vacant territory and therefore use the same inter-patch movement rules. When a habitat patch is encountered, it is searched for breeding quality habitat. If none is found, the search is resumed for a new patch. If breeding habitat is found, then depending on its occupancy status, a new territory is established, a pair formed or, if no suitable vacancy exists, the disperser is forced to search for further suitable habitat within the wood, or to search the matrix for another wood. The resultant inter-patch dispersal paths were nearly straight 'zig-zags' across the landscape. The scale chosen for modelling the landscape (1 cell = 1 ha, see the population viability tests section below) meant that features smaller than 1 ha could not be modelled. During dispersal across the matrix, it is likely that a nuthatch would take shelter in single trees or small woods and the actual dispersal path would therefore most likely be more 'zig-zag' than straight. Such dispersal paths are more realistic than straight ones (Samways 1989) and increase the chance of habitat detection (Forman 1995; Zollner and Lima 1999).

The distance over which a particular species is able to distinguish between different landscape elements has been variously defined as its 'radius of detection' or 'reactive distance' (Cain 1985; Adler and Nuernberger 1994), 'detection distance' (Fahrig 1988) or, more recently, its 'perceptual range' (Zollner and Lima 1997; Zollner 2000). For a dispersing individual, the shorter its perceptual range, the longer the time it spends in the matrix before locating a habitat patch. This increases the chance of dispersal mortality through factors such as resource depletion and increased risk of predation (Lima and Zollner 1996; Schooley and Wiens 2003). Perceptual range interacts with physical connectedness to determine the effective connectivity of the landscape and thus may play a key role in species' responses to habitat fragmentation.

To incorporate effects of landscape structure on dispersal patterns (Travis and French 2000), a habitat perceptual range mechanism was included in the basic dispersal rules, allowing the disperser to move directly to the nearest wood, if within the specified range. The perceptual range algorithm searched all cells within the user-selected perceptual range, fanning out progressively from the origin. Implicit in the concept of habitat perceptual range is the species' field of view. Other modelling studies discussing perceptual range looked directly ahead (Zollner and Lima 1999) or used a 360° field of view (Cain 1985; Fahrig 1988), but published coverage of this subject is sparse. For the tests in this study, a 90° field of view was employed, as a compromise between computational efficiency and ensuring that cell coverage was a factor in the resultant model behaviour (Fig. 3). The bird moved to the habitat cell nearest the origin. If more than one cell was found at the same distance, a random choice was made to avoid any directional biasing. The distance at which a disperser perceives a wood should represent the actual habitat perceptual range, but this is not known for the nuthatch (or for many other species) and such data are difficult to estimate (Wennergren et al. 1995). A distance of 2 km was assumed as a suitable perceptual range for a nuthatch. This distance corresponds to the maximum distance over which a human observer at ground level in a similar landscape was able to clearly identify woods (Alderman pers. obs.). To simulate nuthatches flying at canopy height, the observations were taken from hilltops.

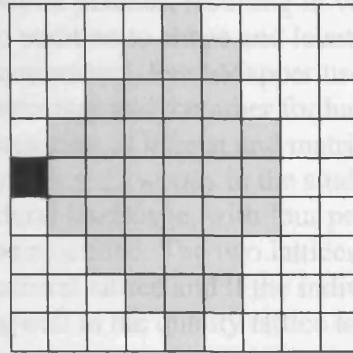


Figure 3: Example search coverage for a disperser with a six-cell perceptual range using a 90° field of view, including corrections for cell diagonal and side dimensions. The black cell is the search origin.

In reality, dispersing individuals are not constrained by arbitrary study area dimensions, they can both leave and enter the study area. PatchMapper models emigration by ‘losing’ an individual once it crosses the landscape edge (an absorbing boundary). To model immigration into the landscape, from a nearby external source for example, both the direction of immigration and its rate were made user-selectable. Immigration takes place in the ‘summer’, with an individual nuthatch entering the landscape from a position chosen at random along a landscape edge. The position was sampled from a uniform distribution, with gender alternating for each immigrant. Immigration rate is modelled as a yearly number of immigrants and is user-selectable, as is immigration direction, which can be from one of the cardinal or quadrantal compass points or from all points.

The predator most likely to be encountered by dispersing nuthatches is the sparrowhawk (*Accipiter nisus*) (Newton 1986), although other avian predators such as kestrel (*Falco tinnunculus*) and hobby (*F. subbuteo*) may also be a threat. Vulnerability, once pursued, would be greater in the open than in woodland. Taking this into consideration, in conjunction with published dispersal mortality estimates (Pulliam et al. 1992; Liu et al. 1995), arbitrary per-step dispersal mortality probabilities equivalent to  $0.05 \text{ km}^{-1}$  were chosen for dispersal within the matrix and  $0.01 \text{ km}^{-1}$  for within-habitat dispersal. (Per-step mortality is the chance that mortality occurs during dispersal, applied at each movement step.) Dispersal in PatchMapper is modelled as movement from one cell to another. The step size for the tests used in this study was 100 m (1 cell = 1 ha, see the population viability tests section below), which meant that mortality probabilities of 0.005 and 0.001 were applied at each step in the matrix and habitat respectively.

### Landscape Modelling

PatchMapper models landscapes in a square celled lattice of  $100 \times 100$ ,  $200 \times 200$ ,  $300 \times 300$  or  $600 \times 600$  cells. The landscapes used for the tests in this study were  $200 \times 200$  cells and were imported from a GIS.

Habitat quality may differ within patches, resulting in variations in population density within a patch. Therefore, in addition to shape and location, patch quality should also be modelled. To meet these requirements, PatchMapper uses two landscapes for each simulation, one for habitat structure and the other for habitat quality. The structural landscape is a binary representation of habitat and matrix, in the form of a cartographic view of the landscape representing all woods in the study area. The quality landscape is the same resolution as the structural landscape, with four possible states, allowing up to four levels of habitat quality to be modelled. The two lattices are coupled. During dispersal, reference is made to the structural lattice and if the individual is on a habitat cell, reference is made to the corresponding cell in the quality lattice to determine whether or not to settle.

For this study, the landscape was modelled with three elements: target habitat, non-target habitat and matrix. Target habitat represents breeding quality woodland habitat. Non-target habitat represents woodland that is unsuitable for breeding, but the difference between breeding quality and non-target woodland cannot be determined from a distance. The matrix represents non-wooded areas, unsuitable for occupancy by nuthatches. The breeding quality habitat areas could support 2 ha territories. Note that individual woods can contain both target and non-target habitat.

## Tests

Firstly, the importance of immigration into the study area was examined, followed by a comparison of the predictions of PatchMapper to observed numbers of nuthatches in target woods (*model comparison tests*). Secondly, the effects of increasing the area of breeding quality habitat on nuthatch population persistence were examined (*population viability tests*). These tests were intended to demonstrate the effects of feasible habitat management plans, rather than to provide a long-term prediction of actual nuthatch population sizes. The tests are described in detail as follows.

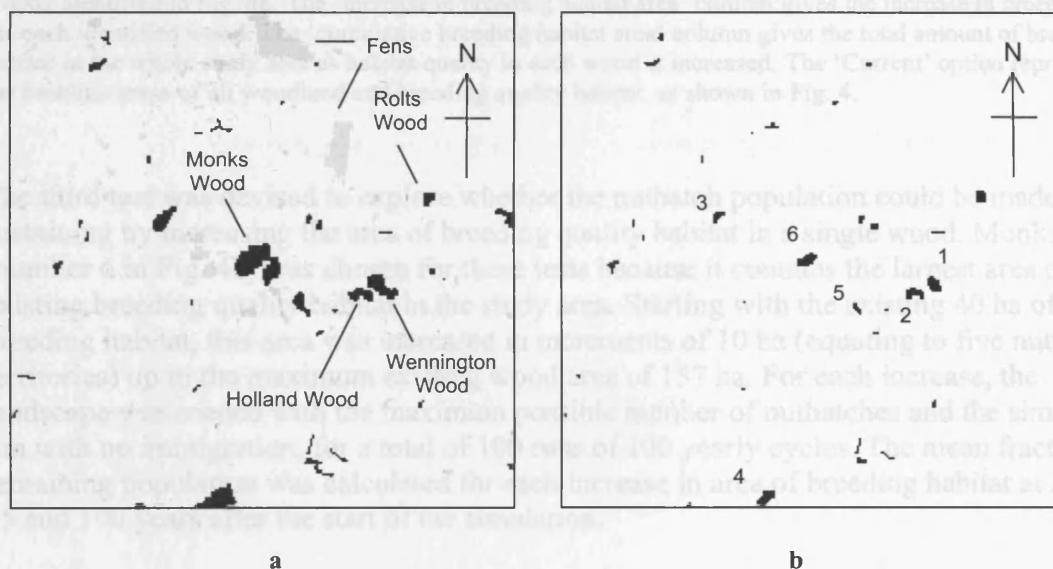
### *Model comparison*

To investigate the role of immigration in population persistence in the study area, the model was run with no immigration (from outside the study area). Emigration still applied, meaning that birds were lost as they crossed the study area boundary. The scenario consisted of 100 runs of 100 yearly-cycles per run and the results were used to calculate the mean time to extinction for the study area population.

The most likely direction of immigration into the study area was westerly (from South Rockingham Forest), but the immigration rate itself was unknown. The comparison tests therefore took the form of a sensitivity analysis, measuring the mean population sizes in Monks, Holland, Wennington and Rolts Woods for immigration rates from 0 to 60 birds per annum. The upper range limit of 60 birds was thought to be well above the most likely actual rate, with the test therefore spanning the actual rate. Tests were run over 10,000 cycles for each tested value, using the presumed nuthatch perceptual range of 2 km. The mean population size in each wood was recorded for each test.

### Population viability

To determine the effects of increasing the amount of breeding quality habitat in the study area on the long-term viability of the nuthatch population, three sets of tests were carried out. In the first set, the amount of breeding quality habitat in the six largest woods in the test landscape which already contained breeding habitat (Fig. 4b) was increased (Fig. 4a). In these tests, any non-breeding habitat was changed to breeding habitat in existing woods, but without any increase in the total area of woodland, making the whole area of each wood suitable for breeding (Table 2). In the second test (the 'All Small' option), all the woods in the study area with the exception of the three largest woodland patches (Monks Wood, Holme Fen and Woodwalton Fen, the latter two woods marked Fens in Fig. 4a), were upgraded to breeding quality habitat in the same manner. This option provided a total of 1099 ha breeding habitat spread over 232 smaller woods, removing the influence of the large habitat patches. (In this instance, Monks Wood retained its existing breeding quality habitat area of 40 ha.)



**Figure 4:** The structural and quality landscapes used with PatchMapper for the model tests. The landscapes are modelled using a  $200 \times 200$  cell grid, with Monks Wood positioned at the centre, representing a  $20 \times 20$  km landscape (1 cell = 1 ha). The structural landscape (a) is a binary representation of the landscape, comprising woods (potential habitat) and matrix. For illustration, woods containing suitable habitat are shown in black, with all other woods shaded light grey. Woods of particular relevance to the study are individually labelled. The quality landscape (b) represents the areas of habitat of sufficient quality to support nuthatch territories. Data extracted from survey results by Bellamy et al. (1998).

Option	Existing total area (ha)	Existing breeding area (ha)	Increased breeding habitat area (ha)	Cumulative breeding habitat area (ha)
Current, all woods	1660	298	0	298
Wood 1	72	30	42	340
Wood 2	35	20	15	355
Wood 3	50	20	30	385
Wood 4	85	32	53	438
Wood 5	32	14	18	456
Wood 6	157	40	117	573

**Table 2:** Woodland area and nuthatch breeding habitat in the whole study area for each of the numbered woods identified in Fig. 4b. The ‘increase in breeding habitat area’ column gives the increase in breeding area for each identified wood. The ‘cumulative breeding habitat area’ column gives the total amount of breeding habitat in the whole study area as habitat quality in each wood is increased. The ‘Current’ option represents the baseline areas of all woodland and breeding quality habitat, as shown in Fig. 4.

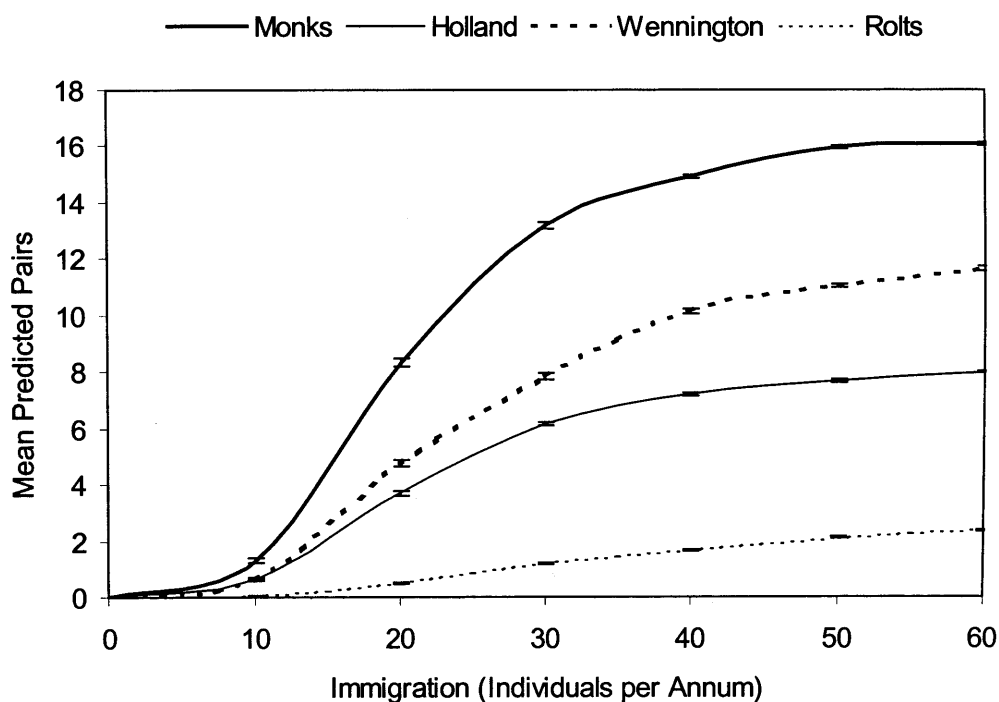
The third test was devised to explore whether the nuthatch population could be made self-sustaining by increasing the area of breeding quality habitat in a single wood. Monks Wood (number 6 in Fig. 4b) was chosen for these tests because it contains the largest area of existing breeding quality habitat in the study area. Starting with the existing 40 ha of breeding habitat, this area was increased in increments of 10 ha (equating to five nuthatch territories) up to the maximum existing wood area of 157 ha. For each increase, the landscape was seeded with the maximum possible number of nuthatches and the simulation run with no immigration, for a total of 100 runs of 100 yearly cycles. The mean fraction of remaining population was calculated for each increase in area of breeding habitat at 25, 50, 75 and 100 years after the start of the simulation.

## Results

### *Model comparison*

The first model comparison test revealed that without immigration, the study area population became extinct after a mean of 8 years  $\pm$  0.5 years (95 % C.I. over 100 runs). Therefore, immigration into the study area was a vital factor in maintaining the existing nuthatch population and needed to be included in the model.

As expected, the predicted population sizes in Monks, Holland, Wennington and Rolts Woods increased with increasing immigration rate (immigration from the west, perceptual range of 2 km). The results showed a lower threshold at approximately 10 individuals per annum, below which the numbers of immigrants reaching the woods were too low to support a population (Fig. 5). The results also showed an upper threshold at approximately 30 - 40 individuals per annum, when the number of immigrants 'saturated' the woods (Fig. 5). The maximum observed numbers were 2 pairs in Monks Wood, 1 pair in Wennington Wood and 0.5 pairs in Holland and Rolts Woods.

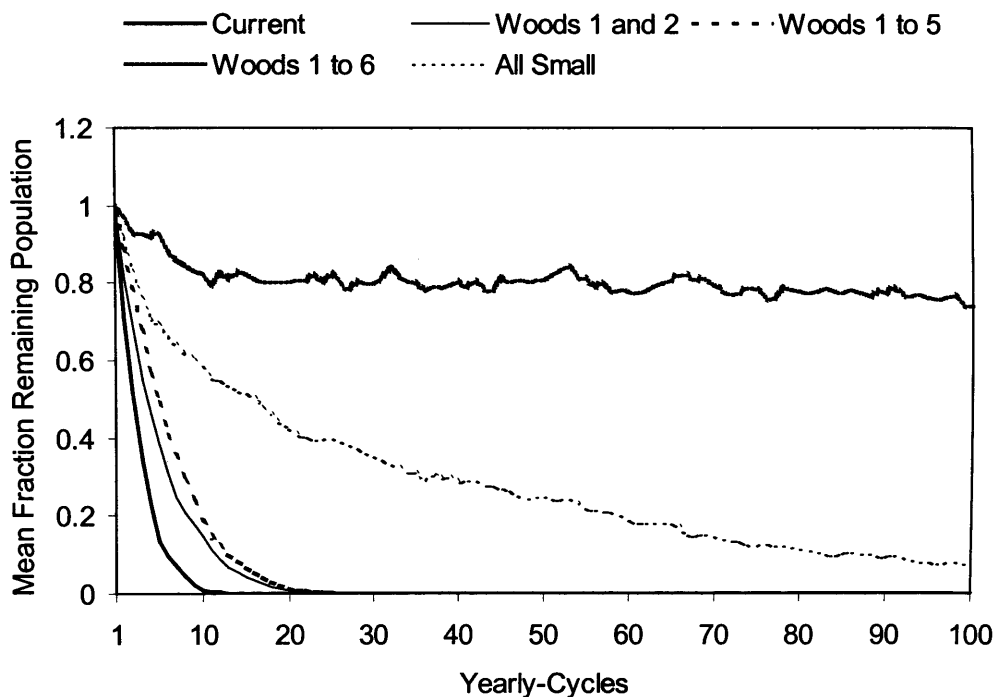


**Figure 5:** Predicted population size (mean number of pairs) in Monks, Holland, Wennington and Rolts Woods, as a function of immigration into the study area. Perceptual range was set at 2 km. The error bars give 95% confidence levels.

### Population viability

The results of increasing the area of breeding habitat in selected woods are given in Fig. 6. For clarity, not all results are shown. With the current amount of breeding quality habitat, the population lasted approximately 10 years. This increased to approximately 20 years when breeding habitat in woods 1 to 5 (Fig. 4b) was increased to occupy the whole of each wood. However, the population only became self-sustaining over the long-term, when the amount of breeding habitat in Monks Wood (wood number 6) was also increased to occupy the whole wood.

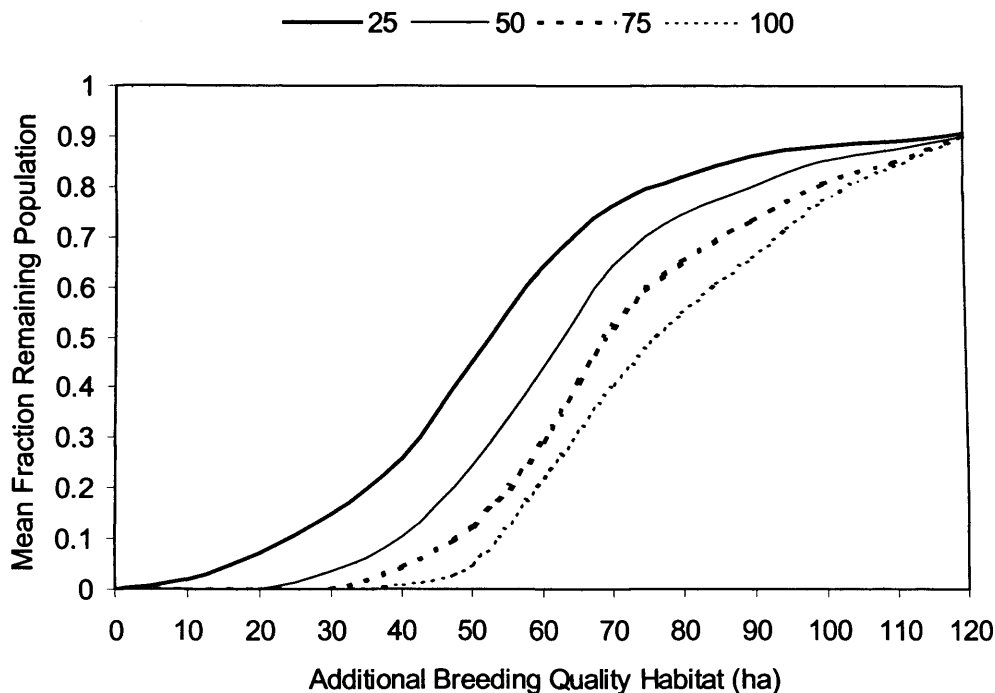
The 'All Small' option provided the largest increase in breeding quality habitat of the three tests (1099 ha compared with 573 ha for the 'wood 6 option' (Table 2)). Of the 232 woods altered by this option, 117 were below 2 ha and hence too small to support a breeding pair, 90 woods were from 2 - 10 ha, leaving 25 woods above 10 ha. Young produced in the smaller woods have little option but to disperse through the matrix, with all the dangers that that entails (plus the possibility of leaving the study area). Despite the large overall increase in breeding quality habitat, the structure of the landscape therefore prevented the nuthatch population from becoming self-sustaining over the long-term under this option.



