THE STABILITY OF MODEL ECOSYSTEMS

SUNNY ELSPETH TOWNSEND

UNIVERSITY
of
GLASGOW

THIS THESIS IS SUBMITTED IN FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DIVISION OF ECOLOGY AND EVOLUTIONARY BIOLOGY
FACULTY OF BIOMEDICAL AND LIFE SCIENCES
UNIVERSITY OF GLASGOW

SEPTEMBER, 2009

This thesis is dedicated to three exceptional people:

Dr. Simon Thirgood, who tragically died in August 2009 during a trip to Ethiopia,

and my grandparents Hardwicke and Elspeth Holderness, who championed human rights in Southern Rhodesia (now Zimbabwe) and strove to establish constitutional reform for black enfranchisement

Abstract

Ecologists would like to understand how complexity persists in nature. In this thesis I have taken two fundamentally different routes to study ecosystem stability of model ecosystems: classical community ecology and classical population ecology. In community ecology models, we can study the mathematical mechanisms of stability in general, large model ecosystems. In population ecology models, fewer species are studied but greater detail of species interactions can be incorporated. Within these alternative contexts, this thesis contributes to two consuming issues concerning the stability of ecological systems: the ecosystem stability-complexity debate; and the causes of cyclic population dynamics.

One of the major unresolved issues in community ecology is the relationship between ecosystem stability and complexity. In 1958 Charles Elton made the conjecture that the stability of an ecological system was coupled to its complexity and this could be a “wise principle of co-existence between man and nature” with which ecologists could argue the case for the conservation of nature for all species, including man. The earliest and simplest model systems were randomly constructed and exhibited a negative association between stability and complexity. This finding sparked the stability-complexity debate and initiated the search for organising principles that enhanced stability in real ecosystems. One of the universal laws of ecology is that ecosystems contain many rare and few common species. In this thesis, I present analytical arguments and numerical results to show that the stability of an ecosystem can increase with complexity when the abundance distribution is characterized by a skew towards many rare species. This work adds to the growing number of conditions under which the negative stability - complexity relationship can been inverted in theoretical studies.

While there is growing evidence that the stability-complexity debate is progressing towards a resolution, community ecology has become increasingly subject to major criticism. A long-standing criticism is the reliance on local stability analysis. There is growing recognition that a global property called permanence is a more satisfactory definition of ecosystem stability because it tests only whether species can coexist. Here I identify and explain a positive correlation between the probability of local stability and permanence, which suggests local stability is a better measure of species coexistence than previously thought. While this offers some relief, remaining issues cause the stability-complexity debate to evade clear resolution and leave community ecology in a poor position to argue for the conservation of natural diversity for the benefit of all species.

In classical population ecology, a major unresolved issue is the cause of non-equilibrium population dynamics. In this thesis, I use models to study the drivers of cyclic dynamics in Scottish populations of mountain hares (*Lepus timidus*), for the first time in this system. Field studies currently favour the hypothesis that parasitism by a nematode *Trichostrongylus retortaeformis* drives the hare cycles, and theory predicts that the interaction should induce cycling. Initially I used a simple, strategic host-parasite model parameterised using available empirical data to test the superficial concordance between theory and observation. I find that parasitism could not account for hare cycles. This verdict leaves three options: either the parameterisation was inadequate, there were missing important biological details or simply that parasites do not drive host cycles.

Regarding the first option, reliable information for some hare-parasite model parameters was lacking. Using a rejection-sampling approach motivated by Bayesian methods, I identify the most likely parameter set to predict observed dynamics. The results imply that the current formulation of the hare-parasite model can only generate realistic dynamics when parasite effects are significantly larger than current empirical estimates, and I conclude it is likely that the model contains an inadequate level of detail.

The simple strategic model was mathematically elegant and allowed mathematical concepts to be employed in analysis, but the model was biologically naïve. The second model is the antipode of the first, an individual based model (IBM) steeped in biological reality that can only be studied by simulation. Whilst most highly detailed tactical models are developed as a predictive tool, I instead structurally perturb the IBM to study the ecological processes that may drive population cycles in mountain hares. The model allows delayed responses to life history by linking maternal body size and parasite infection to the future survival and fecundity of offspring. By systematically removing model structure I show that these delayed life history effects are weakly destabilising and allow parameters to lie closer to empirical estimates to generate observed hare population cycles.