**Figure 6:** The mean fraction of remaining population in the study area, resulting from increasing the area of breeding quality habitat in selected woods (Fig. 4b), as per the legend. Perceptual range was set at 2 km.



The results of increasing the area of breeding quality habitat in Monks Wood alone are given in Fig. 7. The results showed a lower threshold at an addition of approximately 40 - 50 ha, with an upper threshold of approximately 65 - 75 ha.



**Figure 7:** The mean fraction of remaining population in the study area, at 25, 50, 75 and 100 years (as per the legend), resulting from increasing the area of breeding habitat in Monks Wood. Perceptual range was set at 2 km.

## Discussion

The model comparison tests demonstrated that, as suspected, the fragmented structure of the existing suitable habitat in the study area was incapable of supporting a nuthatch population without external immigration. The current landscape is effectively acting as a sink. Information on nuthatch distribution in eastern England obtained from local county bird reports and atlas data (Gibbons et al. 1993; Bircham et al. 1994; Clark 1996) revealed two likely sources of immigrant nuthatches. The main source is probably South Rockingham Forest, which lies some 12 km to the west of the study area, the other is a more wooded area to the northwest of Peterborough and of the study area (Smith and Gilbert 2002). With immigration rate affecting the predicted population sizes in target woods (Fig. 5), identification of these sources and their likely emigration rates are necessary to increase the accuracy of PatchMapper's predictions.

PatchMapper's predictions, using a presumed nuthatch perceptual range of 2 km and a range of westerly immigration rates (from Rockingham Forest), over-estimated the mean population sizes for Monks, Wennington and Rolts Woods at the higher immigration rates (Fig. 5). To match the observed numbers of nuthatches in the study area, the model required an annual immigration rate of about 10 - 15 birds, which seems not unrealistic. These results showed that PatchMapper was capable of producing a close match to observed population sizes, although the work was based on feasible, but unvalidated, parameters.

The results from the model were based on a static landscape. In reality, the current population may be a result of historical changes in land-cover. Historically, deforestation was widespread in the UK by the 14<sup>th</sup> century and the county of Cambridgeshire was poorly wooded (c. 1.5% cover) until the mid 20<sup>th</sup> century (Smith and Gilbert 2002). Recent increases (up to about 4%) in woodland cover are unlikely to have altered the distribution of breeding habitat for nuthatches, especially since much of this increase is recent and the trees have yet to mature. This was thought to eliminate changes in amount or configuration of suitable habitat as a possible cause of the current patch occupancy levels. However, an increase in unsuitable woodland patches may make it easier for nuthatches to disperse but more difficult to find a suitable breeding site, reducing the chance of dispersers settling to breed.

Comparative analyses of patch occupancy and spatial structure have shown that the distribution of patch occupancy is not only a function of patch heterogeneity, but also depends on a species' degree of habitat specialisation. Biedermann (2004), for example, found that for two hemipterans sharing the same host plant (*Brachypodium pinnatum* L.), the habitat specialist *Neophilaenus albipennis* was present in 20% fewer patches than the habitat generalist *Adarrus multinotatus* Boheman. A similar effect was also found for butterfly species with specialist and generalist host plant requirements (Steffan-Dewenter and Tscharrntke 2000). With its dependence on mature deciduous woodland, the nuthatch can be considered a habitat specialist. Patch occupancy levels for the nuthatch were low in the highly fragmented woodland habitat of the study area, suggesting both patch heterogeneity and habitat specialisation as causes of the existing patchy distribution. The results of increasing the quality of existing habitat, analogous to increasing the availability of the species specialist requirements, supported this conclusion.

In this study, to reduce the dependence of the resident nuthatch population on immigration, three 'habitat management' plans were tested by increasing woodland habitat quality rather than total woodland area. The first two plans had little effect until Monks Wood was included (Fig. 6). Without changing Monks Wood, the population still declined, even when all woods except the largest three (the 'All Small' option) were improved. This suggested that the largest suitable wood in the area (Monks Wood) was a key feature and that, for this study area, improving the quality of core woods would be more effective than improving that of smaller, more dispersed ones. The third plan (Fig. 7) revealed that a lower threshold of approximately 40 - 50 ha of the unsuitable habitat in Monks Wood was required to mature and/or be managed to increase quality, to enable the study area nuthatch population to become largely self-sustaining. Increasing the amount of breeding quality habitat above this threshold increased emigration from Monks Wood to the surrounding woods, thereby increasing the 'self-sustainability' of the whole study area population. This continued until the whole wood was converted to breeding quality habitat, with saturation starting to occur at an upper threshold of 65 - 75 ha. The area of existing habitat being below a critical

persistence threshold is therefore suggested as one cause of the low occupancy levels and patchy distribution of the nuthatch in the study area. The population in Monks Wood is predicted to be self sustaining with an area of suitable habitat much smaller than when all small woods converted to suitable habitat failed to create a sustainable population. This suggests that both the total amount of suitable habitat and the configuration of the habitat are important in determining the viability of the population.

Species with greater dispersal abilities are more likely to have higher population sizes, and to occupy more patches, in fragmented landscapes than those with restricted dispersal abilities (Laurance 1991). Landscapes have, as an example, been found to be more connected for the habitat generalist white-footed mouse (*Peromyscus leucopus* Rafinesque) than for the habitat specialist eastern chipmunk (*Tamias striatus* L.) (Henein et al. 1998). As a further example, Wang et al. (2004) in a butterfly study, found that the highly mobile *Melitaea phoebe* Denis and Schiffermuller had a higher number of local populations than the less mobile *Euphydryas aurina* Rottemburg. Dispersal ability is another possible cause of patch occupancy levels which can also be investigated with PatchMapper. Perceptual range as well as landscape configuration and mobility may affect connectivity or dispersal ability within fragmented habitat by enabling individuals to find more isolated habitat patches. The results of the tests in this study were based on a perceptual range of 2 km; the effect of perceptual range on population viability is the subject of a separate study (Alderman in prep.).

The identification of the true causes of population distribution within a fragmented landscape by empirical experimentation presents considerable challenges (Walsh and Harris 1996; Ormerod and Watkinson 2000), but the possibility of experimentation by computer simulation presents a practical alternative (Turner 1989). As distribution maps are used widely to assess species' status, an understanding of the reasons behind the distribution of species is essential (Cowley et al. 2000). The results of the tests in this study showed that an individual-based SEPM, such as PatchMapper, which models the movement of individuals is one type of model that can be used for this purpose.

## Acknowledgements

Thanks to Ruth Swetnam for supplying the digital landscapes.

## References

- Adler R.A. and Nuernberger B. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* 45: 41-75.
- Alderman J., McCollin D., Hinsley S., Bellamy P., Picton P. and Crockett R. 2004. Simulating population viability in fragmented woodland: nuthatch (*Sitta europaea* L.) population survival in a poorly wooded landscape in eastern England. pp. 76-83. *In* Landscape ecology of trees and forests: Proceedings 12th Annual IALE(UK) Conference. Edited by R. Smithers. Royal Agricultural College, Cirencester. 21<sup>st</sup> – 24<sup>th</sup> June 2004. IALE(UK).
- Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*. 71: 355-366.
- Bellamy P.E., Brown N.J., Enoksson B., Firbank L.G., Fuller R.J., Hinsley S.A. and Schotman A.G.M. 1998. The influences of habitat, landscape structure and climate on local distribution patterns of the nuthatch (*Sitta europaea* L.). *Oecologia* 115: 127-136.
- Biedermann R. 2004. Patch occupancy of two hemipterans sharing a common host plant. *Journal of Biogeography* 31: 1179-1184.
- Bircham P.M.M., Rathmell J.C.A. and Jordan W.J. 1994. An atlas of the breeding birds of Cambridgeshire (vice county 29). Cambridge Bird Club.
- Cain M.L. 1985. Random search by herbivorous insects: a simulation model. *Ecology* 66: 876-888.
- Clark J.S. 1996. The birds of Huntingdon and Peterborough. J.S. Clark, Hilton.
- Cowley M.J.R., Wilson R.J., Leon-Cortes J.L., Gutierrez D., Bulman C.R. and Thomas C.D. 2000. Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *Journal of Applied Ecology* 37: 60-72.
- Currie D. and Matthysen E. 1998. Nuthatches *Sitta europaea* do not delay postfledging dispersal in isolated forest fragments. *Belg. J. Zool.* 128: 49-54.
- Dunning J., Stewart D., Danielson B., Noon B., Root T., Lamberson, R. and Stevens, E. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5: 3-11.
- Enoksson B., Angelstam P. and Larsson K. 1995. Deciduous forest and resident birds: the problem of fragmentation in a coniferous forest landscape. *Landscape Ecology* 10: 267-275.
- Fahrig L. 1988. A general model of populations in patchy habitats. *Applied Mathematics and Computation* 27: 53-66.

- Forman R. 1995. Land mosaics: the ecology of landscapes and regions. 1<sup>st</sup> ed. Cambridge: Cambridge University Press, The Edinburgh Building, Cambridge, UK.
- Gibbons D.W., Reid J.B. and Chapman R.A. 1993. The new atlas of breeding birds in Britain and Ireland: 1988-1991. T. & A.D Poyser.
- Halstead A. J. 2004. Berberis sawfly, *Arge berberidis* Schrank (hymenoptera: argidae), a pest new to Britain. British Journal of Entomology and Natural History 17: 131-135.
- Hanski L. 1998. Metapopulation dynamics. Nature 396: 41-49.
- Henein K., Wegner J. and Merriam G. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. Oikos 81: 168-186.
- Hinsley S.A., Bellamy P.E., Newton I. and Sparks T.H. 1995. Habitat and landscape factors influencing the presence of individual bird species in woodland fragments. Journal of Avian Biology 26: 94-104.
- Hinsley, S.A., Pakeman, R.J., Bellamy, P.E. & Newton, I. 1996. Influence of habitat fragmentation on bird species distributions and regional population sizes. Proceedings of the Royal Society of London, Series B, 263: 307-313.
- Jones R.A. 2004. Brachycarenum tigrinus (Schilling) (hemiptera: rhopalidae) new to Britain. British Journal of Entomology and Natural History 17: 137-141.
- Lande R., Engen S., Saether B.E. 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. American Naturalist 154: 271-281.
- Laurance W.F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5: 79-89.
- Lennon J.J., Kunin W.E., Corne S., Carver S. and van Hees W.W.S. 2002. Are Alaskan trees found in more favourable sites in marginal areas? Global Ecology and Biogeography 11: 103-114.
- Lima S.L. and Zollner P.A. 1996. Towards a behavioural ecology of ecological landscapes. TREE 11: 131-134.
- Liu J., Dunning J.B. and Pulliam H.R. 1995. Potential effects of a forest management plan on Bachman's sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. Conservation Biology 9: 62-75.
- Lurz P.W.W., Rushton S.P., Wauters L.A., Bertolino S., Currado I., Mazzoglio P. and Shirley M.D.F. 2001. Predicting grey squirrel expansion in north Italy: a spatially explicit modelling approach. Landscape Ecology 16: 407-420.
- Matthysen E. 1986. Some observations on sex-specific territoriality in the nuthatch. Ardea 74: 117-183.

- Matthysen E. 1989a. Nuthatch *Sitta europaea* demography, beech mast and territoriality. *Ornis Scandinavica* 20: 278-282.
- Matthysen E. 1989b. Territorial and nonterritorial settling in juvenile eurasian nuthatches (*Sitta europaea* L.) in summer. *The Auk* 106: 560-567.
- Matthysen E. 1990. Behavioural and ecological correlates of territory quality in the eurasian nuthatch (*Sitta europaea*). *The Auk* 107: 86-95.
- Matthysen E. 1998. *The Nuthatches*. London: T & AD Poyser Ltd.
- Matthysen E. and Adriaensen F. 1998. Forest size and isolation have no effect on reproductive success of eurasian nuthatches (*Sitta europaea*). *The Auk* 115: 955-963.
- Matthysen E., Adriaensen F. and Dhondt A.A. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* 72: 375-381.
- Newton I. 1986. *The sparrowhawk*. Calton: T & AD Poyser Ltd.
- Nilsson S.G. 1976. Habitat, territory size and reproductive success in the nuthatch *Sitta europaea*. *Ornis Scandinavica* 7: 179-184.
- Nilsson S. 1987. Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *Journal of Animal Ecology* 56: 921-937.
- Oostermeijer J.G.B., Luijten S.H., Ellis-Adam A.C. and den Nijs J.C.M. 2002. Future prospects for the rare, late-flowering *Gentianella germanica* and *Gentianopsis ciliate* in Dutch nutrient-poor calcareous grasslands. *Biological Conservation* 104: 339-350.
- Opdam P., Rijdsdijk G. and Hustings F. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biological Conservation* 34: 333-352.
- Ormerod S.J. and Watkinson A.R. 2000. Editors' introduction: birds and agriculture. *Journal of Applied Ecology* 37: 1-5.
- Pravosudov V.V. 1993a. Breeding biology of the eurasian nuthatch in northeastern Siberia. *Wilson Bulletin* 105: 475-482.
- Pravosudov V.V. 1993b. Social organisation of the nuthatch (*Sitta europaea*). *Ornis Scandinavica* 24: 290-296.
- Pulliam H., Dunning J. and Liu, J. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2: 165-177.
- Ricketts T. 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158: 87-99.
- Ruckelshaus M., Hartway C. and Kareiva P. 1996. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* 11: 1298-1306.

- Samways M.J. 1989. Insect conservation and landscape ecology: a case-history of bush crickets Tettigoniidae) in Southern France. *Environmental Conservation* 16: 217-226.
- Saunders D.A., Hobbs R.J. and Margules C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Biological Conservation* 1: 18-30.
- Schippers P., Verboom J., Knaapen J.P. Apeldoorn R.C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography* 19: 97-106.
- Schooley R.L. and Wiens J.A. 2003. Finding habitat patches and directional connectivity. *Oikos* 102: 559-570.
- Simberloff D.S. 1995. Habitat fragmentation and the extinction of bird populations. *Ibis* 137 [Suppl] 1: 105-111
- Smith S. and Gilbert J. 2002. National Inventory of woodland and trees – county report for Cambridgeshire. Woodland Surveys Branch of Forestry Research, Forestry Commission, 231 Corstorphine Road, Edinburgh, EH12 7AT.
- Steffan-Dewenter I. and Tschardt T. 2000. Butterfly community structure in fragmented habitats. *Ecology letters* 3: 449-456.
- Sutcliffe O. and Thomas C.D. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology* 10: 1359-1365.
- Travis J. and French D. 2000. Dispersal functions and spatial models: expanding our dispersal toolbox. *Ecology Letters* 3: 163-165.
- Turner M.G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecological Systems* 20: 171-197.
- Villard M., Trzcinski M.K. and Merriam G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* 13: 774-783.
- Walsh A.L. and Harris S. 1996. Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. *Journal of Applied Ecology* 33: 519-529.
- Wang R., Wang Y., Chen J., Lei G. and Xu R. 2004. Contrasting movement patterns in two species of chequerspot butterflies, *Euphydryas aurina* and *Melitaea phoebe*, in the same patch network. *Ecological Entomology* 29: 367-374.
- Wennergren U., Ruckelshaus M. and Kareiva P. 1995. The promise and limitations of spatial models in conservation biology. *Oikos* 74: 349-356.

Wesolowski T. and Stawarczyk T. 1991. Survival and population dynamics of nuthatches *Sitta europaea* breeding in natural cavities in a primeval temperate forest. *Ornis Scandinavica* 22: 143-154.

Wiens J.A. 1994. Habitat fragmentation: island v landscape perspectives on bird conservation. *Ibis* 137: 97-104.

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

With K. 1997. The application of neutral landscape models in conservation biology. *Conservation Biology* 11: 1069-1080.

With K.A. and King A.W. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314-326.

Zollner P.A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented landscapes. *Landscape Ecology* 15: 523-533.

Zollner P.A. and Lima S.L. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* 80: 51-60.

Zollner P.A. and Lima S.L. 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80: 1019-1030.



---

## **Appendix C: Survey Results**

This appendix presents the results of the various surveys carried out as part of the research for this thesis:

C.1 Population ecology models

C.2 Published SEPMs

C.3 Commonly used landscape resolutions

C.4 Tree diameters

## Appendix C.1: Population Ecology Models

Paper	Model type	Species	Explicit landscape	Dynamic landscape	Individual/population	Focus
Nee and May (1992)	Differential Equation	2	N	Not Stated (D)	Individual	Competition
Palmer (1992)	Grid-based	10	Y	N	Population	Competition
Dytham (1994)	Grid-based	2	Y	Not Stated (D)	Individual	Competition
Donovan <i>et al.</i> (1995)	Spreadsheet Based	1	N	N	Individual	Parameterisation
Dytham (1995)	Grid-based	2	Y	N (D)	Individual	Competition
Dytham and Shorrocks (1995)	Grid-based	1	Y	N	Individual	Genetic diversity
Moilanen and Hanski (1995)	Incidence Function	2	N	N (D)	Population	Competition
Fahrig (1997)	Grid-based	1	Y	N (D)	Individual	Fragmentation thresholds
Ruckelshaus <i>et al.</i> (1996)	Grid-based	1	Y	N (D)	Individual	Parameterisation errors
Boswell <i>et al.</i> (1998)	Grid-based	1	Y	N	Population	Environmental fragmentation

**Table C.1.1:** A survey of population ecology model types. Y means that the feature is included, N that it is not. The 'Explicit Landscape' column lists those models that use a realistic landscape. The 'Dynamic Landscape' column lists those models that change the landscape during a simulation run. (D) means that the effects of changing landscapes are studied. The 'Individual/Population' column entries for grid-based models are recorded as 'individual' if one cell contains one occupant or 'population' if each cell can contain more than one occupant, even if the study says the model is individual-based.

Paper	Model type	Species	Explicit landscape	Dynamic landscape	Individual/population	Focus
Drechsler and Wissel (1998)	Differential Equation	1	N	N	Population	Metapopulation viability
Fahrig (1998)	Grid-based	1	Y	Y (D)	Individual	Fragmentation thresholds
Frank and Wissel (1998)	Markov Chain	1	N	N	Population	Spatial configuration
Travis and Dytham (1998)	Differential Equation	1	Y	N	Population	Dispersal
Hill and Caswell (1999)	Grid-based	1	Y	N (D)	Individual	Fragmentation thresholds
South (1999)	Array Based	1	N	N	Population	Dispersal success
Taneyhill (2000)	Dynamical System	2	N	N	Population	Competition
Fahrig (2001)	Grid-based	1	Y	N (D)	Population	Fragmentation thresholds
With and King (2001)	Grid-based	1	Y	N (D)	Breeding Pairs	Spatial structure
Clinchy <i>et al.</i> (2002)	Incidence Function	1	N	N	Population	Parameterisation
Dennis (2002)	Diffusion	1	N	N	Population	Allee effects

**Table C.1.1 (cont.):** A survey of population ecology model types. Y means that the feature is included, N that it is not. The ‘Explicit Landscape’ column lists those models that use a realistic landscape. The ‘Dynamic Landscape’ column lists those models that change the landscape during a simulation run. (D) means that the effects of changing landscapes are studied. The ‘Individual/Population’ column entries for grid-based models are recorded as ‘individual’ if one cell contains one occupant or ‘population’ if each cell can contain more than one occupant, even if the study says the model is individual-based.

Paper	Model type	Species	Explicit landscape	Dynamic landscape	Individual/population	Focus
Flather and Bevers (2002)	Grid-based	1	Y	N (D)	Population	Spatial structure
Kerr <i>et al.</i> (2002)	Grid-based	3	N	N	Individual	Competition
Sondgerath and Schroder (2002)	Grid-based	1	Y	N	Individual	Habitat connectivity

**Table C.1.1 (cont.):** A survey of population ecology model types. Y means that the feature is included, N that it is not. The 'Explicit Landscape' column lists those models that use a realistic landscape. The 'Dynamic Landscape' column lists those models that change the landscape during a simulation run. (D) means that the effects of changing landscapes are studied. The 'Individual/Population' column entries for grid-based models are recorded as 'individual' if one cell contains one occupant or 'population' if each cell can contain more than one occupant, even if the study says the model is individual-based.

## Appendix C.2: Published SEPMs

Reference	Landscapes	Habitat quality	Dynamic land./qual.	Species modelled	Immig.	Pcep. range	Visual output	Misc. info
PatchMapper	Neutral Realistic (GIS and user drawn)	Y	Y	Nuthatch ( <i>Sitta europaea</i> ), Black Hairstreak ( <i>Satyrrium pruni</i> ), White Footed Mouse Generic (4 off)	Y	Y	Y	Correlated random walk Wrapped boundaries Absorbing boundaries Directional immigration
Cain (1985)	Neutral	N	N	Generic insect	N	Y	N	Individual based Random walk dispersal Absorbing boundaries
Doak <i>et al.</i> (1992)	Neutral	N	N	Generic	N	N	N	Random dispersal Reflecting boundaries
Pulliam <i>et al.</i> (1992)	Neutral	Y	Habitat suitability and availability	Bachman's sparrow ( <i>Aimophila aestivalis</i> )	N	N	N	BACHMAP Female based Random walk

**Table C.2.1:** A survey of published SEPMs, showing their characteristics and common areas. The first entry, PatchMapper, describes the model developed for this thesis and is shown for comparison. Habitat quality = Y means that more than one habitable type of cover is modelled. Dynamic Land./Qual column details models that can vary habitat and/or quality during the simulation run. Immig. = Y means that immigration is allowed into the landscape, rather than patches within the landscape. Pcep. Range = Y means that perceptual range is explicitly modelled. Visual Output = Y means that a real-time (computer) display of individual or population positions in the landscapes is generated.

Reference	Landscapes	Habitat quality	Dynamic landscape	Modelled species	Immig.	Pcep. range	Visual output	Misc. info
Turner <i>et al.</i> (1993)	Neutral Realistic (GIS)	Y	Food source availability	Generic large ungulate	N	Y	N	Individual based Perception like: 10 cell limited dispersal
Turner <i>et al.</i> (1994)	Realistic (GIS)	Y	Food source availability	Elk ( <i>Cervus elaphus</i> L.) Bison ( <i>Bison bison</i> L.)	N	Y	N	Individual or group based A perceptual-range like parameter Reflective boundaries
Wu and Levin (1994)	Neutral	Y	Habitat disturbance	Annual forbs: <i>Bromus mollis</i> L. <i>Lasthenia californica</i> Lindley	N	N	N	PATCHMOD Links patch and plant models
Liu <i>et al.</i> (1995)	Realistic (GIS)	Y	Habitat management plans: habitat ageing	Bachman's Sparrow ( <i>Aimophila aestivalis</i> )	N	N	N	ECOLECON Individual based Female only Random walk
Lindenmayer and Possingham (1996)	Realistic (GIS)	Y	Habitat suitability	Leadbeaters's Possum ( <i>Gymnobelideus leadbeateri</i> McCoy)	N	N	N	Individual based Female only

**Table C.2.1 (cont.):** A survey of published SEPMs, showing their characteristics and common areas. The first entry, PatchMapper, describes the model developed for this thesis and is shown for comparison. Habitat quality = Y means that more than one habitable type of cover was modelled. Dynamic Land./Qual column details models that can vary habitat and/or quality during the simulation run. Immig. = Y means that immigration was allowed into the landscape, rather than patches within the landscape. Pcep. Range = Y means that perceptual range was explicitly modelled. Visual Output = Y means that a real-time (computer) display of individual or population positions in the landscapes was generated.

Reference	Landscapes	Habitat quality	Dynamic landscape	Modelled species	Immig.	Pcep. range	Visual output	Misc. info
Ruckelshaus <i>et al.</i> (1996)	Neutral	N	N	Generic	N	N	N	Random dispersal Absorbing boundaries
Schippers <i>et al.</i> (1996)	Realistic (GIS)	Y	N	European badger ( <i>Meles meles</i> )	N	N	N	GRIDWALK Individual based Foraging model Correlated random walk
Venier and Fahrig (1996)	Neutral	Y	N	Generic	N	N	N	Individual based Population / cell Random dispersal Wrapped boundaries
Henein <i>et al.</i> (1998)	Neutral	Y	N	Eastern chipmunk ( <i>Tamias striatus</i> L.) White-footed mouse	N	N	N	Individual based

**Table C.2.1 (cont.):** A survey of published SEPMs, showing their characteristics and common areas. The first entry, PatchMapper, describes the model developed for this thesis and is shown for comparison. Habitat quality = Y means that more than one habitable type of cover was modelled. Dynamic Land./Qual column details models that can vary habitat and/or quality during the simulation run. Immig. = Y means that immigration was allowed into the landscape, rather than patches within the landscape. Pcep. Range = Y means that perceptual range was explicitly modelled. Visual Output = Y means that a real-time (computer) display of individual or population positions in the landscapes was generated.

Reference	Landscapes	Habitat quality	Dynamic landscape	Modelled species	Immig.	Pcep. range	Visual output	Misc. info
Carter and Finn (1999)	Neutral	Y	N	Red fox ( <i>Vulpes vulpes</i> L.), striped skunk ( <i>Mephitis mephitis</i> Schreber)	N	N	N	MOAB Individual based Foraging model Random dispersal Reflective boundaries
Travis and Dytham (1999)	Neutral	Y	Habitat availability and suitability	Generic	N	N	N	Population / cell Individuals disperse Random walk Wrapped boundaries
Zollner and Lima (1999a)	Neutral	N	N	Generic	N	Y	N	Individual based Correlated random walk Absorbing boundaries 5 steps fixed perceptual range
Tischendorf and Fahrig (2000a)	Neutral	Y (?)	N	Generic	N	N	N	Individual based Uses three cover types Torus boundaries

**Table C.2.1 (cont.):** A survey of published SEPMs, showing their characteristics and common areas. The first entry, PatchMapper, describes the model developed for this thesis and is shown for comparison. Habitat quality = Y means that more than one habitable type of cover was modelled. Dynamic Land./Qual column details models that can vary habitat and/or quality during the simulation run. Immig. = Y means that immigration was allowed into the landscape, rather than patches within the landscape. Pcep. Range = Y means that perceptual range was explicitly modelled. Visual Output = Y means that a real-time (computer) display of individual or population positions in the landscapes was generated.



Reference	Landscapes	Habitat quality	Dynamic landscape	Modelled species	Immig.	Pcep. range	Visual output	Misc. info
Lurz <i>et al.</i> (2001)	Realistic (GIS linked)	Y	N	Grey squirrel	N	N	N	Individual based Saturation based dispersal to nearest site
King and With (2002)	Neutral	N	N	Generic	N	N	N	Individual based Random dispersal
Travis (2002)	Neutral	N	Habitat loss from climate change	Generic	N	N	N	Population based Dispersal to neighbouring patches
Bender <i>et al.</i> (2003)	Neutral Realistic (GIS)	N	N	Generic	N	N	N	No gender 5 cell limited dispersal Wrapped boundaries
Lurz <i>et al.</i> (2003)	Realistic (GIS linked)	Y	Habitat management plans: habitat availability	Red squirrel Grey squirrel	N	N	N	Individual based Two species Saturation based dispersal to nearest site

**Table C.2.1 (cont.):** A survey of published SEPMs, showing their characteristics and common areas. The first entry, PatchMapper, describes the model developed for this thesis and is shown for comparison. Habitat quality = Y means that more than one habitable type of cover was modelled. Dynamic Land./Qual column details models that can vary habitat and/or quality during the simulation run. Immig. = Y means that immigration was allowed into the landscape, rather than patches within the landscape. Pcep. Range = Y means that perceptual range was explicitly modelled. Visual Output = Y means that a real-time (computer) display of individual or population positions in the landscapes was generated.

Reference	Landscapes	Habitat quality	Dynamic landscape	Modelled species	Immig.	Pcep. range	Visual output	Misc. info
Macdonald and Rushton (2003)	Realistic (GIS linked)	Y	N	American mink ( <i>Mustela vison</i> Schreber), Pine marten ( <i>Martes martes</i> L.), Doormouse ( <i>Muscardinus avellanarius</i> L.), Water vole ( <i>Arvicola terrestris</i> L.)	N	N	N	Correlated random walk Single cell dispersal
Tischendorf <i>et al.</i> (2003)	Neutral	Y	N	Generic	N	N	N	Individual based Correlated random walk Torus based boundaries
Gardner and Gustafson (2004)	Neutral Realistic (GIS and user-drawn)	N	N	Generic	N	N	Y	Individual based Dispersal modelling Correlated random walk Absorptive boundaries Visual output not discussed and no examples given

**Table C.2.1 (cont.):** A survey of published SEPMS, showing their characteristics and common areas. The first entry, PatchMapper, describes the model developed for this thesis and is shown for comparison. Habitat quality = Y means that more than one habitable type of cover was modelled. Dynamic Land./Qual column details models that can vary habitat and/or quality during the simulation run. Immig. = Y means that immigration was allowed into the landscape, rather than patches within the landscape. Pcep. Range = Y means that perceptual range was explicitly modelled. Visual Output = Y means that a real-time (computer) display of individual or population positions in the landscapes was generated.

## Appendix C.3: Commonly Used Landscape Resolutions

Paper (Square Lattice)	Outline study area	Grid size	Cell scale	Extent	Why chosen (given or deduced)
Inghe (1989)	Genet and ramet survival	60 x 60	2cm <sup>2</sup>	1.2m <sup>2</sup>	Scale of data source
Hassell <i>et al.</i> (1991)	Insect population dynamics	30 x 30			Pure modelling
Gustafson and Parker (1992)	Patch spatial metric behaviour	120 x 120 200 x 200			Matching Thematic Mapper images of agricultural landscapes
O'Neill <i>et al.</i> (1992)	Hierarchical random map generation	64 x 64			Pure modelling
Palmer (1992)	Population survival in fractal landscapes	32 x 32			Pure modelling
Green (1994)	Critical thresholds in landscapes	100 x 100			Pure modelling
Scheuring <i>et al.</i> (1994)	Investigating chaos in natural populations	16 x 16			Pure modelling
Hulshoff (1995)	Cross-landscape metrics evaluation	200 x 200	50m <sup>2</sup>		Scale of data source
Lavorel <i>et al.</i> (1995)	Plant dispersal in hierarchical landscapes	100 x 100	10cm <sup>2</sup>	10m <sup>2</sup>	Scale of data source
Childress (1997)	Spatial pattern dynamics	20 x 20			Pure modelling
Dunkerley (1997)	Causes of banding in vegetation	50 x 50	1m <sup>2</sup>	2500m <sup>2</sup>	Matching vegetation size

**Table C.3.1:** Survey of commonly used landscape resolutions, showing outline subject area, grid size, cell scale and modelled extent, where given. Pure modelling studies do not test against a real landscape.

Paper (Square Lattice)	Outline study area	Grid size	Cell scale	Extent	Why chosen (given or deduced)
Li and Archer (1997)	New metric (Weighted mean patch size)	64 x 64			Pure modelling
Hargis <i>et al.</i> (1998)	Landscape metric behaviour analysis	101 x 101	30m <sup>2</sup>	918 ha	Matching LANDSAT grain and extent
With and King (1998)	Determination of extinction thresholds	128 x 128			Pure modelling
With and King (1999)	Dispersal success on neutral landscapes	128 x 128			Pure modelling
Hong <i>et al.</i> (2000)	New spatial pattern metric (Aggregation)	1024 x 1024	1m <sup>2</sup>		Pure modelling
Keitt (2000)	Food web stability	100 x 100			Pure modelling
Tischendorf and Fahrig (2000a)	Landscape connectivity response analysis	200 x 200			Pure modelling
Elkie and Rempel (2001)	Detecting scales in landscape patterns	800 x 800			Scale comparisons
Tischendorf (2001)	Links between pattern and process	200 x 200	25m <sup>2</sup>		Matching LANDSAT grain and extent
Wu and Sui (2001)	New metric (Segregation measure)	100 x 100			Pure modelling
Gardner and Gustafson (2004)	Dispersal modelling	1024 x 1024			Pure modelling

**Table C.3.1 (cont.):** Survey of commonly used landscape resolutions, showing outline subject area, grid size, cell scale and modelled extent, where given. Pure modelling studies do not test against a real landscape

Paper (Hexagonal Lattice)	Outline study area	Grid size	Cell scale	Extent	Why chosen (given or deduced)
O'Neill <i>et al.</i> (1996)	Scale problems with landscape metrics	1505 hexagons	640km <sup>2</sup>		Matching sampling design used by the U.S. Environmental Protection Agency
Roberts (1996)	Vegetation modelling using fuzzy systems	400 hexagons			Pure modelling

**Table C.3.1 (cont.):** Survey of commonly used landscape resolutions, showing outline subject area, grid size, cell scale and modelled extent, where given. Pure modelling studies do not test against a real landscape

## Appendix C.4: Tree Diameters

Name	Grid ref.	Ash ( <i>Fraxinus excelsior</i> L.)	Beech ( <i>Fagus sylvatica</i> L.)	Field Maple ( <i>Acer campestre</i> L.)	Oak ( <i>Quercus robur</i> L.)	Sweet Chestnut ( <i>Castanea sativa</i> Mill.)	Sycamore ( <i>Acer pseudoplatanus</i> L.)
Brigstock	SP965855 (Sheet 141)	38.2 - 44.9 41.32 ± 2.93 (n=4)			30.2 - 49.68 38.4 ± 5.6 (n=12)		
Everdon Stubbs	SP605565 (Sheet 152)		111.9 (n=1)	41.71 (n=1)	47.45 - 94.9 69.1 ± 12.077 (n=23)	65.6 - 92.9 80.97 ± 11.35 (n=4)	79.29 (n=1)
Glaphorn Cow Pastures	TL004905 (Sheet 141)	43 - 55 49 ± 8.48 (n=2)			44 - 100 59.4 ± 13.76 (n=18)		
Titchmarsh Woods	SP976830 (Sheet 141)	27.38 - 61.46 14.96 ± 4.96 (n=4)			28.34 - 47.13 35.78 ± 5.97 (n=17)		

**Table C.4.1:** Results of the survey into tree diameters at breast height. The size is given as the minimum to maximum range, in cm and the mean value ± 1 SD. Grid references were taken using the Ordnance Survey Landranger 1:50,000 series maps from the given sheet numbers.

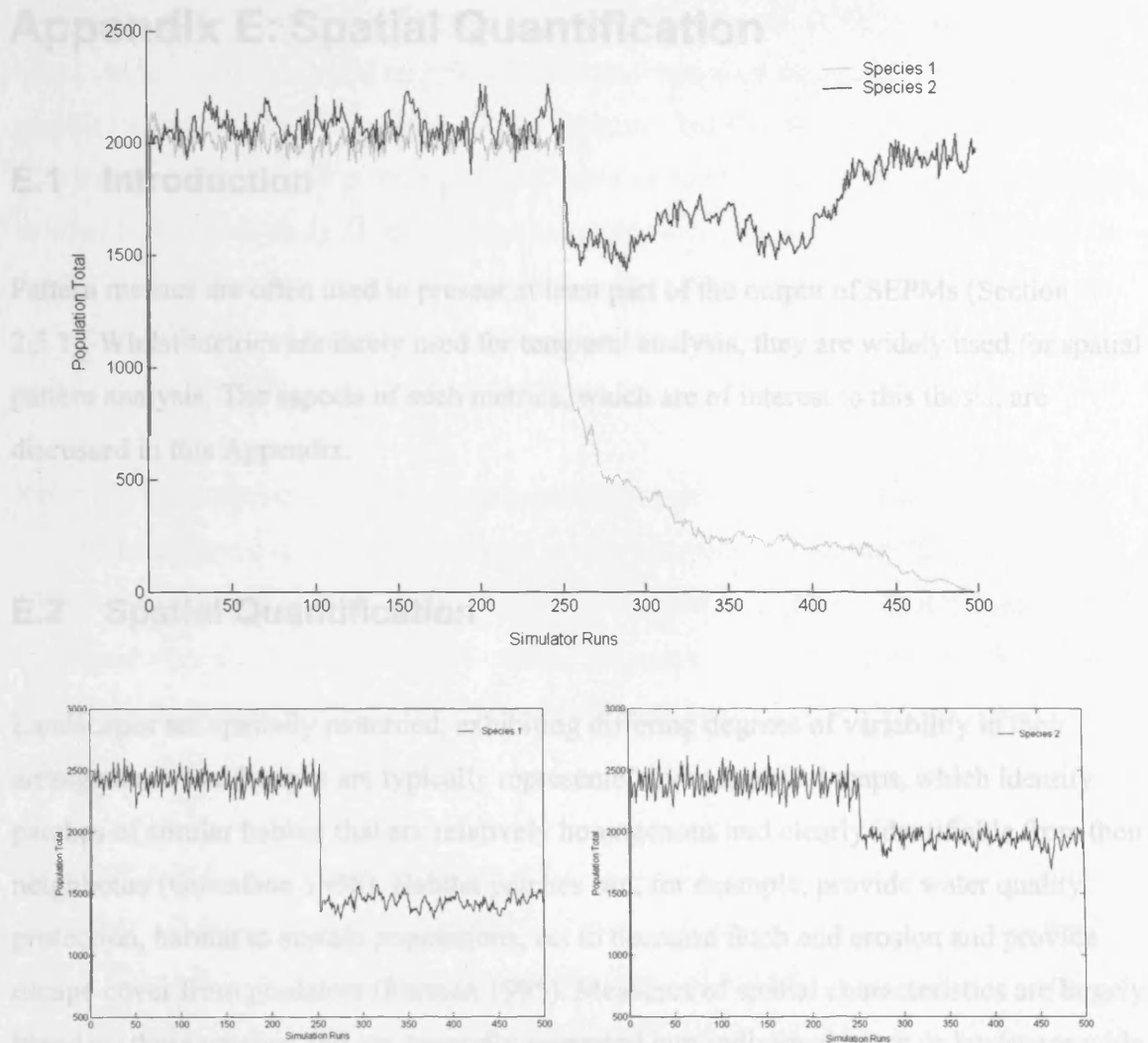
## **Appendix D: Multi-Species Modelling**

### **D.1 Introduction**

If species interactions are not considered, then there is a danger that the results given by modelling individual species separately may be quite different than that when modelled together. This appendix presents an illustrative example of two generic species inhabiting fragmenting habitat, modelled with PatchMapper. The same two species were used for all tests, with the landscape suffering a 50 % habitat loss half way through the simulation.

### **D.2 The Example**

When the two species were modelled together, species 1 entered a steady terminal decline following the habitat loss, but species 2 suffered an initial loss and then recovered towards its original level. However, if each species is modelled separately then the results suggested that both could cope with the habitat loss (Figure D.1). This could give the false impression that both species would survive if a land-use scheme resulting in a 50 % habitat loss were implemented, whereas the opposite would in fact be true.



**Figure D.1:** The results of modelling two generic species inhabiting a landscape suffering a 50 % habitat loss, generated using PatchMapper. The upper plot shows the results of simultaneous modelling with species 1 entering a terminal decline following the habitat loss and species 2 recovering from an initial loss. The lower plots show the results of modelling the same species separately. Both species suffer a loss, but neither goes extinct.



## Appendix E: Spatial Quantification

### E.1 Introduction

Pattern metrics are often used to present at least part of the output of SEPMs (Section 2.5.1). Whilst metrics are rarely used for temporal analysis, they are widely used for spatial pattern analysis. The aspects of such metrics, which are of interest to this thesis, are discussed in this Appendix.

### E.2 Spatial Quantification

Landscapes are spatially patterned, exhibiting differing degrees of variability in their arrangement. Landscapes are typically represented by categorical maps, which identify patches of similar habitat that are relatively homogenous and clearly identifiable from their neighbours (Gustafson 1998). Habitat patches can, for example, provide water quality protection, habitat to sustain populations, act to decrease fetch and erosion and provide escape cover from predators (Forman 1995). Measures of spatial characteristics are largely based on these patches and are generally separated into individual patch or landscape wide metrics (McGarigal and Marks 1995). Efforts to quantify spatial characteristics began in the early 1980s and have accelerated so that there are now hundreds of metrics available to the researcher (Gustafson 1998). Sample papers are Haines-Young and Chopping (1996) (56 metrics), Cain *et al.* (1997) (28 metrics) and Trani and Giles (1999) (24 metrics).