In a third model I structurally modify the simple strategic host-parasite model to make it spatially explicit by including diffusion of mountain hares and corresponding advection of parasites (transportation with host). From initial simulations I show that the spatially extended host-parasite equations are able to generate periodic travelling waves (PTWs) of hare and parasite abundance. This is a newly documented behaviour in these widely used host-parasite equations. While PTWs are a new potential scenario under which cyclic hare dynamics could be explained, further mathematical development is required to determine whether adding space can generate realistic dynamics with parameters that lie closer to empirical estimates. In the general thesis discussion I deliberate on whether a hare-parasite model has been identified which can be considered the right balance between abstraction and relevant detail for this system.

Table of Contents

ABSTRACT .... **III**

TABLE OF CONTENTS .... **V**

LIST OF TABLES .... **VII**

LIST OF FIGURES .... **VIII**

ACKNOWLEDGEMENTS .... **X**

CANDIDATE'S DECLARATION .... **XII**

CHAPTER 1. GENERAL INTRODUCTION **1**

STABILITY - COMPLEXITY RELATIONSHIPS 1
PERIODIC FLUCTUATIONS IN THE NUMBERS OF MOUNTAIN HARES 5

CHAPTER 2. SPECIES ABUNDANCE DISTRIBUTIONS AND MODEL ECOSYSTEM RESILIENCE - INTERACTIVITY RELATIONSHIPS **10**

ABSTRACT 10
1. INTRODUCTION 11
2. MODELLING ECOSYSTEMS USING THE LOTKA-VOLTERRA EQUATIONS (LVE) 13
    (2a) Lotka vs. Volterra: generality vs. ecological transparency *13*
    (2b) Model formulation *14*
3. DO EQUITABLE ECOSYSTEMS HAVE DIFFERENT STABILITY-INTERACTIVITY RELATIONSHIPS TO INEQUITABLE? 18
    (3a) Analytical study of the effect of variance in the diagonal elements of the Jacobian on resilience - interactivity relationships *18*
    (3b) Numerical study of the effect of variance in the diagonal elements of the Jacobian on resilience - interactivity relationships *20*
    (3c) Numerical study of the effect of variance in the relative abundance distribution on resilience - interactivity relationships *21*
4. DISCUSSION 22
    (4a) The species abundance distribution and stability - complexity relationships *22*
    (4b) Limitations and extensions of the analytical approaches for studying stability - complexity relationships *24*
APPENDIX: DERIVATION OF THE VARIANCE OF EIGENVALUES IN TERMS OF THEIR REAL AND IMAGINARY PARTS 33

CHAPTER 3. ON THE GENERALITY OF STABILITY - COMPLEXITY RELATIONSHIPS IN LOTKA-VOLTERRA ECOSYSTEMS **35**

ABSTRACT 35
INTRODUCTION 36
METHODS 38
    Model ecosystems *38*
    Stability analyses *40*
RESULTS 41
    Permanence-complexity relationships *41*
    Permanence and local stability *43*
    The boundary equilibria and permanence *44*
DISCUSSION 45
APPENDIX: ELEMENTS OF THE JACOBIAN MATRIX FOR INTERIOR AND BOUNDARY EQUILIBRIA OF THE LOKTA-VOLTERRA EQUATIONS 54

CHAPTER 4. CAN PARASITES DRIVE POPULATION CYCLES IN MOUNTAIN HARES? **56**

ABSTRACT 56
INTRODUCTION 57
METHODS 58
RESULTS 59
    Model parameterisation within empirically defined plausibility envelope *59*
    Parameter changes which generate dynamics with the observed properties *60*
    Can small changes in parameters account for variability in dynamical properties? *61*
DISCUSSION 61
    Are key elements of the interaction represented sufficiently realistically? *61*

Are important ways in which the parasites influence hare demography omitted? *63*
A secondary role for parasites? *64*
Conclusion *64*
Appendix 4.1: Parameter estimation 71
Appendix 4.2: Analysis 74
Equilibrium hare and parasite density *74*
Stability *75*
Elasticity analysis *76*