The plethora of metrics has resulted in a large number that are closely inter-correlated (Riitters *et al.* 1995; Gardner and Gustafson 2004). The aim should be to reduce redundancy by using metrics that correlate closely to processes (Haines-Young and Chopping 1996; Tischendorf 2001) and to avoid those which simply correlate with each other (O'Neill *et al.* 1988). A number of successful studies which identified inter-

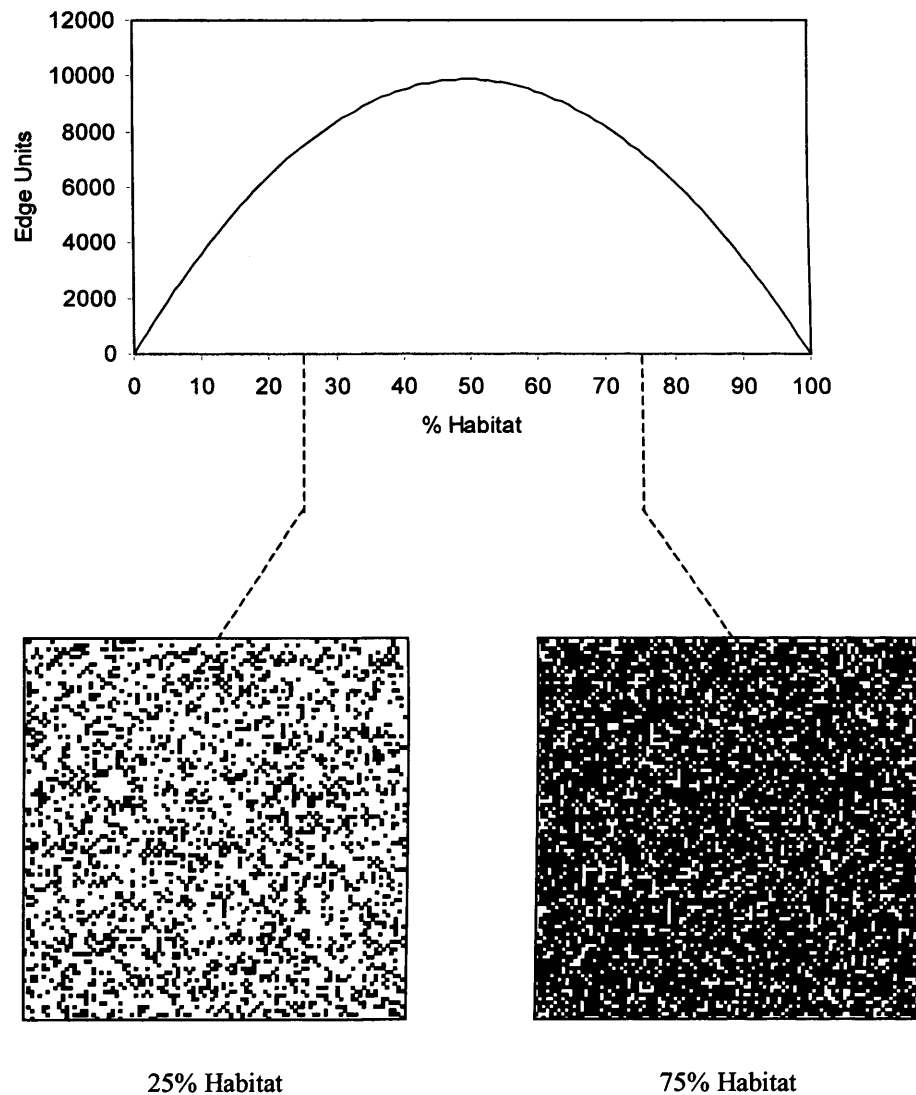
correlating metrics have been undertaken, such as Riitters *et al.* (1995) who found that an initial set of 55 metrics could be reduced to 26 and then used factor analysis to determine 6 significant factors. Further analysis revealed that the first five factors could be explained with just 5 metrics. Another example was Cain *et al.* (1997) who conducted factor analysis on various data sets using 28 metrics and found that 4 or 5 factors could be extracted. These results indicate that care should be taken in the selection of metrics, if meaningful results are to be produced and that the search for orthogonal metrics should continue (O'Neill *et al.* 1996; Cain *et al.* 1997; Bourgeron *et al.* 1999).

Recently, measures have become more sophisticated as researchers attempt to isolate specific landscape characteristics, such as habitat perimeter irregularity (Bogaert *et al.* 1999), aggregation (He *et al.* 2000), landscape fragmentation (Jaeger 2000), connectivity (Tischendorf and Fahrig 2000a), perforation (Bogaert *et al.* 2001) and segregation (Wu and Sui 2001). Such specialisation should, hopefully, reduce the inter-metric correlation problem.

When measured over their full possible range, most patch-based metrics (such as Number of Patches, Mean Patch Size and Total Edge) demonstrate non-monotonicity (Tischendorf 2001). Figure E.1 shows the misleading results than can arise from the use of a single metric to quantify spatial pattern. To avoid this problem, a combination of metrics should therefore be used, as exemplified by Ripple *et al.* (1991), who used five groups of metrics for their forestry based landscape pattern analysis. Hulshoff (1995) and Bourgeron *et al.* (1999) found that differences among habitats in landscape patterns were most successfully characterised using combinations of patch and landscape metrics, as they provided information about different aspects of spatial variability.

A further problem is that pattern metrics often fail to take the individual characteristics of species' into account, either during their calculation or in the application of their results. Isolation metrics, for example, are usually based on inter-patch distance, with the

assumption that the matrix is a homogeneous quantity as far as species dispersal is concerned (Verbeylen *et al.* 2003). As an example, Moilanen and Hanski (1998) looking at habitat quality with a detailed model landscape stated ‘.. the study of many species at the metapopulation level may be profitably based on the effects of just the two variables in the heart of the classical metapopulation concept: patch area and isolation’.



**Figure E.1:** A demonstration of the misleading results than can arise from the use of a single metric to quantify spatial pattern. This example shows the Total Edge metric graph resulting from a transformation of a landscape from 0 % to 100 % habitat, generated using PatchMapper, with each cell being changed from matrix to habitat at random.

One of the main uses of landscape metrics is for comparative analyses between landscapes or between different instances of the same landscape. The problem with undertaking such comparisons is that currently available patch-based metrics are sensitive to grain and extent, or scale (Haines-Young and Chopping 1996; O'Neill *et al.* 1996; Gustafson 1998; Tischendorf 2001).

Although many metrics exist which are useful for evaluating landscape heterogeneity, few metrics quantify landscape response at different scales (Li and Archer 1997). One that stands out is the lacunarity index, which can be used to detect points at which landscape scales change. Examples of its use can be seen in With and King (1999) in their study of dispersal success, Wu *et al.* (2000) in their measures of tiger bush fragmentation and Elkie and Rempel (2001) with an investigation into the detection of scales of pattern in boreal forest landscapes.

### **E.3 Commonly Used Landscape Pattern Metrics**

To determine whether or not there is a tendency to employ a common group of metrics, this author carried out a survey of 22 papers that used metrics for landscape studies. The results are given in Table E.1. Only metrics explicitly used in the studies were recorded. The survey revealed that five metrics were commonly used: Mean Patch Size, Class Area, Mean Nearest Neighbour, Number of Patches and Total Edge. These metrics were calculated in a common manner, as described in Fragstats (McGarigal and Marks 1995). The results suggested that fractal dimension and perimeter/area ratio are also widely used, but these were calculated using different algorithms. This also applied to the diversity, shape and contagion measures. The survey results were potentially misleading in that the five common metrics are based on the cell geometry of square lattices and form the basis of most of the other metrics recorded. Nevertheless it can be seen that despite the large number of available metrics, there is a tendency to use a common subset, with emphasis on the simpler metrics. Due to the different methods used to calculate metrics beyond the common subset, comparisons between studies becomes problematic and does not aid researchers in their choice of metrics.

Paper	MPS PS	CA	MNN NEAR	Perimeter/ Area	NP	TE EDGE	FRACT	Diversity	CONTAG	SHAPE	Connectivity	LPI
Turner (1990)		X		X		X	X	X	X			
Ripple <i>et al.</i> (1991)	X	X	X	X		X	X	X				
Gustafson and Parker (1992)	X		X			X	X		X			
Moss and Davis (1994)	X	X	X	X	X	X					X	
Simpson <i>et al.</i> (1994)		X		X	X			X				
Hulshoff (1995)	X	X		X	X							
Lavorel <i>et al.</i> (1995)			X									
O'Neill <i>et al.</i> (1996)	X					X			X	X		
Cain <i>et al.</i> (1997)	X			X	X			X	X			X
Li and Archer (1997)	X											
Hargis <i>et al.</i> (1998)			X	X			X		X			
Swetnam <i>et al.</i> (1998)			X	X								
Baskent (1999)						X						
Bourgeron <i>et al.</i> (1999)	X	X					X				X	
Haydon and Pianka (1999)	X	X			X							
Nikora <i>et al.</i> (1999)				X			X					
Trani and Giles (1999)	X	X	X		X	X		X			X	
Saveraid <i>et al.</i> (2001)	X		X									
Tischendorf and Fahrig (2000a)		X	X	X						X	X	
Wu <i>et al.</i> (2000)		X	X							X		
Herzog <i>et al.</i> (2001)	X				X			X		X		X
Tischendorf (2001)	X	X	X		X	X	X	X	X	X		X
<b>Totals (22 Papers):</b>	<b>13</b>	<b>11</b>	<b>11</b>	<b>10</b>	<b>8</b>	<b>8</b>	<b>7</b>	<b>7</b>	<b>6</b>	<b>5</b>	<b>4</b>	<b>3</b>

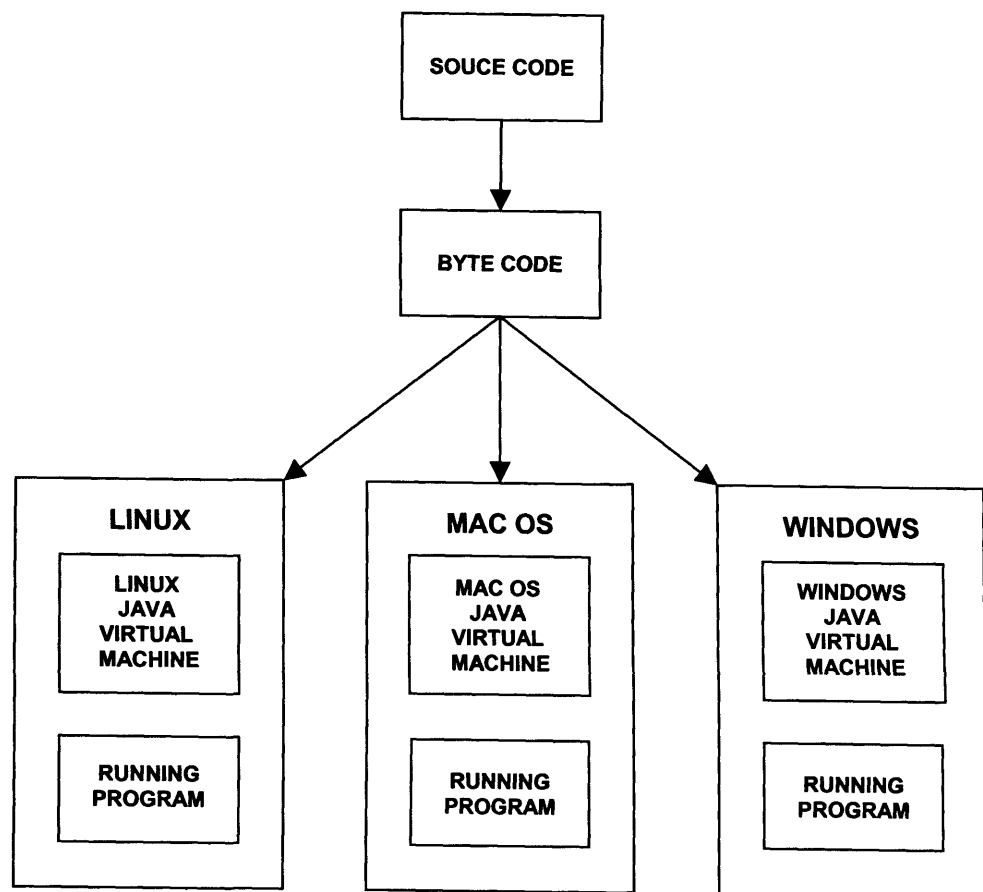
**Table E.1:** A survey of the metrics most commonly used for landscape studies. Shape measurements other than Fractal Dimension, Diversity or Perimeter/Area are recorded under SHAPE.

## Appendix F: The Principles of Java

Various programming languages are suitable for programming an individual-based Spatially Explicit population Model (SEPM), but if the model is to be widely used it must run on as many platforms as possible. Developed by Sun Microsystems, Java is a interpreted, object oriented programming language (Wright 1998) whose portability exactly matches the portability requirements for a SEPM.

Rather than the more usual method of compiling source code to operating system specific machine code, a Java program is produced by compiling the source code to bytecode. An interpreter, known as a Java Virtual Machine (JVM), is then required to run the bytecode. JVMs are platform specific and are available for many operating systems, such as Linux, Macintosh OS, Solaris and the various flavours of Windows, with the result that the program can be written once and run on many machines without recompilation.

Figure F.1 gives a graphical description of the JVM paradigm. It is this portability that gives Java its advantage over other programming languages (Linden 1999). The other major advantage of Java is that the development system and JVMs are (currently) free and providing third-party libraries are avoided, any distributed programs are also royalty free.



**Figure F.1:** The *write once run many* advantage of the Java programming language

## Appendix G: Program Structure

This appendix presents details of the population lattices and the habitat and quality file formats used with PatchMapper:

G.1 Population lattice bit-fields

G.2 Habitat and quality file formats



## Appendix G.1: Population Lattice Bit-Fields

### G.1.1 Introduction

This Appendix presents the use of the bit-fields in the population lattice (Section 3.3) for modelling the nuthatch (*Sitta europaea*), the white-footed mouse (*Peromyscus leucopus*) and the black hairstreak (*Satyrium pruni*). The lattice is coded as a two-dimensional array and holds a combination of species-specific multi-bit data elements and single-bit flags. The data elements are accessed via shift left/right commands. The flags are accessed via Boolean algebraic AND/OR commands. The specific functions of the lattice bit-fields are detailed in the following Sections and Tables.

### G.1.2 The Nuthatch

Each nuthatch territory has one main cell and a number of territory cells, depending on the territory size (Section 4.2.6). The main cell uses one plane of the lattice and contains details of the occupants (Table G.1.1). The territory cell/s use both planes of the lattice and point to the location of the associated main cell (Tables G.1.2 and G.1.3).

### G.1.3 The White-Footed Mouse

Each white-footed mouse territory has one main cell and a number of territory cells, depending on the territory size (Section 4.4.3). The main cell uses one plane of the lattice and contains details of the occupants (Table G.1.4). The territory cell/s use both planes of the lattice and point to the location of the associated main cell (Tables G.1.5 and G.1.6).

### G.1.4 The Black Hairstreak

The black hairstreak model uses both planes of the lattice, which are used to store details of the occupants and the age of the cell's habitat (Tables G.1.7 and G.1.8).

Bit number	31-28	27	26	25	24-12	11	10	9-5	4-0
Function	Unused	Occupied Flag 0 = empty 1 = occupied	Nuthatch Flag 0 = not a nuthatch 1 = nuthatch	Territory Flag 0 = main cell 1 = territory cell	Unused	Pair Flag 0 = single 1 = pair	Gender Flag 0 = male 1 = female	Male Age	Female Age
Comments		Territory occupied by a pair or a single bird. Used to test for a vacancy.	Cell occupied by a nuthatch. For multi-species modelling.	Cell type (main or territory)		Signifies occupancy by a pair or a single bird. Used when testing the gender of the occupant.	The gender of a single occupant. Only used to signify the gender of a single occupant.	Age of male occupant	Age of female occupant

**Table G.1.1:** Functions of the plane 0 population lattice main-cell bit-fields when modelling the nuthatch.

Bit number	31-28	27	26	25	24-15	14-5	4-0
Function	Unused	Occupied Flag 0 = empty 1 = occupied	Nuthatch Flag 0 = not a nuthatch 1 = nuthatch	Territory Flag 0 = main cell 1 = territory cell	Unused	Main Cell Row	Unused
Comments		Territory occupied by a pair or a single bird. Used to test for a vacancy.	Cell occupied by another species. For multi-species modelling.	Cell type (main or territory)		Row location of the associated main cell	

**Table G.1.2:** Functions of the plane 0 population lattice territory-cell bit-fields when modelling the nuthatch.

Bit number	31-10	9-0
Function	Unused	Main Cell Column
Comments		Column location of the associated main cell

**Table G.1.3:** Functions of the plane 1 population lattice territory-cell bit-fields when modelling the nuthatch.

Bit number	25	24-21	20-17	16-14	13	12	11-6	5-0
Function	Territory Flag 0 = main cell 1 = territory cell	Unused	Young	Unused	Pair Flag 0 = single 1 = pair	Gender Flag 0 = male 1 = female	Male Age	Female Age
Comments	Cell type (main or territory)		Records the number of young produced by the pair occupying the cell		Signifies occupancy by a pair or a single mouse. Used when testing the gender of the occupant.	The gender of a single occupant. Only used to signify the gender of a single occupant.	Age of male occupant	Age of female occupant

Bit number	31-30	29	28	27	26
Function	Unused	Young Flag 0 = no young 1 = got young	White-footed Mouse Flag 0 = not a WFM 1 = WFM	Occupied Flag 0 = empty 1 = occupied	Unused
Comments		Signifies whether the pair have produced young.	Cell occupied by a white-footed mouse. For multi-species modelling.	Territory occupied by a pair or a single bird. Used to test for a vacancy.	

Table G.1.4: Functions of the plane 0 population lattice main-cell bit-fields when modelling the white-footed mouse.

Bit number	31	30	29-26	25	24-10	9-0
Function	Unused	Juvenile Flag 0 = no juveniles 1 = juvenile	Unused	Territory Flag 0 = main cell 1 = territory cell	Unused	Main Cell Row
Comments		Indicates that the territory cell is occupied by a juvenile		Cell type (main or territory)		Row location of the associated main cell

Table G.1.5: Functions of the plane 0 population lattice territory-cell bit-fields when modelling the white-footed mouse.

Bit number	31-15	14-5	4-0
Function	Unused	Main Cell Column	Unused
Comments		Column location of the associated main cell	

Table G.1.6: Functions of the plane 1 population lattice territory-cell bit-fields when modelling the white-footed mouse.

Bit number	31-28	27	26-21	20	19-15	14-0
Function	Unused	Occupied Flag 0 = empty 1 = occupied	Unused	Black hairstreak Flag 0 = not a black hairstreak 1 = black hairstreak	Unused	Egg Counter
Comments		Cell occupied by one or more individuals. Used to test for a vacancy.		Cell occupied by a black hairstreak. Used for multi-species modelling.		Keeps track of the number of eggs in the cell. Used for density control.

**Table G.1.7:** Functions of the plane 0 population lattice cell bit-fields when modelling the black hairstreak.

Bit number	31-15	14-6	5-0
Function	Unused	Adult Counter	Habitat Age
Comments		Records the number of adults occupying the cell	Records the age of the cell's habitat

**Table G.1.8:** Functions of the plane 1 population lattice cell bit-fields when modelling the black hairstreak.

## Appendix G.2: Habitat and Quality File Formats

### G.2.1 Introduction

The imported habitat and quality landscapes can be generated from a number of sources, such as a GIS or user-drawn via a graphics package. The habitat and quality landscape file formats are presented in the following Sections.

### G.2.2 Habitat Landscape File Format

The habitat landscape is modelled in binary form (Section 3.3), with habitat represented by black cells and matrix by white cells. Files must be in 24-bit bitmap format, with a '.bmp' file extension. Table G.2.1 shows the RGB codes for the two states. When loaded into PatchMapper, the black (habitat) cells are displayed in green and the white (matrix) cells displayed in buff (Figure 3.4).

Type	Colour	R	G	B
Habitat	Black	255	255	255
Matrix	White	0	0	0

**Table G.2.1:** The RGB codes used to represent habitat and matrix in the imported landscape maps.

### G.2.3 Quality Landscape File Format

The quality landscape models quality using four states (Section 3.3), labelled Q1, Q2, Q3 and Q4 on the appropriate user-screens (Appendix I). The use of the quality option depends on the species being modelled, but could, for example, represent territory size, with the user selecting the size in cells, to suit habitat quality levels within the modelled study area (Section 4.2.6). The different quality levels (Q1 – Q4) are modelled as different coloured cells, using the RGB codes given in Table G.2.2. Files must be in 24-bit bitmap format, with a '.bmp' file extension.

Level	Colour	R	G	B
Q1	Yellow	255	255	0
Q2	Light orange	255	192	0
Q3	Dark orange	255	128	0
Q4	Red	255	0	0

**Table G.2.2:** the RGB codes used to represent the four quality levels in the imported quality maps.



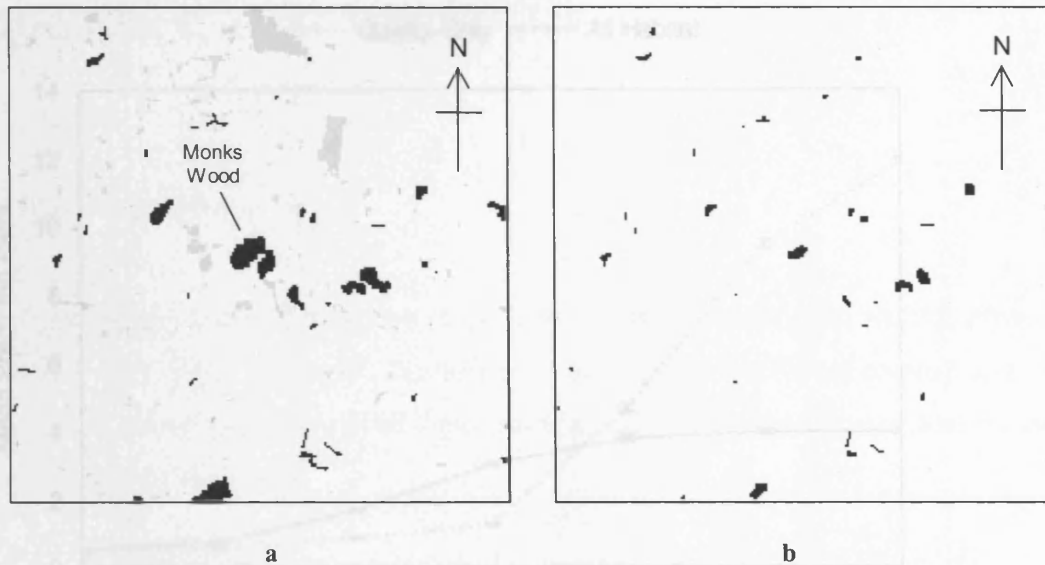
## Appendix H: Habitat and Quality Modelling

### H.1 Introduction

Small patches may be used as staging posts or stepping-stones between territories (Thomas and Harrison 1992; Fischer and Lindenmayer 2002). This suggests that dispersal flow will be affected both by target and non-target habitat patches and as a consequence, all useable habitat and not just potential breeding habitat should be included when modelling dispersal. An investigation into the usefulness of modelling with breeding quality and non-breeding quality habitat is presented in this Appendix.