CHAPTER 5. DISSECTING THE DRIVERS OF POPULATION CYCLES: INTERACTIONS BETWEEN PARASITES AND MOUNTAIN HARE DEMOGRAPHY 77

Abstract 77
Introduction 78
Ecology of the mountain hare – T. retortaeformis system *79*
A tactical approach *80*
Methods 81
The model *81*
Characterising real hare time series and parasite burdens *82*
Characterising simulated hare time series and parasite burdens *82*
Model performance *83*
Structural changes to the best fit model *83*
Changes to the parameterisation of models *84*
Results 84
Does making the timing of breeding dependent on maternal body size and parasite burden generate delayed life history effects (DLHEs)? *85*
Do DLHEs reduce the strength of direct parasite effects necessary to reproduce observed dynamics? *85*
How do different transmission mechanisms affect the dynamics? *86*
Can the wide geographical diversity of observed dynamics across Scottish populations be recovered? *86*
Discussion 87
Appendix 5.1: Body size 102
Appendix 5.2: Birthdate 102
Appendix 5.3: Litter size 103
Appendix 5.4: Adult hare mortality 104
Appendix 5.5: Parasite transmission 104

CHAPTER 6. PERIODIC TRAVELLING WAVES IN A SIMPLE HOST-PARASITE MODEL PARAMETERISED USING APPROXIMATE BAYESIAN INFERENCE 109

Abstract 109
1. Introduction 110
2. Methods 112
(2a) The host-parasite model *112*
(2b) Empirical parameter estimation *113*
(2c) Parameter estimation using rejection-based approximate Bayesian inference *113*
(2d) Summary statistics of hare and parasite time series *115*
(2e) Spatial extension *116*
3. Results 117
(3a) Temporal dynamics *117*
(3b) Spatio-temporal dynamics *119*
4. Discussion 119
Appendix 6.1: Re-analysis of empirical parameter estimates 131
Appendix 6.2: Numerical scheme for the spatial host-parasite model 132

CHAPTER 7. GENERAL DISCUSSION 138

The stability - complexity debate 138
Periodic fluctuations in the numbers of mountain hares 143

CITED LITERATURE 147

List of Tables

Table 2.1. Spillover and union in Geršgorin discs 27

Table 4.1. Parameter estimates and plausible limits from field experiments and related host-parasite systems with which to parameterize the hare - *Trichostrongylus retortaeformis* model 65

Table 5.1. Individual based model parameter values and their plausible ranges used in model analyses 92

Table 5.2. Mean (and range) of four characteristic properties of real and simulated mountain hare time series and parasite burdens 93

Table 5.3. The effect of structural changes on the stability of modelled dynamics and fit to four characteristic properties of observed mountain hare time series and parasite burdens 94

Table 5.4. Elasticity analysis showing the proportional effect of changes in parameters of the best fit model on four characteristic properties of mountain hare time series and parasite burdens 95

Table 6.1. Model parameter estimates from empirical data sources and approximate Bayesian inference. 124

Table 6.2. Summary statistics of real and modelled mountain hare and *T. retortaeformis* population dynamics 125

List of Figures

Figure 2.1. Equitable and inequitable relative distributions 28

Figure 2.2. Geršgorin discs in the complex plane..29

Figure 2.3. Effect of variance in the diagonal elements of stable Jacobians (var(g_{ii})) on the relationship between model ecosystem resilience ($\mathrm{Re}\,\lambda_d$) and interactivity 30

Figure 2.4. Effect of variance in the equilibrium relative abundance distribution ($\mathbf{N}^*$) on ecosystem stability at different levels of interactivity..31

Figure 2.5. Brauer Cassini ovals 32

Figure 3.1. The probability of permanence with increasing complexity 49

Figure 3.2. The probability that ecosystems were permanent as skew towards weak interactions was increased..50

Figure 3.3. The probability that ecosystems were permanent, had a locally stable interior equilibrium point or were both permanent and locally stable, with increasing complexity...51

Figure 3.4. The probability an ecosystem was permanent but locally unstable and the probability an ecosystem was locally stable but not permanent with increasing complexity...52

Figure 3.5. Attractors on the boundary that cause non-permanence 53

Figure 4.1. Simulated population dynamics based on the empirical information available on the hare-parasite interaction 66

Figure 4.2. Parameter changes required to obtain dynamical properties observed in wild hare populations 67

Figure 4.3. Simulated population dynamics after parameter changes to get closer to the observed dynamical properties..68