### H.2 Methods

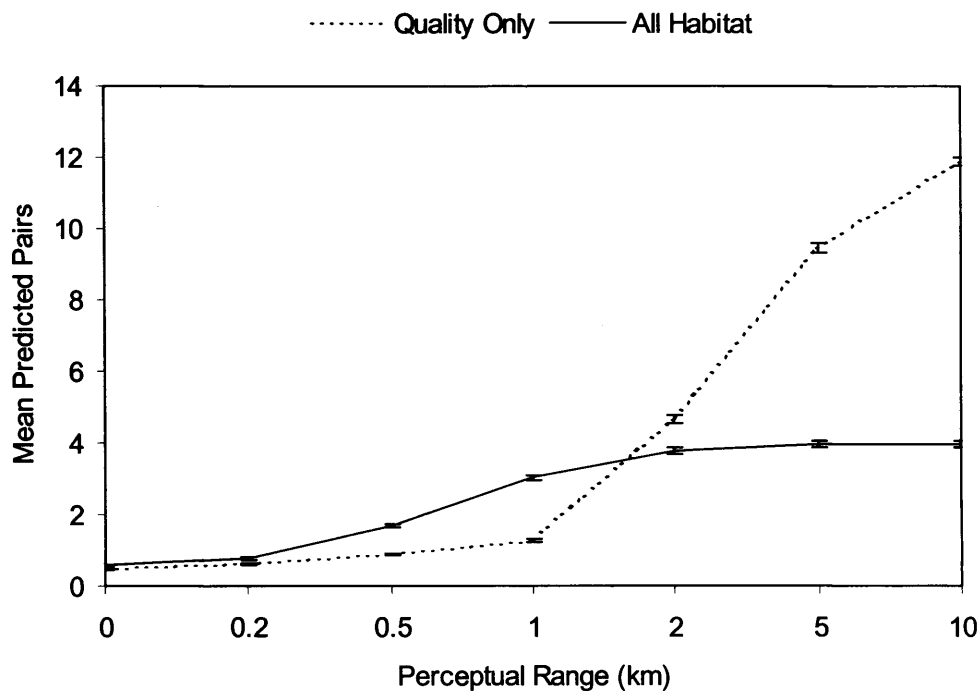
Using PatchMapper's two-map method of modelling habitat structure and habitat quality (Section 3.3), the first test used the landscape containing all habitat patches (Figure H.1a) as the habitat landscape and the identified good quality habitat areas (Figure H.1b) as the quality landscape. The second test used the identified good quality areas (Figure H.1b) for both the structural and quality landscapes. These tests represent two possible choices of modelling, one using all habitat (suitable and unsuitable) and the other using only the identified good quality habitat. Both tests recorded the mean population size in Monks Wood, for an annual immigration rate of 30 birds per annum into the study area, using a perceptual range of 0 - 10 km and a 90-degree field-of-view. This rate was chosen to ensure that any differences between tests would be detectable. Each test was run for 10,000 yearly cycles.



**Figure H.1:** The habitat (Figure H.1a) and quality (Figure H.1b) centralised landscapes used with PatchMapper for the initial study tests. The landscapes are modelled using a 200 x 200 cell grid, with Monks Wood positioned at the centre, representing a 20 x 20 km landscape (1 cell = 1 ha). The structural landscape (Figure H.1a) is a binary representation of the landscape, comprising woods (potential habitat) and matrix. For illustration, woods containing suitable habitat are shown in black, with all other woods shaded light grey. The quality landscape (Figure H.1b) represents the areas of habitat of sufficient quality to contain nuthatch territories. The 'good' quality category (Table 4.2) was used, resulting in a territory size of two cells. Data extracted from survey results by Bellamy et al. (1998).

### H.3 Results

Both habitat modelling tests revealed a general rise in predicted population size in line with perceptual range (Figure H.2). Both options resulted in similar predictions up to a perceptual range of approximately 200 m. Modelling the landscape with all potentially suitable habitat resulted in the predicted number of pairs in Monks Wood levelling off at a threshold of perceptual range of approximately 2 km. The landscape using only good quality woods showed a similar pattern. There was little increase in populations with increase in perceptual range up to 1 km, then a more rapid increase in population with increasing perceptual range. At the presumed 2 km nuthatch perceptual range (Section 4.2.4.4), both options gave similar predictions.



**Figure H.2:** Mean predicted nuthatch pairs in Monks Wood as a function of the two different habitat patch modelling methods, based on the ‘centralised’ landscape (Figure H.1). The different configurations are described in the text. The error bars give 95% confidence intervals.

## H.4 Discussion

Most grid-based SEPMs that model dispersal between habitat patches were found to use only two landscape elements: habitat and non-habitat (Section 2.3.3). The inclusion of habitat quality is a useful element of PatchMapper, allowing a more realistic modelling of target and non-target habitat within a landscape. When using the presumed nuthatch perceptual range of 2 km (Section 4.2.4.4), the results of these tests (Figure H.2) gave very similar predicted population sizes in Monks Wood for both habitat modelling options. Taken at face value this could lead to the conclusion that only target habitat needs to be modelled. An examination of patterns of dispersal flow paths (Section 5.4.3.1; Appendix B.4) showed that both target and non-target habitat patches are visited during dispersal, pointing to the importance of including all potentially suitable habitat in the model and not just the good quality breeding habitat.

# Appendix I: User Guide

## I.1 Introduction

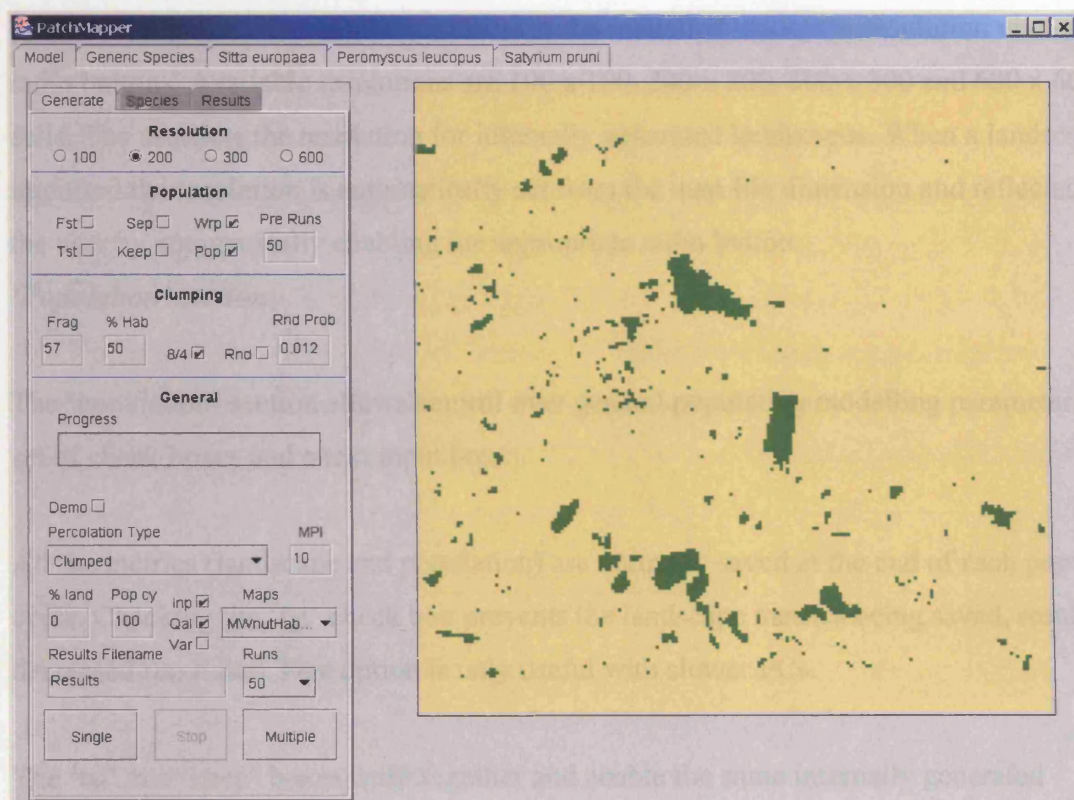
This Appendix presents a description of the user-accessible screens and controls provided as the user interface of the model. During model development, different controls and options were added and although all the controls are described, not all were used for the tests described in this thesis.

## I.2 'Model' Screen

The 'model' screen is used to control the simulation itself and for displaying the landscapes and the simulation results (Figure I.1). The screen is divided in three sub-screens: 'generate', 'species' and 'results'. Each of the sub-screens has its own set of controls, which are described in the following sub-sections.

The sub-screens are positioned to the left of the model screen. A panel to the right of the screen is used to display the landscapes and the simulation results, such as the position of individuals and dispersal trails, in real-time (computer). Figure 3.4 provides an example of the positions of nuthatches in a modelled landscape.

### I.2.3 'Generate' Sub-Screen



**Figure I.1:** The 'generate' sub-screen showing a 200 x 200 cell imported landscape.

The 'generate' sub-screen enables the user to exercise control over the general simulation parameters, including starting (and stopping) the simulation (Figure I.1). This screen is divided into four sections: 'resolution', 'population', 'clumping' and 'general'.

Un-checking the 'pop' box enables a test to be run without a population. Examples uses for this option include looking at an imported map, or investigating landscape dynamics.

The 'wrp' box is used in conjunction with the generic species. Checking this box ensures that individuals cannot leave the landscape. Any that try to move beyond the landscape boundaries reappear on the opposite side of the landscape. If this box is unchecked then individuals can leave the landscape (absorptive boundaries). This control has no effect with the specific species, which have their own wrapping controls.

*'Resolution' section*

The 'resolution' section allows control over the modelled landscape resolution via four radio buttons. Available resolutions are 100 x 100, 200 x 200, 300 x 300 and 600 x 600 cells. The user sets the resolution for internally generated landscapes. When a landscape is imported the resolution is automatically set from the map file dimension and reflected to the user by automatically enabling the appropriate radio button.

*'Population' section*

The 'population' section allows control over general population modelling parameters via a set of check boxes and a text input box.

All the metrics (landscape and population) are normally saved at the end of each population cycle. Checking the 'fst' check box prevents the landscape metrics being saved, resulting in decreased run times. This option is only useful with slower PCs.

The 'tst' and 'keep' boxes work together and enable the same internally generated landscape to be used for a set of tests. This is accomplished by checking both the 'tst' and 'keep' boxes and creating an internally generated map using the 'clumped' option. A copy of the displayed landscape will then be stored. If the landscape is suitable, un-check the 'tst' box and leave the 'keep' box checked. The displayed landscape will then be used for all subsequent tests, as long as the 'clumped' option is selected. (Internally generated map options are detailed later in this section.)

Un-checking the 'pop' box enables a test is to be run without a population. Example uses for this option include looking at an imported map, or investigating landscape dynamics.

The 'wrp' box is used in conjunction with the generic species. Checking this box ensures that individuals cannot leave the landscape. Any that try to move beyond the landscape boundaries reappear on the opposite side of the landscape. If this box is unchecked then individuals can leave the landscape (absorptive boundaries). This control has no effect with the specific species, which have their own wrapping controls.

The population metrics are recorded over the whole landscape. The user can extract population metrics for a single patch or a group of patches within the landscape by drawing two boxes on the landscape. The principles behind and example uses of the two boxes, along with details of the 'box' metrics are given in Section 3.8.4. To draw the boxes, check the 'sep' box. Display a map (internal or imported), then position the mouse in an appropriate position on the map and select the upper left and lower right corner positions of the first box using the left-hand mouse button. On selection of the lower right hand position the first box is drawn. Reposition the mouse and draw a second box in the same fashion. The first box is shown in black and the second in white. The habitat area (in cells) contained within each box is displayed at the bottom of the screen underneath the map display. Pressing the right-hand mouse button erases each box in turn, the first press erasing the second box and the second press the first box. This allows the boxes to be repositioned as required.

To allow a population time to reach equilibrium, a number of population cycles are undertaken during which no metrics are recorded. Following these 'pre runs', the main population run takes place. Entering a value in the 'pre run' text input box sets the required number of 'pre runs'.

### *'Clumping' section*

The 'clumping' section allows the user to control the structure of the internally generated neutral landscapes. The generation algorithm is described in Section 3.6.2.

The 'frag' input box governs how fragmented the landscape is, by giving a rough control over the number of habitat patches. The '% hab' input box controls the exact number of habitat cells. When the landscape is created, the total number of habitat cells are counted and the landscape adjusted, by adding or removing habitat cells, until the required total is met. The '8/4' input controls how patches are formed. Selecting the box means that all

eight neighbouring cells are changed, causing larger patches to be generated. De-selecting the box means that only cells in the cardinal directions are affected, generating more, but smaller patches. This option offers a fine control over the fragmentation process.

The 'rnd' and 'rnd prob' controls are used in conjunction with the internal landscape transformation algorithm (Section 3.6.5.1). The basic transformation algorithm 'eats' into the edges of habitat patches, changing them to matrix cells. Checking the 'rnd' box enables a randomising option whereby, in accordance with the probability entered in the 'rnd prob' input box, habitat cells are selected at random and changed to matrix cells. This changes the nature of the transformation from a smooth removal of habitat to a totally random removal of habitat, governed by the entered 'rnd' probability.

#### *'General' section*

The 'general' section contains the main simulation run controls. Pressing the 'single' button causes the simulation to run for a user-selectable number of years, controlled by the number of pre-runs ('pre run' input box in the 'population' section) and the number of years entered in the 'pop cy' input box. Population metrics are recorded for each year, over the number of years entered in the 'pop cy' box. At the end of the simulation cycle the population metrics are saved under the filename prefix entered in the 'results filename' input box. Pressing the 'multiple' box causes the simulation cycle to be repeated 50, 100 or 250 times according to the value selected in the 'runs' drop-down list box. The 'pre run' and 'pop cy' inputs function as per the single run, with results being saved at the end of each simulation cycle. The simulation can be halted at any time by pressing the 'stop' button.

Landscapes can be imported by checking the 'inp' box and selecting a suitable map from the 'maps' drop-down list box. Checking the 'qal' box imports the associated quality map. The 'var' control is used for modelling habitat management schemes where different landscapes are loaded at set years (Section 3.6.5.2). Example uses of this feature are given in Chapters 4 and 5.



De-selecting the 'inp' and 'qal' boxes enables the internal landscape generator. The type of landscape to be generated is selection from the 'percolation type' drop-down list box. The first landscape type is the 'clumped' landscape, which generated neutral landscapes as detailed in the 'clumping section'. The second option is 'uniform random', which selects habitat cells at random and changes them matrix cells, transforming the landscape from all habitat to all matrix. Other landscape transformation algorithms are provided, but these are not described here.

A dynamic transformation algorithm is available, which converts the habitat cells to matrix cells, which is enabled by entering a value greater than 0 in the '% land' input box. The value denotes the percentage of cells (of the total possible) which are changed from habitat to matrix at the end of each 'year'. The changes in the landscapes at 5% intervals can be viewed via the 'map' controls in the 'results' sub-screen. Note that the '% land' results in a progressive uniform removal of habitat.

Feedback of the simulation progress is provided via the 'progress' bar display. Checking the 'demo' box causes a 'speed' bar to be displayed. This enables the simulation to be slowed down for demonstration purposes.

The last control is the 'mpi' input box. This is used to enter the mean proximity index (MPI) threshold in number of cells.

## I.2.2 'Species' Sub-Screen

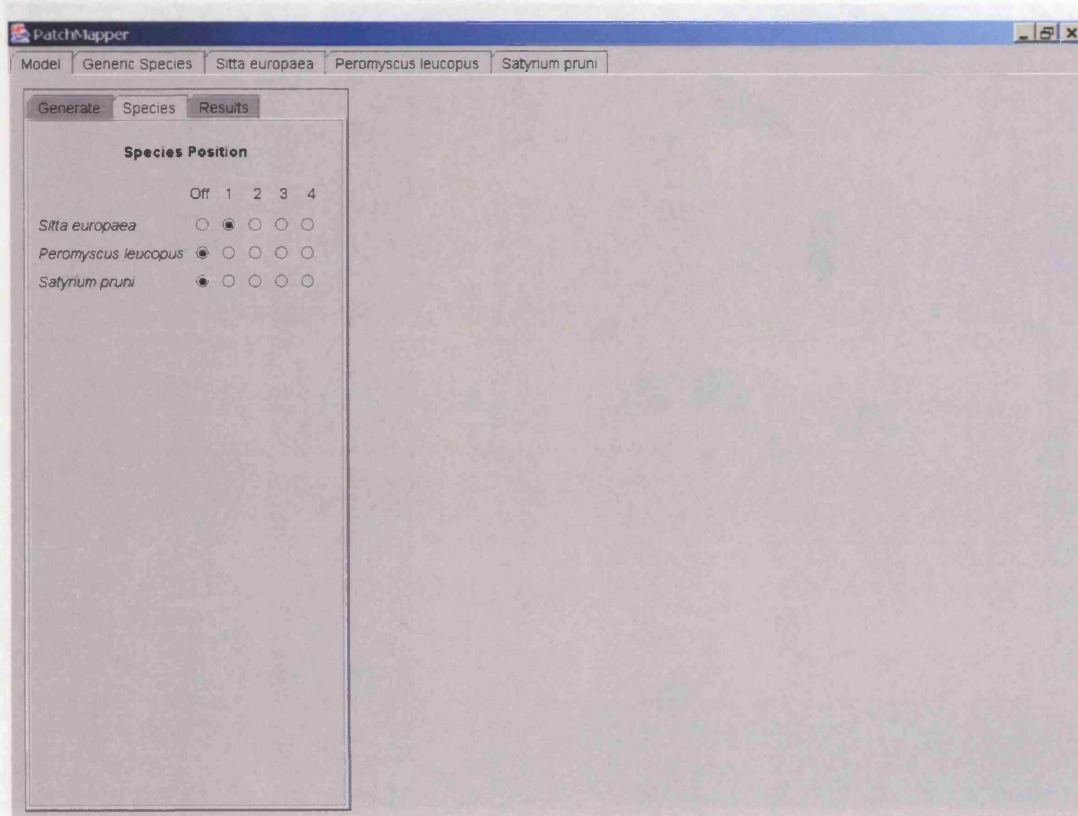


Figure I.2: The 'species' sub-screen.

The 'species' sub-screen enables the user to select one of the specific species (Figure I.2). Species are selected by 'pressing' one of the radio buttons in position 1 to 4. The example screen-shot shows that the nuthatch (*Sitta europaea*) has been selected in position 1.

The species positioning allows simultaneous modelling of up to four species. A priority order is given to the species, with position 1 given the highest priority and position 4 the lowest priority. One example use for this is to allow the modelling of competition for habitat type. Currently only one specific species can be modelled at a time, but one specific species can be modelled with up to three generic species. Alternatively, up to four generic species can be modelled simultaneously, in which case all the specific species should be in the 'off' position. See Section I.3 for details on the generic species modelling screen and sections Q.4, Q.5 and Q.6 for the specific species screens.

### 1.2.3 'Results' Sub-Screen

The 'W/O' check-box allows the transformed landscapes to be displayed in monochrome, for use in cases where colour diagrams are not possible.

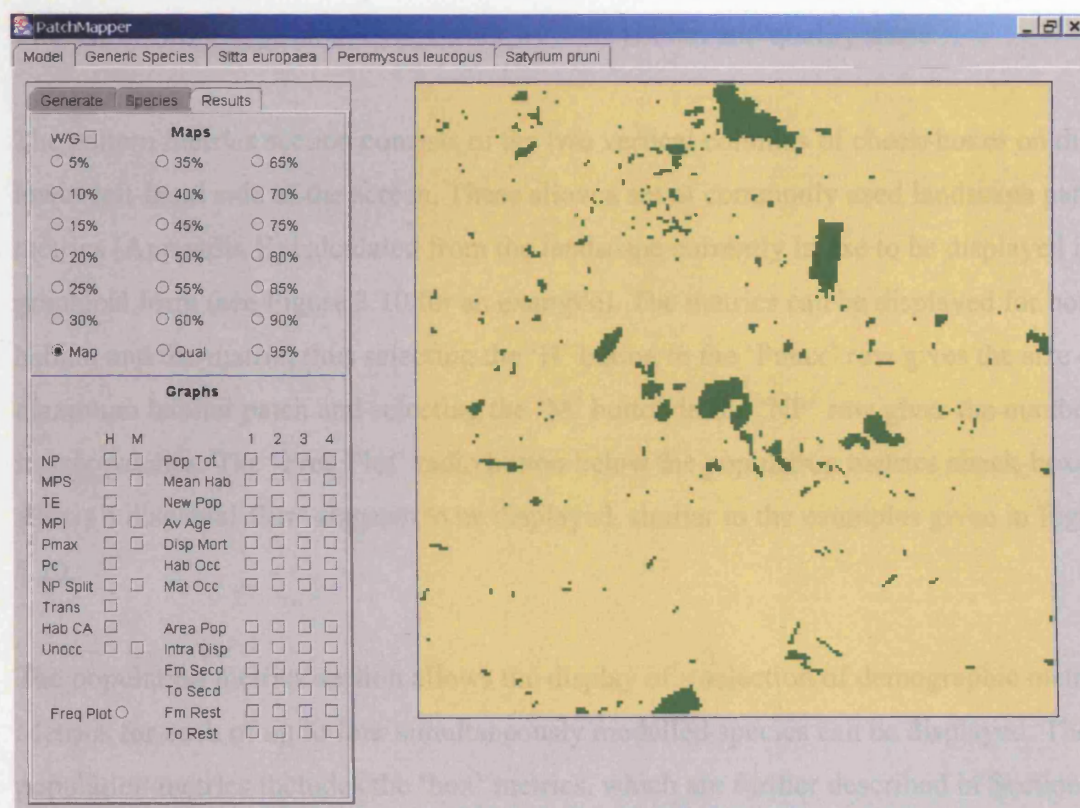


Figure I.3: The 'results' sub-screen.

The 'results' sub-screen enables the user to display the habitat and quality maps and a selection of metrics (Figure I.3). The controls are on the left-hand side of the screen, while the results are displayed in a panel on the right-hand side of the screen. The 'results' sub-screen is split into three sections: maps, pattern-based metrics and population-based metrics. The map section allows the user to show the imported habitat and quality maps via two radio buttons labelled 'Map' and 'Qual'. The example screen-shot (Figure I.3) shows an example habitat landscape (habitat patches in green, matrix in buff). Quality maps are colour-coded as detailed in Appendix G.2. Figure 5.3b shows an example quality landscape. The other radio buttons in the map section allow the display of a transformed landscape in 5% intervals. This option is used in conjunction with the dynamic landscape

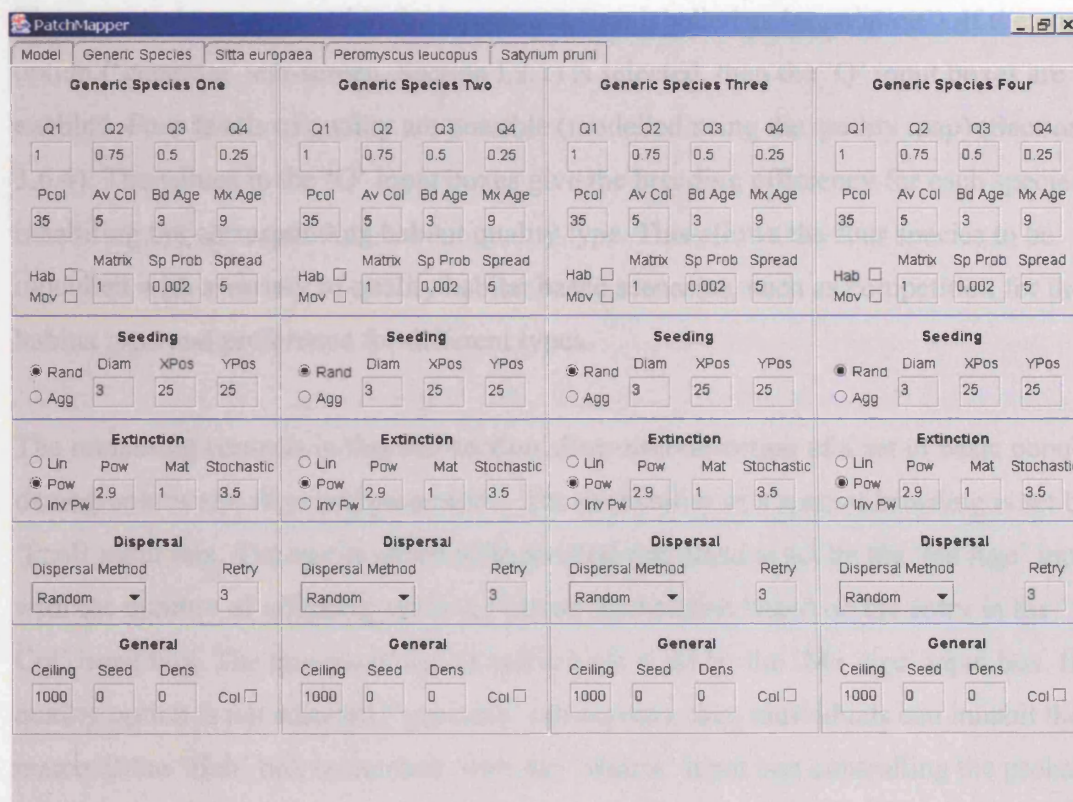
option (detailed in Section I.2.1). The 'W/G' check-box allows the transformed landscapes to be displayed in monochrome, for use in cases where colour diagrams are not possible. The monochrome option does not work with the habitat and quality maps.

The pattern metrics section consists of the two vertical columns of check-boxes on the lower left-hand side of the screen. These allow a set of commonly used landscape pattern metrics (Appendix E) calculated from the landscape currently in use to be displayed in graphical form (see Figure 3.10 for an example). The metrics can be displayed for both the habitat and the matrix, thus selecting the 'H' button in the 'Pmax' row gives the size of the maximum habitat patch and selecting the 'M' button in the 'NP' row gives the number of matrix patches. The 'Freq Plot' radio button below the population metrics check-boxes allows a dispersal-flow diagram to be displayed, similar to the examples given in Figure 5.20.

The population metrics section allows the display of a selection of demographic metrics. Metrics for each of up to four simultaneously modelled species can be displayed. The population metrics includes the 'box' metrics, which are further described in Section 3.8.4.



### I.3 'Generic Species' Screen



The screenshot shows the 'Generic Species' screen in PatchMapper. The window title is 'PatchMapper'. At the top, there are tabs for 'Model', 'Generic Species', 'Sitta europaea', 'Peromyscus leucopus', and 'Satyrus pruni'. The main area is divided into four columns, each for a generic species. Each column contains several sections of input fields:

- Generic Species One:**
  - Q1: 1, Q2: 0.75, Q3: 0.5, Q4: 0.25
  - Pcol: 35, Av Col: 5, Bd Age: 3, Mx Age: 9
  - Matrix: 1, Sp Prob: 0.002, Spread: 5
  - Seeding: ☒ Rand, Diam: 3, XPos: 25, YPos: 25
  - Extinction: ☐ Lin, ☒ Pow (2.9), ☐ Mat (1), ☐ Stochastic (3.5)
  - Dispersal: Dispersal Method: Random, Retry: 3
  - General: Ceiling: 1000, Seed: 0, Dens: 0, Col: ☐
- Generic Species Two:** (Identical to Generic Species One)
- Generic Species Three:** (Identical to Generic Species One)
- Generic Species Four:** (Identical to Generic Species One)

Figure I.4: The 'generic species' screen

The 'generic species' screen allows the user to set parameters for the four generic species (Figure I.4). The screen is split into four columns, one for each species. Each species screen is split into a set of population, seeding, extinction, dispersal and general controls.

*'Population' section*

These controls are grouped in the top section (not labelled as 'population'). If the quality option ('generate' sub-screen, Section I.2.1) is selected, then the 'Q' input boxes are enabled. Four levels of quality are possible (modelled using the quality map) (Section 3.6.4). The values in the 'Q' input boxes give the breeding efficiency for each species inhabiting the corresponding habitat quality type. This allows the four species to be modelled with a variety of quality habitat based scenarios, such as competition for the same habitat type and preference for different types.

The remaining controls in this sub-section allow user-selection of a set of basic population demographics and dispersal parameters. The probability of a species breeding is set by the 'Pcol' input box. The age at which an individual can breed is set by the 'Bd Age' input box, with the number of offspring set by a Poisson distribution based on the entry in the 'Av Col' input box. The maximum age of individuals is set by the 'Mx Age' input box. If the quality option is not selected ('generate' sub-screen), then individuals can inhabit the matrix if the 'Hab' box is checked, with the 'Matrix' input box controlling the probability of breeding in the matrix taking place. If the 'Mov' box is checked, then individuals can move around the matrix. The maximum distance an individual can disperse is set by the 'Spread' input box, with a probability that this distance can be exceeded controlled by the 'Sp Prob' box, allowing occasional long distance dispersal.

*'Seeding' section*

The seeding controls govern how the initial population is seeded. The 'Rand' option places individuals at random on the habitat. The 'Agg' option enables seeding to be concentrated in an circular area of habitat whose diameter is set by the 'Diam' input box and centre position by the 'XPos' and 'YPos' input boxes.

*'Extinction' section*

Two causes of mortality are modelled: overwintering and dispersal. Overwintering mortality is stochastic, based on the probability entered in the 'Stochastic' input box. Mortality is increased for individuals inhabiting the matrix by adding the factor entered in the 'Mat' input box to the stochastic probability. Dispersal mortality is modelled as an age-based probability, using a choice of three functions: linear, power and inverse power. The linear function, selected with the 'Lin' button, increases mortality linearly from 0 up to a probability of one at the set maximum age ('Mx age' input box). The power function, selected via the 'Pow' button uses a 'bathtub' probability function, with the lower and upper 'curves' shaped by the exponential values entered in the 'Pow' input box. The inverse power function, selected via the 'Inv Pw' button, uses an inverse power function, based on the exponential value entered in the 'Pow' input box.

*'Dispersal' section*

Two types of dispersal are possible: 'random' and 'nearest', selected via the 'Dispersal Method' drop-down list. The 'random' dispersal algorithm moves the individual to a point selected at random within a radius of the spread distance ('spread' input box) from the individual's location. The 'nearest' dispersal algorithm moves the individual in one of eight randomly selected directions (cardinal and quadrantal), up to the spread distance ('spread' input box). A dispersal mortality probability is applied at each dispersal step, as detailed in the 'Extinctions' section. Individuals are given a number of chances to find a suitable vacancy, as determined by the entry in the 'Retry' input box.

*'General' section*

The maximum number of individuals inhabiting the landscape is controllable via the 'Ceiling' input box. To prevent an abrupt ceiling, the overwintering stochastic probability (see the 'Population' section) is increased as the population exceeds the ceiling limit. The number of seeded individuals is set via the 'Seed' input box. A breeding density factor, entered via the 'Dens' input box, increases the litter size if all adjacent cells in the cardinal directions are unoccupied.

In order to distinguish the different species on the real-time (computer) display, individuals of each generic species are given a different colour. Species one is coloured red, species two is white, species three is blue and species four is green. The 'Col' box shows individuals in age-related shades of their default colour.



## 1.4 'Sitta europaea' (nuthatch) Screen

**Territory (ha)**

Q1	Q2	Q3	Q4	Qual	Explore
2	6	10	0	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>

**Breeding**

Var	Success	Min	Max	Median	Min	Max	M/F
<input checked="" type="checkbox"/>	75	4	6	7	70	90	0.5

**Seeding**

<input checked="" type="radio"/> Rand	Diam	XPos	YPos	Pairs
<input type="radio"/> Agg	3	25	25	350

**Survival**

Var	Winter	Adult	Juve	Low	High	Summer	Adult	Low	High
<input checked="" type="checkbox"/>		54	42	40	60		75	81	93

**Dispersal**

Dispersal Mortality	Immigration	No Wrap
Matrix	Allow	<input checked="" type="checkbox"/>
0.995	15	
Habitat	Direction	
0.999	Random	
	Var	
	0	20
Pcep Range/Field of View	Search Depth	
20	Winter	
0 <input type="radio"/> 90 <input checked="" type="radio"/> 180 <input type="radio"/> Full	Summer	
Trails	50	
100	40	

Figure I.5: The 'nuthatch' screen

The 'nuthatch' screen is divided into five sections, allowing user control over territorial, breeding, seeding, survival and dispersal parameters (Figure I.5). The controls are initialised to a set of default demographic parameters taken from the literature, as detailed in Section 4.2.2.

### 'Territory' section

Nuthatch territory size is a function of habitat quality (Section 4.2.6). To model this, territory sizes in cells, for the four possible habitat quality levels are entered in the 'Q' input boxes. For the scale of one cell to one hectare chosen for the nuthatch model comparison

and sensitivity analysis tests in this thesis (Chapters 4 and 5), the entry in the 'Q' boxes gives the nuthatch territory size in hectares. Checking the 'Qual' box enables this feature (the quality option also has to be selected from the 'Generate' screen (Section I.2.1)). If the 'Qual' box is un-checked, then all habitat is assumed to be suitable, with territory size governed by the entry in the 'Q1' input box. This is irrespective of whether the quality option is selected ('Generate' screen (Section I.2.1)).

Un-checking the 'Explore' box limits the total number of nuthatch territories in the landscape to the number established when seeding takes place. Checking the 'Explore' box enables the more realistic situation of allowing territories to be established by dispersing individuals in addition to those established during the seeding process.

### *'Breeding' section*

The controls in this section govern breeding success and litter size. Two sets of values are available: stochastic and deterministic. Checking the 'Var' box enables the stochastic method. In this case, breeding success and litter size are taken from a value chosen at random, using a uniform distribution, lying between the values entered in the 'Min' and 'Max' input boxes. If the 'Var' box is un-checked, then the deterministic method is enabled, whereby the percentage of successful breeding pairs and the litter size are governed by the values entered in the 'Success' and 'Median' input boxes respectively. The ratio of male to female nestlings is governed by the entry in the 'M/F' input box. This is a deterministic input, which is applied to all litters during the simulation.

### *'Seeding' section*

The seeding controls govern how the initial population is seeded. The 'Rand' option places individuals at random on the habitat. The 'Agg' option enables seeding to be concentrated in a circular area of habitat whose diameter is set by the 'Diam' input box and centre position by the 'XPos' and 'YPos' input boxes. The number of seeded pairs is set via the 'Pairs' input box.

*'Survival' section*

The controls in this section govern winter and summer survival rates. Two types of rates are available: stochastic and deterministic. Checking the 'Var' box enables the stochastic method. In this case, winter and summer survival percentage rates are taken from a value chosen at random, using a uniform distribution, lying between the values entered in the 'Low' and 'High' input boxes. If the 'Var' box is un-checked, the deterministic method is enabled, whereby survival rates are governed by the values entered in the 'Adult' and 'Juve' input boxes.

*'Dispersal' section*

This section provides the user with control over the dispersal parameters. The per-step probability of dispersal mortality in the habit and matrix is set by the values in the 'Habitat' and 'Matrix' input boxes.

Immigration into the study area is possible, enabled by checking the 'Allow' box. Immigration direction is selectable via the 'Direction' drop-down list box. Available directions are random (from any direction) and one of the cardinal and quadrantal directions. If the 'Var' box is un-checked, immigration rate is fixed to the level (in immigrating individuals per year) entered in the input box to the right of the 'Allow' check box. If the 'Var' box is checked, then the annual immigration rate varies in accordance with a uniform distribution, between the values entered in the two input boxes to the right of the 'Var' check box.

Perceptual range is also modelled. The perceptual range itself is set as a number of cells entered in the 'Pcep' input box. Fields of view of straight-ahead, 90 and 180 degrees are selected via the '0', '90' and '180' radio buttons. Checking the 'Full' box enables the full search algorithm, un-checking this box enables the basic search algorithm. Both search algorithms are described in Sections 4.2.4 and 4.2.5 and Appendix B.3.

Un-checking the 'No Wrap' box ensures that individuals cannot leave the landscape. Any that try to move beyond the landscape boundaries reappear on the opposite side of the landscape. If this box is checked then individuals can leave the landscape (absorptive boundaries).

In order to provide some visual feedback on the effect of the structure of the landscape on dispersal patterns, it is possible to display the inter-patch movement tracks of individuals. Counters are provided for each cell, which are incremented each time an individual enters that cell. At the end of each run, the results are saved as a file called 'flow.csv' in the 'PatchMapperStats' directory. The 'flow.csv' file is in the form of an array with the same dimensions as the modelled landscape and can be further processed to produce a dispersal flow diagram (see Figure 5.20, for an example). A dispersal-flow diagram can also be displayed using the 'Freq Plot' radio button ('results' sub-screen). If dispersal trails are to be displayed, then the 'Trails' box should be checked. The number of trails being displayed is given by the value entered in the input box to the right of the 'Trails' check-box. Checking the 'I' box displays the trails of individuals immigrating into the study area, checking the 'C' box displays the trails of dispersers originating from patches within the study landscape. The trails are shown in grey, but checking the 'P' box shows the part of the movement trail which is influenced by the individuals perceptual range in red. This is used to provide visual feedback on the effect of perceptual range and field of view on movement patterns.

The two remaining input boxes labelled 'Winter' and 'Summer' control the intra-patch search depth for pair formation following winter mortality and the summer juvenile dispersal respectively. Figure 4.5 shows an example intra-patch search pattern.

## I.5 'Peromyscus leucopus' (white-footed mouse) Screen

**PatchMapper**

Model Generic Species Sitta europaea **Peromyscus leucopus** Stryum pruni

**Territory (ha)**

Size: 6 Explore ☒

**Breeding**

Min	Max	Low	Mod	High
3	5	.7	.8	.9

**Seeding**

☒ Rand ☐ Agg

Diam	XPos	YPos	Pairs
3	25	25	350

**Survival**

Winter	Nesting	Juvenile	Sub Adt	Adult
25	.75	.9	.93	.96

**Dispersal**

Mortality

Q1	Q2	Q3	Q4	Steps Juvenile	Steps Single
0.99	0.98	0.97	0.96	25	50

Perception: 6 No Wrap ☒

Figure I.6: The 'white-footed mouse' screen

The 'white footed mouse' screen is divided into five sections, allowing user control over territorial, breeding, seeding, survival and dispersal parameters (Figure I.6). The controls are initialised to a set of default demographic parameters taken from the literature, as detailed in Section 4.4.2.

*'Territory' section*

The size of the white footed mouse territories is variable and set by the value entered in the 'Size' input box. Un-checking the 'Explore' box limits the total number of black hairstreak territories in the landscape to the number established when seeding takes place. Checking the 'Explore' box enables the more realistic situation of allowing territories to be established by dispersing individuals in addition to those established during the seeding process.

*'Breeding' section*

The controls in this section govern litter size and breeding success. Litter size is taken from a value chosen at random, using a uniform distribution, lying between the values entered in the 'Min' and 'Max' input boxes. The values entered in the 'Low', 'Mod' and 'High' input boxes are used as the seasonal probability of successful breeding based on week numbers, as detailed in Section 4.4.2.

*'Seeding' section*

The seeding controls govern how the initial population is seeded. The 'Rand' option places individuals at random on the habitat. The 'Agg' option enables seeding to be concentrated in an circular area of habitat whose diameter is set by the 'Diam' input box and centre position by the 'XPos' and 'YPos' input boxes. The number of seeded pairs is set via the 'Pairs' input box.

*'Survival' section*

The values entered in the 'Winter', 'Nestling', 'Juvenile', 'Sub Adt' and 'Adult' input boxes govern the different life-stage survival rates, as detailed in Section 4.4.2.

*'Dispersal' section*

This section provides the user with control over dispersal parameters. Dispersal mortality is modelled with a habitat quality based per-step probability, set for the four possible quality levels by entering values in the 'Q' input boxes.

Perceptual range is also modelled. The perceptual range itself is set as a number of cells entered in the 'Pcep' input box.

To prevent clustering around the natal site, it is possible to limit settlement until a set number of dispersal steps have been undertaken. For juveniles this is controlled via the 'Juvenile' input box and for sub-adult and adult dispersers via the 'Single' input box.

Un-checking the 'No Wrap' box ensures that individuals cannot leave the landscape. Any that try to move beyond the landscape boundaries reappear on the opposite side of the landscape. If this box is checked then individuals can leave the landscape (absorptive boundaries).



## I.6 ‘Satyrium pruni’ (black hairstreak) Screen

**PatchMapper**

Model | Generic Species | Sitta europaea | Peromyscus leucopus | **Satyrium pruni**

**General**

Ceiling ☐ Hab Col ☒  
 Qual ☐ Hab Only ☐ Var Qual ☐ Hab Ageing ☒

**Breeding**

Var ☒  
 Eggs/Fem Min Max Eggs/Step Min Max Dec Age  
 90 80 100 45 40 50 20

**Seeding**

Var Hab Age ☒  
☒ Rand Diam XPos YPos Cells Eggs/Cell Age Pw  
 3 25 25 500 1000 4  
☐ Agg

**Mortality**

Var ☒  
 Egg Low High Pupae Low High  
 35 25 35 80 60 80  
 Instar 1 45 30 60 Instar 2 45 30 60  
 Instar 3 45 30 60 Instar 4 45 30 60

**Dispersal**

Init Disp Mort Prob Immigration Direction  
 5 0.02 0.05 Allow ☐ 50 Random  
 Trails ☐ 100 I ☐ C ☐

**Figure I.7:** The ‘black hairstreak’ screen

The ‘black hairstreak’ screen is divided into five sections, allowing user control over breeding, seeding, mortality, dispersal and general parameters (Figure I.7). The controls are initialised to a set of default demographic parameters taken from the literature, as detailed in Section 4.5.2.