Figure 4.4. The effect of small, plausible changes in parameters on the amplitude of the limit cycles 69

Figure 4.5. The effect of small, plausible changes in parameters on stability and period70

Figure 5.1. Schematic diagrams showing structure in the model 96

Figure 5.2. Simulated population dynamics from a single run of the best fit model........97

Figure 5.3. Summary statistics for four characteristic properties of mountain hare time series and parasite burdens...98

Figure 5.4. Simulated hare and parasite population dynamics following structural changes to the best fit model..99

Figure 5.5. Comparing variation in four characteristic properties of mountain hare time series and parasite burdens across different models and to the observed variation 100

Figure 5.6. The relationship between the amplitude of hare cycles and the 'overall' parasite effect on hare fecundity when maternal effects on leveret birthdate were removed from the best fit model 101

Figure 6.1. Population dynamics of the non-spatial mountain hare - *T. retortaeformis* model parameterised with estimates using empirical data sources and approximate Bayesian inference 126

Figure 6.2. Parameter prior distributions based on empirical data and posterior distributions based on ABC using summary statistic vector 1...............................127

Figure 6.3. Parameter prior distributions based on empirical data and posterior distributions based on ABC using summary statistic vector 2...............................128

Figure 6.4. The spatial mountain hare - *T. retortaeformis* model parameterised with empirical point estimates generates a wave front of hares and parasites...............129

Figure 6.5. Spatio-temporal dynamics of the spatial mountain hare - *T. retortaeformis* model parameterised with the most likely estimates using summary statistic vector 2. A wave front moves across the spatio-temporal domain with succeeding periodic travelling waves 130

Supplemental Figure 5.1. Schematic diagrams showing the conceptual difference between two approaches to setting burden thresholds in the allocation of fecundity in female hares 107

Supplemental Figure 5.2. Manipulation of burden thresholds in the allocation of ova shed to female hares in the second litter 108

Supplemental Figure 6.1. Periodic travelling waves (PTWs) generated within the empirical parameter plausible envelope...135

Supplemental Figure 6.2. Slowing hare diffusion rate appears increases the spatial period and amplitude of periodic travelling waves...136

Supplemental Figure 6.3. Speeding up hare diffusion rate decreases the spatial period and amplitude of periodic travelling waves 137

Acknowledgements

I consider myself extremely lucky in the supervision, team and department within which I have found myself. I was primarily under the wing of Dan Haydon with additional nurturing by Louise Matthews. Both have been endlessly supportive and forgiving despite my wavering confidence, poor time management skills and volatile emotions. Dan has challenged me in all ways, from the mental to the physical and sometimes both simultaneously – like being probed for thoughts on Geršgorin discs whilst walking in the Highlands. I thank Dan for providing me with opportunity and for eternally enriching my life.

The members of the theoretical ecology group and the Boyd Orr Centre for Population and Ecosystem Health have been a network of support, and along the way I have had the privilege of consulting with some great minds, including Christina Cobbold, Richard Reeves, Hawthorne Beyer, Heather Ferguson, Graeme Ruxton, Jan Lindstrom, Marco Morelli and Gaël Thébaud. I have to particularly thank Douglas Kerlin and Anaid Diaz for being my companions on this journey into the world of modelling. We all started our PhDs at the same time and we grew together (although not at the same rate: Douglas and Anaid finished 6 months ago!).

I have had the pleasure of collaborating with great people outside the department. I thank Scott Newey and Simon Thirgood for trusting me with their hares. They also had to witness me get out and do some field work, with all the accompanying calamities - definitely the worst was dropping my car key somewhere on a knee-deep heather moor. Working with Steve Webb on the spatial hare model was my first solo mission without Dan, and I thank Steve for making it very enjoyable.

People I have to thank for getting me to the point of signing up: my father John Townsend for initially planting the seeds of the idea of finding a niche by intersecting disciplines, which I let germinate and sprout as mathematics and ecology; Richard Law for guiding my first steps into mathematical ecology without any pain; Simon Jennings and Nick Dulvy for encouraging me to take the PhD studentship where I was forced to write equations on a white board during my interview.

I moved to Glasgow to take up this challenge and I have to thank the city as it is the best place I have ever lived. During my time here I have met some wonderful people. Davina Hill was the first person I befriended in Glasgow, and has remained a loyal and caring friend throughout my time. Christine Donaldson became a very special friend and exercise enforcer. I met my partner Nick Beevers here, who made me laugh when things were getting overwhelming and had a wonderful skill for distracting my mind away from

Geršgorin discs. The rest of lunch hay-day crew must also be mentioned, Chris Foote, Patrick Walsh, Steve Larcombe, Richard Inger, Tom Pike and Ashley Le-Vin with whom I spent my favourite part of the day.

I am forever grateful to the Unity centre for helping me keep my own privileged circumstances in perspective, and for introducing me to so many remarkable personalities, especially Ahmadi, Mark, Jane, Stephen, Jamie and Phill. The CRAG and climate march organisers have been immensely important at keeping my mind alert to the world outside the academic bubble and through which I have met incredible people including Andy, Liz Irene and Kathy. I lived in four different flats during my studies. I had great times living with Tom (Geck), Sandra, Robin and Daniel. Some of my happiest days were spent eating homemade banoffee pie with Lulu. I have delighted in the re-ignition of an old flame with Katherine: Countdown. Some of the other great people I have met here: Peter Hoebe, Clare Marsden, Ally Donaldson, Andy Higginson, Liz Masden, Annabelle Haudry, Lilianna D'Alba, Pierre Bize, Angus Cameron, Flavie Vial, Tim Burton, Donald Malone, Andrew Jackson and Jo Mould.

I am grateful to old friends for still being my friends despite long periods of PhD-induced rubbishness on my part: Helen Dickinson has been my rock, Nick Berry for spurring me on, Despina Psarra, Lucy White, Natalie Coltman and Nick Askew, Alice and Nick Hardiman, Bjorn and Helfrid.

I realise I am very lucky to have the family I do. Such rich minds, philosophies and pursuits. I would like to thanks my parents, Dinah and John, and my brother Jack, and his partner Andrea, for their imperturbable support and love, and my aunt Grizelda Holderness for her inspirational personality and art (front page).

Finally I must thank NERC for keeping me in popcorn and laptops, and Lorna Kennedy, Florence McGarrity and Felicity Huntingford for it never being too much trouble.

During the course of my PhD some events occurred that I would like to acknowledge here: the transition of my father from a potty doctor to a professional, award-winning potter; the passing of my heroic grandfather Hardwick Holderness; the growing frailty of my equally strong-willed and liberal-minded grandmother Elspeth Holderness; Carolyn and Gael had a baby girl; Christine Gould became Christine Donaldson; Alice Davies became Alice Hardiman; Lucy Taylor became Lucy White; Barack Obama became the president of the USA.

S.E.T.

Candidate's declaration

I declare that the work recorded in this thesis is entirely my own, except where otherwise stated, and that it is also of my own composition. Much of the material included in this thesis has been produced in co-authorship with others and some has been presented for publication. My personal contribution to each chapter is as follows:

Chapter 2.	In preparation for submission as: Sunny E. Townsend, Louise Matthews & Daniel T. Haydon. Species abundance distributions and model ecosystem resilience - interactivity relationships. The idea was suggested by DTH and jointly developed by DTH and SET. SET performed all model simulations and analysis, and drafted the manuscript. Mathematical support provided by LM. Drafts enhanced by DTH and LM.
Chapter 3.	Submitted to the Journal of Theoretical Biology as: Sunny E. Townsend, Louise Matthews & Daniel T. Haydon. On the generality of stability - complexity relationships in Lotka-Volterra ecosystems. Concepts developed by LM, DTH and SET. SET performed all model simulations and analysis, and drafted the manuscript. Drafts enhanced by DTH and LM.
Chapter 4.	Published as: Sunny E. Townsend, Scott Newey, Simon J. Thirgood, Louise Matthews & Daniel T. Haydon. Can parasites drive population cycles in mountain hares? Proceedings of the Royal Society B: Biological Sciences, 276, 1611-1617. Data collection and compilation by SN. Initial concept by SN, SJT, DTH and developed by DTH, LM and SET. Data analysis, model simulations and analysis conducted by SET. Drafts enhanced by SN, SJT, LM and DTH.
Chapter 5.	In preparation for submission as: Sunny E. Townsend, Scott Newey, Simon J. Thirgood, Louise Matthews & Daniel T. Haydon. Dissecting the drivers of population cycles: interactions between parasites and mountain hare demography. Conception of ideas jointly by SN, DTH and SET. SET performed all model simulations and analysis, and drafted the manuscript. Mathematical support from LM and DTH. Drafts enhanced by SN, SJT, LM and DTH.
Chapter 6.	Periodic travelling waves in a simple host-parasite model parameterised using approximate Bayesian inference. Conception and development of ideas by Steve Webb and SET. Mathematical support from SW, statistical support from Hawthorne Beyer. Drafts enhanced by SW, HB and DTH. A version which will develop the mathematics further is in preparation for submission as: Sunny E. Townsend, Steven Webb, Scott Newey, Simon J. Thirgood & Daniel T. Haydon. Periodic travelling waves in a simple host-parasite model.