The controls in this section govern the number of eggs laid by each female and the number of eggs laid in each cell. Two sets of values are available: stochastic and deterministic. The ‘General’ section box enables the stochastic method. In this case, the number of eggs laid by each female and the number of eggs laid in each cell are taken from a value chosen at

The black hairstreak model is a combined habitat (blackthorn) and species model (Section 4.5) In conjunction with elements of the ‘breeding’ and ‘seeding’ sections, the ‘general’ section allows the user a certain degree of control over the integration of the two models.



The habitat model includes an ageing algorithm whereby the blackthorn is aged in yearly steps. The blackthorn is unsuitable for colonisation until it is seven years old and becomes unsuitable (dies off) again at a later age, but never becoming older than 50 years. This option is suitable when modelling habitat management schemes and is enabled by checking the 'Hab Ageing' box. Un-checking this box disables the ageing algorithm and in this case, habitat is always suitable for colonisation and never ages. This option is more suited to modelling at the landscape scale. To use the variable habitat option, the 'Var Qual' box must be checked. See Section 4.5 for an example use of this option. To use a combination of habitat and habitat quality for landscape modelling, the 'Qual' box must be checked.

The age at which the habitat starts to die off is governed by the value entered in the 'Dec Age' input box in the 'breeding' section. Habitat dies off in accordance with a power function, whose exponent is set in the 'Age Pw' input box in the 'seeding' section.

It is possible to seed the landscape with habitat aged between 7 to 20 years. This option is enabled by checking the 'Var Hab Age' box in the 'seeding' section. Un-checking this box seeds all habitat with an age of seven years.

Visual feedback of the habitat age is enabled via the 'Hab Col' box. In this case, habitat under seven years old is shown in light green, habitat from 7 to 19 years old is shown in a 'mid' green and habitat 20 years or older is shown in dark green. If this option is not selected, then all habitat is shown in the 'mid' green colour.

### *'Breeding' section*

The controls in this section govern the number of eggs laid by each female and the number of eggs laid in each cell. Two sets of values are available: stochastic and deterministic. Checking the 'Var' box enables the stochastic method. In this case, the number of eggs laid by each female and the number of eggs laid in each cell are taken from a value chosen at

random, using a uniform distribution, lying between the values entered in the 'Min' and 'Max' input boxes. If the 'Var' box is un-checked, then the deterministic method is enabled, whereby the number of eggs laid by each female and the number of eggs laid in each cell are governed by the values entered in the 'Eggs/Fem' and 'Eggs/Step' input boxes respectively. During the simulation run, eggs are laid in different cells until the maximum number of eggs per female is reached.

### *'Seeding' section*

The seeding controls govern how the initial population is seeded. The 'Rand' option places individuals at random on the habitat. The 'Agg' option enables seeding to be concentrated in an circular area of habitat whose diameter is set by the 'Diam' input box and centre position by the 'XPos' and 'YPos' input boxes. The number of cells seeded with eggs is set via the 'Cells' input box and the number of eggs seeded into each cell is set via the 'Eggs/Cell' input box.

It is possible to seed unsuitable as well as suitable habitat by checking the 'Hab Only' box in the 'general' section.

### *'Mortality' section*

The controls in this section govern the various life-cycle mortality rates, entered as percentages. Two types of rates are available: stochastic and deterministic. Checking the 'Var' box enables the stochastic method. In this case, the mortality rates are taken from a value chosen at random, using a uniform distribution, lying between the values entered in the 'Low' and 'High' input boxes. If the 'Var' box is un-checked, the deterministic method is enabled, whereby survival rates are governed by the values entered in the 'Egg', 'Instar' and 'Pupae' input boxes.

*'Dispersal' section*

Black hairstreak dispersal is thought to be limited (Section 4.5.2). Eggs are normally laid in adjacent cells up to the eggs-per-cell value entered in the 'Eggs/Cell' input box in the 'seeding' section. To cater for occasional longer-range dispersal, at each laying step the individual is given a small chance of dispersing. The probability of longer-range dispersal is governed by the value entered in the 'Prob' input box. The value entered in the 'Init Disp' input box sets the number of cells that a dispersing individual moves before egg laying can take place. This forces dispersal (when it takes place) away from the natal cell or patch. Dispersal can also be forced if the eggs laid-per-cell limit is reached ('seeding' section) by checking the 'Ceiling' box in the 'general' section. At each movement step (egg laying or dispersal), a per-step probability of mortality is applied, set by the value entered in the 'Mort' input box.

Immigration into the study area is possible, enabled by checking the 'Allow' box. Immigration direction is selectable via the 'Direction' drop-down list box. Available directions are random (from any direction) and one of the cardinal and quadrantal directions. The immigration rate is fixed to the level (in immigrating individuals per year) entered in the input box to the right of the 'Allow' check box.

To provide some visual feedback on the effect of the structure of the landscape on dispersal patterns, it is possible to display the inter-patch movement paths of individuals, as described in Section I.4. If dispersal trails are to be displayed, then the 'Trails' box should be checked. The number of trails being displayed is given by the value entered in the input box to the right of the 'Trails' check-box. Checking the 'I' box displays the trails of individuals immigrating into the study area, checking the 'C' box displays the trails of dispersers originating from patches within the study landscape. The trails are shown in grey.

## REFERENCES

- Adler R.A. and Neebnerger B. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* 45: 41-75.
- Aleksanyan H. 2000. Viability analysis with habitat-based metapopulation models. *Population Ecology* 42: 43-53.
- Alderman J., McCullin D., Hinsley S., Bellamy P., Fieion P. and Crockett R. 2004. Simulating population viability in fragmented woodland: nuthatch (*Sitta europaea* L.) population survival in a poorly wooded landscape in eastern England. pp. 76-83. *In*: Landscape ecology of trees and forests: Proceedings 12th Annual IALE (UK) Conference. Edited by R. Smothers. Royal Agricultural College, Cirencester, 21<sup>st</sup> - 24<sup>th</sup> June 2004. IALE(UK).
- Anderson G.S. and Dorsetson B.J. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landscape Ecology* 12: 261-271.
- Andersson H.P., Bjorholm E., Carlson P.G., Gundersen G. and Gundersen H. 1998. Visual cues as determinants of perceptual range in root voles *Microtus oeconomus*. *Acta Theriologica* 43: 371-378.
- Andren H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.
- Barnes D.J. and Hopkins T.R. 2003. The impact of programming paradigms on the efficiency of an individual-based simulation model. *Simulation Modelling Practice and Theory* 11: 557-569.
- Bati J. 1995. Acceptance criteria for using individual-based models to make management decisions. *Ecological Applications* 5: 411-420.
- Baskett E. 1999. Controlling spatial structure of forested landscapes: a case study towards landscape management. *Landscape Ecology* 14: 83-97.
- Baudry J. and Taton T. 1993. Changes in landscape patterns and vegetation dynamics in Provence, France. *Landscape and Urban Planning* 24: 153-159.
- Baudry J., Burel P., Avon S., Martin M., Ouan A., Pain G. and Theriault C. 2003. Temporal variability of connectivity in agriculture landscapes: do farming activities help? *Landscape Ecology* 18: 303-314.
- Begon M., Harper J.L. and Townsend C.R. 1996. *Ecology* 3<sup>rd</sup> ed. Blackwell Science, Oxford, UK.

## REFERENCES

- Adler R.A. and Nuernberger B. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* 45: 41-75.
- Akcakaya H. 2000. Viability analyses with habitat-based metapopulation models. *Population Ecology* 42: 45-53.
- Alderman J., McCollin D., Hinsley S., Bellamy P., Picton P. and Crockett R. 2004. Simulating population viability in fragmented woodland: nuthatch (*Sitta europaea* L.) population survival in a poorly wooded landscape in eastern England. pp. 76-83. *In* Landscape ecology of trees and forests: Proceedings 12th Annual IALE(UK) Conference. Edited by R. Smithers. Royal Agricultural College, Cirencester. 21<sup>st</sup> – 24<sup>th</sup> June 2004. IALE(UK).
- Anderson G.S. and Danielson B.J. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landscape Ecology* 12: 261-271.
- Andreassen H.P., Bjornbom E., Carlson R.G., Gunderson G. and Gunderson H. 1998. Visual cues as determinants of perceptual range in root voles *Microtus oeconomus*. *Acta Theriologica* 43: 371-378.
- Andren H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.
- Barnes D.J. and Hopkins T.R. 2003. The impact of programming paradigms on the efficiency of an individual-based simulation model. *Simulation Modelling Practice and Theory* 11: 557-569.
- Bart J. 1995. Acceptance criteria for using individual-based models to make management decisions. *Ecological Applications* 5: 411-420.
- Baskent E. 1999. Controlling spatial structure of forested landscapes: a case study towards landscape management. *Landscape Ecology* 14: 83-97.
- Baudry J. and Taton T. 1993. Changes in landscape patterns and vegetation dynamics in Provence, France. *Landscape and Urban Planning* 24: 153-159.
- Baudry J., Burel F., Aviron S., Martin M., Ouin A., Pain G. and Thenail C. 2003. Temporal variability of connectivity in agricultural landscapes: do farming activities help? *Landscape Ecology* 18: 303-314.
- Begon M., Harper J.L. and Townsend C.R. 1996. *Ecology*. 3<sup>rd</sup> ed. Blackwell Science, Oxford, UK.

- Beissinger R. and Westphal M. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 63: 821-841.
- Bellamy P.E., Brown N.J., Enoksson B., Firbank L.G., Fuller R.J., Hinsley S.A. and Schotman A.G.M. 1998. The influences of habitat, landscape structure and climate on local distribution patterns of the nuthatch (*Sitta europaea* L.). *Oecologia* 115: 127-136.
- Bender D.J., Tischendorf L. and Fahrig L. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecology* 18: 17-39.
- Bergman K. and Kindvall O. 2004. Population viability analysis of the butterfly *Lopinga achine* in a changing landscape in Sweden. *Ecography* 27: 49-58.
- Bircham P.M.M., Rathmell J.C.A. and Jordan W.J. 1994. An atlas of the breeding birds of Cambridgeshire (vice county 29). Cambridge Bird Club.
- Bogaert J., Van Hecke P., Moermans R. and Impens I. 1999. Twist number statistics as an additional measure of habitat perimeter irregularity. *Environmental and Ecological Statistics* 6: 275-290.
- Bogaert J., Eysenrode D., Van Hecke P., Impens I. and Ceulemans R. 2001. Land-cover change: quantification metrics for perforation using 2-D gap features. *Acta Biotheoretica* 49: 161-169.
- Boswell G., Britton N. and Franks N. 1998. Habitat fragmentation, percolation theory and the conservation of a keystone species. *Proc. R. Soc. Lond. B* 265: 1921-1925.
- Boudjemadi K., Lecomte J. and Clobert J. 1999. Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. *Journal of Animal Ecology* 68: 1207-1224.
- Bourgeron P., Humphries H., Barber J., Turner S., Jensen M. and Goodman I. 1999. Impact of broad- and fine-scale patterns on regional landscape characterisation using AVHRR-derived land cover data. *Ecosystem Health* 5: 234-258.
- Bourn N.A.D. and Warren M.S. 1998. Species action plan: black hairstreak *Satyrrium pruni*. The British Butterfly Conservation Society, Dorset, UK.
- Burt W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24: 346-352.
- Butler M.J. 2003. Incorporating ecological process and environmental change into spiny lobster population models using a spatially-explicit individual-based approach. *Fisheries Research* 65: 63-79.
- Cain M.L. 1985 Random search by herbivorous insects: A Simulation Model. *Ecology* 66: 876-888.

- Cain D., Riitters K. and Orvis K. 1997. A multi-scale analysis of landscape statistics. *Landscape Ecology* 12: 199-212.
- Carter J. and Finn J.T. 1999. MOAB: a spatially explicit, individual-based expert system for creating animal foraging models. *Ecological Modelling* 119: 29-41.
- Childress W. 1997. Predicting dynamics of spatial automata models using Hamiltonian equations. *Ecological Modelling* 96: 293-303.
- Childress W., Rykiel E., Forsythe W., Li B. and Wu H. 1996. Transition rule complexity in grid-based automata models. *Landscape Ecology* 11: 257-266.
- Clark J.S. 1996. *The birds of Huntingdon and Peterborough*. J.S. Clark, Hilton.
- Clinchy M., Haydon D. and Smith A. 2002. Pattern does not equal process: what does patch occupancy really tell us about metapopulation dynamics? *The American Naturalist* 159: 351-362.
- Conradt L., Bodsworth E.J., Roper T.J., Thomas C.D. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proc. R. Soc. Lond. B* 267: 1505-1510.
- Conradt L., Roper T.J., Thomas C.D. 2001. Dispersal behaviour of individuals in metapopulations of two British butterflies. *Oikos* 95: 416-424.
- Crist T.O. and MacMahon J.A. 1991. Individual foraging and components of harvester ants: movement patterns and seed patch fidelity. *Insectes Sociaux* 38: 379-396.
- Currie D. and Matthysen E. 1998. Nuthatches *Sitta europaea* do not delay postfledging dispersal in isolated forest fragments. *Belgian Journal of Zoology* 128: 49-54.
- Debinski D. and Holt R. 1999. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14: 342-355.
- Dennis B. 2002. Allee effects in stochastic populations. *Oikos* 96, 389-401.
- Doak D.F., Marino P.C. and Kareiva P.M. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Population Biology* 41: 315-336.
- Donovan T., Lamberson R., Kimber A., Thompson F. and Faaborg J. 1995. Modelling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. *Conservation Biology* 9: 1396-1407.
- Drechsler M. and Wissel C. 1998. Trade-offs between local and regional scale management of metapopulations. *Biological Conservation* 83: 31-41.

- Dunkerley D. 1997. Banded vegetation: development under uniform rainfall from a simple cellular automation model. *Plant Ecology* 129: 103-111.
- Dunning J., Stewart D., Danielson B., Noon B., Root T., Lamberson R. and Stevens E. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5: 3-11.
- Durrett R. and Levin S. 1994. Stochastic spatial models: a user's guide to ecological applications. *Phil. Trans. R. Soc. Lond. B* 343: 329-350.
- Dytham C. 1994. Habitat destruction and competitive coexistence: a cellular model. *Journal of Animal Ecology* 63: 490-491.
- Dytham C. 1995. The effect of habitat destruction pattern on species persistence: a cellular model. *Oikos* 74: 340-344.
- Dytham C. and Shorrocks B. 1995. Aggregation and the maintenance of genetic diversity: an individual-based cellular model. *Evolutionary Ecology* 9: 508-519.
- Elkie P. and Rempel R. 2001. Detecting scales of pattern in boreal forest landscapes. *Forest Ecology and Management* 147: 253-261.
- Elmhagen B. and Angerbjorn A. 2001. The applicability of metapopulation theory to large mammals. *Oikos* 94: 89-100.
- Enoksson B. 1988. Age- and sex-related differences in dominance and foraging behaviour of nuthatches *Sitta europaea*. *Journal of Animal Behaviour* 36: 231-238.
- Enoksson B., Angelstam P. and Larsson K. 1995. Deciduous forest and resident birds: the problem of fragmentation in a coniferous forest landscape. *Landscape Ecology* 10: 267-275.
- Fahrig L. 1988. A general model of populations in patchy habitats. *Applied Mathematics and Computation* 27: 53-66.
- Fahrig L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61: 603-610.
- Fahrig L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* 105: 273-292.
- Fahrig L. 2001. How much habitat is enough? *Biological Conservation* 100: 65-74.
- Fahrig L. and Paloheimo J.E. 1987. Interpatch dispersal of the cabbage butterfly. *Canadian Journal of Zoology* 65: 616-622.
- Ferreras P. 2001. Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. *Biological Conservation* 100: 125-136.



- Fischer J. and Lindenmayer D.B. 2002. The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones. *Biodiversity and Conservation* 11: 833-849.
- Flather C. and Bevers M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159: 40-56.
- Forman R. 1995. *Land Mosaics: the ecology of landscapes and regions*. 1<sup>st</sup> ed. Cambridge: Cambridge University Press, Cambridge, UK.
- Frank K. and Wissel C. 1998. Spatial aspects of metapopulation survival – from model results to rules of thumb for landscape management. *Landscape Ecology* 13: 363-379.
- Gardner R.H. and Gustafson E.J. 2004. Simulating dispersal of reintroduced species within heterogeneous landscapes. *Ecological Modelling* 171: 339-358.
- Gibbons D.W., Reid J.B. and Chapman R.A. 1993. *The new atlas of breeding birds in Britain and Ireland: 1988-1991*. T. & A.D Poyser.
- Gillman M. and Hails R. 1997. *An introduction to ecological modelling*. 1<sup>st</sup> ed. Blackwell Science Ltd., Oxford, UK.
- Green D.G. 1989. Simulated effects of fire, dispersal and spatial pattern on competition within vegetation mosaics. *Vegetatio*. 82: 139-153.
- Green D.G. 1994. Connectivity and complexity in landscapes and ecosystems. *Pacific Conservation Biology* In press.
- Green D.G., Tridgell A. and Gill A.M. 1990. Interactive simulation of bushfire spread in heterogeneous fuel. *Journal of Mathematics and Computer Modelling*. 13: 57-66.
- Griffiths R. and Williams C. 2000. Modelling population dynamics of great crested newts (*Triturus cristatus*): a population viability analysis. *Herpetological Journal* 10: 157-163.
- Gustafson E.J. 1998. Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* 1: 143-156.
- Gustafson E.J. and Parker G. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecology* 7: 101-110.
- Gustafson E.J. and Gardner R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonisation. *Ecology* 77: 94-107.
- Haines-Young R. and Chopping M. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. *Progress in Physical Geography* 20: 418-445.

- Hanski I. 1999. *Metapopulation Ecology*. 1<sup>st</sup> ed. Oxford University Press, Oxford, UK.
- Hanski I., Pakkala T., Kuussaari M. and Lee G. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* 72: 21-28.
- Hargis C., Bissonette J. and David J. 1998. The behaviour of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology* 13: 167-186.
- Hassell M., Comins H. and May R. 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353: 255-258.
- Haydon D. and Pianka R. 1999. Metapopulation theory, landscape models and species diversity. *Ecoscience* 6: 316-328.
- He H., DeZonia B. and Mladenoff D. 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. *Landscape Ecology* 15: 591-601.
- Henein K. and Merriam G. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecology* 4: 157-170.
- Henein K., Wegner J. and Merriam G. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small animals. *Oikos* 81: 168-186.
- Herzog F., Lausch A., Muller E., Thulke H., Steinhardt U. and Lehmann S. 2001. Landscape metrics for assessment of landscape destruction and rehabilitation. *Environmental Management* 27: 91-107.
- Hill M. and Caswell H. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecology Letters* 2: 121-127.
- Hinsley S.A., Bellamy P.E., Newton I. and Sparks T.H. 1995. Habitat and landscape factors influencing the presence of individual bird species in woodland fragments. *Journal of Avian Biology* 26: 94-104.
- Hinsley S.A., Bellamy P.E. and Wyllie I. 2004. The Monks Wood avifauna. *In* Monks Wood 50<sup>th</sup> Anniversary Symposium. English Nature Research Report. Edited by C. Gardener and T.H. Sparks. In press.
- HMSO. 1981. *The Wildlife and Countryside Act 1981*. HMSO, London, UK.
- HMSO. 1994. *Biodiversity: the UK action plan*. HMSO, London, UK.
- HMSO. 1995. *Biodiversity: the UK steering group report*. HMSO, London, UK.
- Hogeweg P. 1988. Cellular automata as a paradigm for ecological modelling. *Journal of Applied Mathematical Computing*. 27: 81-100.

- Hogeweg P. and Hesper B. 1990. Crowns crowding: an individual oriented model of the *Acanthaster* phenomenon. In *Acanthaster* and the coral reef: a theoretical perspective. Edited by R.H. Bradbury. Springer-Verlag, Berlin, Germany.
- Hokit D., Stith B. and Branch L. 2001. Comparison of two types of metapopulation models in real and artificial landscapes. *Conservation Biology* 15: 1102-1113.
- Hong H., DeZonia B. and Mladenoff D. 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. *Landscape Ecology* 15: 591-601.
- Hubbell S. 2001. The unified neutral theory of biodiversity and biogeography. 1<sup>st</sup> ed. Princeton University Press, Oxfordshire, UK.
- Hulshoff R. 1995. Landscape indices describing a Dutch landscape. *Landscape Ecology* 10: 101-111.
- Inghe O. 1989. Genet and ramet survivorship under different mortality regimes – cellular automata model. *Journal of Theoretical Biology* 138: 257-270.
- Jaeger J. 2000. Landscape division, splitting index and effective mesh size: new measures of landscape fragmentation. *Landscape Ecology* 15: 115-130.
- Jeffers J.N.R. 1982. Outline studies in Ecology: Modelling. 1<sup>st</sup> ed. Chapman and Hall, London, UK.
- Jenerette G. and Wu J. 2001. Analysis and simulation of land-use change in the central Arizona-Phoenix region, USA. *Landscape Ecology* 16: 611-626.
- Jones R., Gilbert N., Guppy M., Neals V. 1980. Long-distance movement of *Pieris rapae*. *Journal of Animal Ecology* 49: 629-642.
- Keeling M. 2002. Using individual-based simulations to test the Levins metapopulation paradigm. *Journal of Animal Ecology* 71: 270-279.
- Keitt T.H. 1997. Stability and complexity on a lattice: coexistence of species in an individual-based food web model. *Ecological Modelling* 102: 243-258.
- Keitt T.H. 2000. Spectral representation of neutral landscapes. *Landscape Ecology* 15: 479-493.
- Kerr B., Riley M., Feldman M. and Bohannan B. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418: 171-174.
- Kirby K.J. 2004. Balancing site-based protection versus landscape-scale measures in English woodland. pp. 263-270. In *Landscape ecology of trees and forests: Proceedings 12th Annual IALE(UK) Conference*. Edited by R. Smithers. Royal Agricultural College, Cirencester. 21<sup>st</sup> – 24<sup>th</sup> June 2004. IALE(UK).