I further declare that no part of this work has been submitted as part of any other degree.

Sunny Elspeth Townsend
University of Glasgow
September 2009

Chapter 1. General introduction

In 1958 Charles Elton identified that a “wise principle of co-existence between man and nature” was needed to argue the case for nature conservation under the intensifying press of humanity. He recognised that it was not likely, or right, that animals would be put before humans, nor that preservation of the natural world as something of pure intrigue or aesthetic pleasure should come at the cost of human survival. However he did identify a practical reason for the conservation of diversity, “because it tends to promote ecological stability”, giving resistance to our crops, forests, fisheries etc. against destructive population explosions and invasive species. Elton’s reflections provide a noble motivation to study the stability of ecosystems. In contemplating the coupling of ecological diversity and stability he continues,

> “for if this can be shown to be anywhere near the truth, it will have to be admitted that there is something very dangerous about handling cultivated land as we handle it now, and even more dangerous if we continue to go farther down the present road of ‘simplification for efficiency’…the whole matter is supremely important to the future of every species that inhabits the world”.

Stability - complexity relationships

Elton was not able to provide proof of the coupling between stability and diversity, only a list of observations which appeared to support the relationship (Elton, 1958). He called for additional research and threw down the gauntlet to ecologists to provide a reason for ecosystems to be respected. It is understandable therefore that the relationship between the diversity and stability of ecosystems has been one of the most consuming topics in ecology for decades.

Early on the message was clear, even close to dogma (Pimm, 1991), that ecological diversity and stability went hand in hand. An early notion of ecosystem stability was Odum’s (1953) stability principle based on the second law of thermodynamics, that states that energy spontaneously tends to flow only from being concentrated in one place to becoming dispersed. He wrote:

> “According to this concept any natural closed system, whether the earth itself or a smaller unit, such as a lake, tends to change until a stable state, with self-regulating mechanisms is developed. Self-regulating mechanisms …bring about a return to constancy if a system is caused to change from the stable state by a momentary outside influence”.

The major contribution of Robert MacArthur, the man who came to be considered the father of theoretical ecology, was made in 1955. Using Odum’s stability principle, he argued that if the amount of choice energy has in following paths up through the food web is greater, then the effect of excesses in energy i.e. caused by overpopulation of one species, will have a lower impact on the rest of the community (MacArthur, 1955). This paper has been cited as proving that the stability-diversity relationship should be positive, including by MacArthur’s professor G. Evelyn Hutchinson in his seminal paper on the diversity of animals (Hutchinson, 1959). In fact MacArthur does not provide a mathematical proof, which May (1971) picked up on: “...this work, cogent and insightful though it is, is not (as it is sometimes mistaken to be) a "formal [mathematical] proof of the increase in stability of a community as the number of links in its food web increases".” (May’s quote is taken from Hutchinson (1959)). The first mathematical modelling was undertaken by Gardner & Ashby (Gardner and Ashby, 1970) on generic systems with connected dynamic components that were assumed to be at equilibrium, which May’s 1971 paper, subsequent Nature paper (1972b) and book (1973) expanded in a specifically ecological context. They used simple linear dynamics for which ecosystem complexity and stability could be defined unambiguously: complexity as the number of interacting components (species), the degree of connectance between interacting components and the strength of these interactions; and defined a stable system as one which returned to equilibrium after a perturbation. With both mathematical and computational support, they showed that more complex models had a vanishing probability of being stable. The prevailing view was challenged – were ecosystems stable because of complexity, or in spite of complexity? Despite the final comment in May’s 1971 paper:

> “That stability may usually go with complexity in the natural world, but not necessarily in mathematical models, is not really paradoxical. In nature we deal not with arbitrary complex systems, but rather with ones selected by a long and intricate process… mathematical theorems tend to deal with general complex systems, which are quite another matter”,

most ecologists did perceive a paradox at the centre of ecology.