- King A.W. and With K.A. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behaviour really matter? *Ecological Modelling* 147: 23-39.
- Lamberson R.H., Noon B.R., Voss C. and McKelvey K.S. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. *Conservation Biology* 8: 185-195.
- Langevelde F., Schotman A., Claasen F. and Sparenburg G. 2000. Competing land use in the reserve site selection problem. *Landscape Ecology* 15: 243-256.
- Lavorel S., Gardner R. and O'Neill R. 1995. Dispersal of annual plants in hierarchically structured landscapes. *Landscape Ecology* 10: 277-289.
- 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. Extinction. In: M. Gerstenhaber, *Some Mathematical Problems in Biology*, American Mathematical Society, Providence, RI.
- Li B. and Archer S. 1997. Weighted mean patch size: a robust index for quantifying landscape structure. *Ecological Modelling* 102: 353-361.
- Lima S.L. and Zollner P.A. 1996. Towards a behavioural ecology of ecological landscapes. *TREE* 11: 131-134.
- Linden P. 1999. *Just JAVA 1.2*. 1<sup>st</sup> ed. Sun Microsystems Press, California, USA.
- Lindenmayer D.B. and Possingham H.P. 1996. Modelling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia. *Landscape Ecology* 11: 79-105.
- Liu J. 1993. ECOLECON: An ECOlogical-ECONomic model for species conservation in complex forest landscapes. *Ecological Modelling* 70: 63-87.
- Liu J., Dunning J.B. and Pulliam H.R. 1995. Potential effects of a forest management plan on Bachman's sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. *Conservation Biology* 9: 62-75.
- Lurz P.W.W., Rushton S.P., Wauters L.A., Bertolino S., Currado I., Mazzoglio P. and Shirley M.D.F. 2001. Predicting grey squirrel expansion in north Italy: a spatially explicit modelling approach. *Landscape Ecology* 16: 407-420.
- Lurz P.W.W., Geddes N., Lloyd A.J., Shirley M.D.F., Rushton S.P. and Burlton B. 2003. Planning a red squirrel conservation area: using a spatially explicit population dynamics model to predict the impact of felling and forest design plans. *Forestry* 76: 96-108.

- McGarigal K. and Marks B. 1995. Fragstats: spatial pattern analysis program for quantifying landscape structure. U.S. Forest Service General Technical Report PNW. 351.
- MacArthur R. and Wilson E. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373-387.
- MacArthur R. and Wilson E. 1967. The theory of island biogeography. Monographs in Population Biology. Princeton University Press, New Jersey, USA.
- Macdonald D.W. and Rushton S. 2003. Modelling space use and dispersal of mammals in real landscapes: a tool for conservation. *Journal of Biogeography* 30: 607-62.
- Marsh D. and Trenham P. 2000. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15: 40-49.
- Matthysen E. 1986. Some observations on sex-specific territoriality in the nuthatch. *Ardea* 74: 117-183.
- Matthysen E. 1989a. Nuthatch *Sitta europaea* demography, beech mast and territoriality. *Ornis Scandinavica* 20: 278-282.
- Matthysen E. 1989b. Territorial and nonterritorial settling in juvenile eurasian nuthatches (*Sitta europaea* L.) in summer. *The Auk* 106: 560-567.
- Matthysen E. 1990. Behavioural and ecological correlates of territory quality in the eurasian nuthatch (*Sitta europaea*). *The Auk* 107: 86-95.
- Matthysen E. 1998. The nuthatches. T & AD Poyser Ltd., London, UK
- Matthysen E. 2002. Boundary effects on dispersal between habitat patches by forest birds (*Parus major*, *P. caeruleus*). *Landscape Ecology* 17: 509-515.
- Matthysen E. and Adriaensen F. 1998. Forest size and isolation have no effect on reproductive success of eurasian nuthatches (*Sitta europaea*). *The Auk* 115: 955-963.
- Matthysen E., Adriaensen F. and Dhondt A.A. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* 72: 375-381.
- Matthysen E. and Currie D. 1996. Habitat fragmentation reduces disperser success in juvenile nuthatches *Sitta europaea*: evidence from patterns of territory establishment. *Ecography* 19: 67-72.
- Mech S.G. and Zollner P.A. 2002. Using body size to predict perceptual range. *Oikos* 98: 47-52.
- Milne B. 1988. Measuring the fractal geometry of landscapes. *Applied Mathematics and Computation* 27: 67-79.

- Moilanen A. and Hanski I. 1995. Habitat destruction and coexistence of competitors on a spatially realistic metapopulation model. *Journal of Animal Ecology* 64: 141-144.
- Moilanen A. and Hanski I. 1998. Metapopulation dynamics: effects of habitat quality and landscape architecture. *Ecology* 79: 1-11.
- Moss M. and Davis L. 1994. Measurement of spatial change in the forest component of the rural landscape of southern Ontario. *Applied Geography* 14: 214-231.
- Nee S. and May R. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61: 37-40.
- Newton I. 1986. The sparrowhawk. Calton: T & AD Poyser Ltd.
- Niklas K.J., Tiffney B.H. and Knoll A.H. 1983. Patterns in vascular land plant diversification. *Nature* 303: 614-616.
- Nikora V., Pearson C. and Shankar U. 1999. Scaling properties in landscape patterns: New Zealand experience. *Landscape Ecology* 14: 17-33.
- Nilsson S.G. 1976. Habitat, territory size and reproductive success in the nuthatch *Sitta europaea*. *Ornis Scandinavica* 7: 179-184.
- Nilsson S. 1987. Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *Journal of Animal Ecology* 56: 921-937.
- O'Neill R., Krummel J., Gardner R., Sugihara G., Jackson B., DeAngelis D., Milne B., Turner M., Zygmunt B., Christensen S., Dale V. and Graham R. 1988. Indices of landscape pattern. *Landscape Ecology* 1: 153-162.
- O'Neill R., Gardner R. and Turner M. 1992. A hierarchical neutral model for landscape analysis. *Landscape Ecology* 7: 55-61.
- O'Neill R., Hunsaker C., Timmins S., Jackson B., Jones K., Riitters K. and Wickham J. 1996. Scale problems in reporting landscape pattern at the regional scale. *Landscape Ecology* 11: 169-180.
- Olden J.D., Schooley R.L., Monroe J.B. and Poff N.L. 2004. Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology* 73: 1190-1194.
- Palmer M. 1992. The coexistence of species in fractal landscapes. *The American Naturalist* 139: 375-397.
- Paradis E., Baillie S.R., Sutherland W.J. and Gregory R.D. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67: 518-536.

- Parsons M., Green D. and Waring P. 2000. The action for threatened moths project. *The British Journal of Entomology and Natural History* 13: 57-63.
- Pastor J., Moen R. and Choen Y. 1997. Spatial heterogeneities, carrying capacity and feedbacks in animal landscape interactions. *Journal of Mammalogy* 78: 1040-1052.
- Patten B.C. and Jørgensen S.E. 1995. *Complex ecology: the part-whole relation in ecosystems*. Prentice Hall, New Jersey, USA. pp 705.
- Pech R., McIlroy J.C., Clough M.F. and Green D.G. 1992. A microcomputer model for predicting the spread and control of foot and mouth disease in feral pigs. *In Proceedings 15th Vertebrate Pest Conference*, Newport, USA.
- Phillips J.W. 2000. Butterfly Conservation – action for threatened moths project – an opportunity for participation by BENHS members. *The British Journal of Entomology and Natural History* 13: 63-66.
- Possingham H. 1995. ALEX: A model for the viability analysis of spatially structured populations. *Biological Conservation* 73: 143-150.
- Pravosudov V.V. 1993a. Social organisation of the nuthatch (*Sitta europaea*). *Ornis Scandinavica* 24: 290-296.
- Pravosudov V.V. 1993b. Breeding biology of the eurasian nuthatch in northeastern Siberia. *Wilson Bulletin* 105: 475-482.
- Pulliam H.R., Dunning J.B. and Liu J. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2: 165-177.
- Railsback S.F. 2001. Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecological Modelling* 139: 47-62.
- Ricketts T. 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158: 87-99.
- Ricketts T., Daily G., Ehrlich P. and Fay J. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology* 15: 378-388.
- Riitters K., O'Neill R., Hunsacker C., Wickham J., Yankee D., Timmins S., Jones K. and Jackson B. 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecology* 10: 23-39.
- Ripple W., Bradshaw G. and Spies T. 1991. Measuring forest landscape patterns in the Cascade Range of Oregon, USA. *Biological Conservation* 57: 73-88.
- Roberts D. 1996. Landscape vegetation modelling with vital attributes and fuzzy systems theory. *Ecological Modelling* 90: 175-184.

- Rodwell J.S. 2000. British plant communities. In: Maritime communities and vegetation of open habitats, vol. 5. Cambridge University Press, Cambridge, UK.
- Root R.B. and Kareiva P.M. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequence and adaptive significance of Markovian movements in a patchy environment. *Ecology* 65: 147-165.
- Rouget M., Richardson D., Milton S. and Polakow D. 2000. Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. *Plant Ecology* 152: 79-92.
- RSPB. 2004. RSPB as lead partner.  
[http://www.rspb.org.uk/biodiversity/RSPBbandbiodiversity/lead\\_partner/index.asp](http://www.rspb.org.uk/biodiversity/RSPBbandbiodiversity/lead_partner/index.asp).
- Ruckelshaus M., Hartway C. and Kareiva P. 1996. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* 11: 1298-1306.
- Rushton S., Lurz P., Fuller R. and Garson P. 1997. Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *Journal of Applied Ecology* 34: 1137-1154.
- Ruxton G., Gonzalez-Andujar J.L. and Perry J.N. 1997. Mortality during dispersal stabilises local population fluctuations. *Journal of Animal Ecology* 66: 289-292.
- Saarenmaa H., Stone N.D., Folse L.J., Packard J.M., Grant W.E., Makela M.E. and Coulson R.N. 1988. An artificial intelligence modelling approach to simulating animal/habitat interactions. *Ecological Modelling* 44: 125-141.
- Samways M.J. 1989. Insect conservation and landscape ecology: a case-history of bush crickets (*Tettigoniidae*) in Southern France. *Environmental Conservation* 16: 217-226.
- Saupe D. 1988. Algorithms for random fractals. In: Peitgen, H., Saupe, D. (Eds.), *The Science of Fractal Images*. Springer-Verlag, New York. pp. 71-136.
- Saura S. and Martinez-Milan J. 2000. Landscape patterns simulation with a modified random clusters method. *Landscape Ecology* 15: 661-678.
- Saveraid E., Debinski D., Kindscher K. and Jakubauskas M. 2001. A comparison of satellite data and landscape variables in predicting bird species occurrences in the greater Yellowstone ecosystem, USA. *Landscape Ecology* 16: 71-83.
- Scheuring I., Janosi I., Csilling A. and Pasztor G. 1994. SOC defeats chaos: a new population-dynamic model. *Fractals in the Natural and Applied Sciences* 41: 341-348.
- Schippers P., Verboom J., Knaapen J.P. Apeldoorn R.C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography* 19: 97-106.



- Schooley R.L. and Wiens J.A. 2003. Finding habitat patches and directional connectivity. *Oikos* 102: 559-570.
- Schotman A.G.M. and Meeuwsen H.A.M. 1994. Predicting the effects of defragmentation measures in the Rolde/Gieten area. (In Dutch). IBN report 118, Instituut voor Bos en Natuuronderzoek (IBN-DLO), Wageningen, Netherlands.
- Simberloff D., Berthet P., Boy V., Cousins S.H., Fortin M-J., Goldberg R., Lefkovitch L.P., Ripley B., Scherrer B. and Tonkyn D. 1987. Novel statistical analyses in terrestrial animal ecology: dirty data and clean questions. In: P. Legendre and L. Legendre (Eds.), *Developments in numerical ecology*. NATO ASI series. Vol. G14, Springer, Berlin. pp 559-572.
- Simpson J., Boerner R., DeMers M., Berns L., Artigas F. and Silva A. 1994. Forty-eight years of landscape change on two contiguous Ohio landscapes. *Landscape Ecology* 4: 261-270.
- Smith A.R. 1976. Introduction to and survey of polyautomata theory. *In Automata, languages, development*. Edited by A. Lindemayer and G. Rozenberg. North-Holland, Amsterdam, Holland. pp405-422.
- Smith S. and Gilbert J. 2002. National Inventory of woodland and trees – county report for Cambridgeshire. Woodland Surveys Branch of Forestry Research, Forestry Commission, 231 Corstorphine Road, Edinburgh, EH12 7AT.
- Sondgerath D. and Schroder B. 2002. Population dynamics and habitat connectivity affecting the spatial spread of populations – a simulation study. *Landscape Ecology* 00: 1-14.
- South A. 1999. Dispersal in spatially explicit population models. *Conservation Biology* 13: 1039-1046.
- Stauffer D. and Aharony A. 1994. *Introduction to percolation theory*. 2<sup>nd</sup> ed. Taylor and Francis Limited, London, UK.
- Stiling P. 2002. *Ecology*. 4<sup>th</sup> ed. Prentice Hall, New Jersey, USA.
- Strong D.R., Lawton J.H. and Southwood T.R.E. 1984. *Insects on plants: community patterns and mechanisms*. Blackwell Scientific Publications, Oxford, UK.
- Swetnam R., Ragou P., Firbank L., Hinsley S. and Bellamy P. 1998. Applying ecological models to altered landscapes: scenario-testing with GIS. *Landscape and Urban Planning* 41: 3-18.
- Swetnam R., Wilson J., Bradbury R. and Krebs J. 2001. Modelling the effects of agricultural change on skylark numbers using GIS: a pilot study. In P F Donald and J A Vickey (eds) *The ecology and conservation of skylarks *Alauda arvensis**. RSPB, Sandy. pp 209-219.

- Taneyhill D. 2000. Metapopulation dynamics of multiple species: the geometry of competition on a fragmented habitat. *Ecological Monographs* 70: 495-516.
- Thomas J.A. 1974. Factors influencing the numbers and distribution of the brown hairstreak, *Thecla betulae* and the black hairstreak *Strymonidia pruni*. Ph.D. thesis, Leicester University, UK.
- Thomas J.A. 1975. The black hairstreak, conservation report. Unpublished report ITE/NCC.
- Thomas C.D. and Harrison S. 1992. Spatial dynamics of a patchily distributed butterfly species. *Journal of Animal Ecology* 61: 437-446.
- Thomas C.D., Thomas J.A., Warren M.S. 1992. Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* 92: 563-567.
- Thomas C. and Kunin W. 1999. The spatial structure of populations. *Journal of Animal Ecology* 68: 647-657.
- Thornton P. and Jones P. 1998. A conceptual approach to dynamic agricultural land-use modelling. *Agricultural Systems* 57: 505-521.
- Timm R.M., Howard W.E. 1994. White-footed and deer mice. Prevention and control of wildlife damage, Institute of Agriculture and Natural Resources, University of Nebraska, USA.
- Tischendorf L. 2001. Can landscape indices predict ecological processes consistently? *Landscape Ecology* 16: 235-254.
- Tischendorf L. and Fahrig L. 2000a. How should we measure landscape connectivity? *Landscape Ecology* 15: 633-641.
- Tischendorf L. and Fahrig L. 2000b. On the usage and measurement of landscape connectivity. *Oikos* 90: 7-19.
- Tischendorf L., Bender D.J. and Fahrig L. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* 18: 41-50.
- Trani M. and Giles R. 1999. An analysis of deforestation: metrics used to describe pattern change. *Forest Ecology and Management* 114: 459-470.
- Travis J.M.J. 2002. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. R. Soc. Lond. B* 270: 467-473.
- Travis J.M.J. and Dytham C. 1998. The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. *Proc R. Soc. Lond. B* 265: 17-23.

- Travis J.M.J. and Dytham C. 1999. Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. B* 266:723-728.
- Travis J.M.J. and French D. 2000. Dispersal functions and spatial models: expanding our dispersal toolbox. *Ecology Letters* 3: 163-165.
- Turner M.G. 1990. Spatial and temporal analysis of landscape patterns. *Landscape Ecology* 4: 21-30.
- Turner M.G., Wu Y., Romme W.H. and Wallace L.L. 1993. A landscape simulation model of winter foraging by large ungulates. *Ecological Modelling* 69: 163-184.
- Turner M.G., Wu Y., Wallace L.L., Romme W.H. and Brenkert A. 1994. Simulating winter interactions among ungulates, vegetation and fire in northern Yellowstone park. *Ecological Applications* 4: 472-496.
- Turner M.G., Arthaud G.J., Engstrom R.T., Hejl S.J., Liu J, Loeb S. and Mckelvey K. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* 5: 12-16.
- Valentine J.W. 1970. How many marine invertebrate fossil species? A new approximation. *Journal of Paleontology*. 44: 410-415.
- Venier L.A. and Fahrig L. 1996. Habitat availability causes the species abundance – distribution relationship. *Oikos* 76: 564-570.
- Verboom J., Foppen R., Chardon P., Opdam P. and Luttikhuisen P. 2001. Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. *Biological Conservation* 100: 89-101.
- Watts K. and Griffiths M. 2004. Exploring structural connectivity in welsh woodlands using neutral landscape models. pp. 133-140. *In* Landscape ecology of trees and forests: Proceedings 12th Annual IALE(UK) Conference. Edited by R. Smithers. Royal Agricultural College, Cirencester. 21<sup>st</sup> – 24<sup>th</sup> June 2004. IALE(UK).
- Weisser W. 2000. Metapopulation dynamics in an aphid-parasitoid system. *Entomologia Experimentalis et Applicata* 97: 83-92.
- Wennergren U., Ruckelshaus M. and Kareiva P. 1995. The promise and limitations of spatial models in conservation biology. *Oikos* 74: 349-356.
- Wesolowski T. and Stawarczyk T. 1991. Survival and population dynamics of nuthatches *Sitta europaea* breeding in natural cavities in a primeval temperate forest. *Ornis Scandinavica* 22: 143-154.
- Wiens J.A.; Schooley R.L. and Weeks R.D. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos*. 78: 257-264.

- Wilson E.O. 1985. The biological diversity crisis: a challenge to science. *Issues in Science and Technology* 2: 20-29.
- Wilson E.O. 1994. *Naturalist*. Penguin Books Ltd., London, UK. pp 354-364.
- With K.A. 1997. The Application of neutral landscape models in conservation biology. *Conservation Biology* 11: 1069-1080.
- With K.A. and King A. 1998. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314-326.
- With K.A. and King A. 1999. Dispersal success in fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* 14: 73-82.
- With K.A. and King A. 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. *Biological Conservation* 100: 75-88.
- With K.A., Gardner R.H. and Turner M.G. 1997. Landscape connectivity and population distribution in heterogeneous environments. *Oikos* 78: 151-169.
- Wolfram S. 1984. Cellular automata as models of complexity. *Nature* 311: 419-424.
- Wright C. 1998. *Java*. 1<sup>st</sup> ed. Hodder Headline Plc, London, UK.
- Wu X. and Sui D. 2001. An initial exploration of a lacunarity-based segregation measure. *Environment and Planning B: Planning and Design* 28: 433-446.
- Wu X., Thurow T. and Whisenant S. 2000. Fragmentation and changes in hydrologic function of tiger bush landscapes, south-west Niger. *Journal of Ecology* 88: 790-800.
- Wu Y. and Levin S.A. 1994. A spatial patch dynamic modelling approach to pattern and process in an annual grassland. *Ecological Monographs* 64: 447-464.
- Yeomans S.R. 1995. Water-finding in adult turtles: random search or oriented behaviour. *Animal Behaviour* 49: 977-987.
- Young D. 2001. *Xestia rhomboidea* (Esper) (square spotted clay) (Lepidoptera): request for information. *British Journal of Entomology and Natural History* 14: 92.
- Zipperer W. 1993. Deforestation patterns and their effects on forest patches. *Landscape Ecology* 8: 177-184.
- Zollner P.A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented landscapes. *Landscape Ecology* 15: 523-533.
- Zollner P.A. and Lima S.L. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* 80: 51-60.

## References

---

Zollner P.A. and Lima S.L. 1999a. Search strategies for landscape-level interpatch movements. *Ecology* 80: 1019-1030.

Zollner P.A. and Lima S.L. 1999b. Illumination and the perception of remote habitat patches by white-footed mice. *Journal of Animal Behaviour* 58: 489-500.