On the one hand, it could be argued that the paradox is being resolved. May’s argument became a prediction that the ecosystem structures we observe should contain structure that enhances stability. Fundamental ecological realities lacking from the simple dynamical models were highlighted (Lawlor, 1978, Roberts, 1974) and observing universality across food webs would identify common organising principles across different ecosystems. For example, many empirical studies agree that low connectance and a skew towards weak interaction strengths (few strong, many weak) are common features of large, real ecosystems (Berlow, 1999, Paine, 1992, Bascompte et al., 2006, De Ruiter et al., 1995). This property has been attributed to the architectural features of omnivory (Emmerson and Yearsley, 2004), compartmentalisation (Rejmanek and Stary, 1979, Krause et al., 2003) and long loops (Neutel et al., 2002). Such non-random patterning can increase the stability of competitive communities (Jansen and Kokkoris, 2003, Rozdilsky and Stone, 2001) and food webs (Neutel et al., 2002, De Ruiter et al., 1995, McCann et al., 1998, Emmerson and Yearsley, 2004), allowing complex systems to persist. Another non-random pattern in ecosystems is the ubiquity of inequity in species abundances (McGill et al., 2007). The species abundance distribution is a fundamental measure of ecosystem structure and biodiversity (Magurran, 2004) yet it is rarely linked to the dynamical properties of ecosystems. How relative commonness and rarity affects stability - complexity relationships has remained an open question. This forms the focus of **Chapter 2**.

On the other hand, it may be argued that the paradox eludes resolution because it has been almost impossible to synthesise theory with findings from the field. While theoreticians were making predictions about "what kind of communities we observe and those we do not" (Pimm, 1991), how was an empirical ecologist supposed to test this? Further, the interaction strengths that theoreticians were using were difficult to estimate in the field and not what empiricists typically measured (Berlow et al., 2004). Consequently, ecological stability became a sizeable and complicated subject in which "rarely did two ecologists look at the same question" (Pimm, 1991). For example, Elton (1958), who took his notions of stability largely from the field, implied all of the following: population variability, population recovery, the ease of invasion and the consequences of invasion (Pimm, 1991). Going by the definitions given by Grimm & Wissel (1999), MacArthur was thinking about resistance (dynamics staying essentially unchanged despite the presence of disturbance) whereas May was talking about probability of resilience (returning to reference state after a temporary disturbance).

An obvious criticism of Gardner & Ashby (1970) and May's (1971) mathematical models is that ecological systems are not simple dynamic systems. Unlike physical or chemical processes from which the mathematics was adapted, ecological systems are not largely deterministic but are a unique mixture of deterministic and stochastic forces to comparable degrees (Bjornstad and Grenfell, 2001). Furthermore, ecological systems do not have linear dynamics but contain gross non-linearities, which were left out 'as a first step' (Gardner and Ashby, 1970) for the sake of mathematical tractability. In fact the models are extremely general because they are linearised approximations (by Taylor expansion) at the equilibrium point of unspecified equations of multispecies dynamics. But this generality requires that the equilibrium points are assumed to be feasible. To check feasibility, a specific set of equations does have to be defined - the simplest and most familiar globally defined multispecies population growth model is Volterra's (1926) formulation of the classic Lotka-Volterra (LV) equations. (The distinction between local and general or global and specific applies to Lotka's and Volterra's alternative formulations of the LV equations (Haydon and Lloyd, 1999), and which I discuss further in Chapter 2.) Both local and global models of ecosystem dynamics have been used extensively in the study of stability - complexity relationships. By adopting either approach, ecologists take an equilibrium viewpoint of ecosystems and can only measure whether an equilibrium point is stable against very small perturbations and thus does not guarantee global stability (Law and Blackford, 1992). In 1987, De Angelis & Waterhouse voiced the concern:

> “The equilibrium view of ecological systems, which has always had a fair number of skeptics, now seems unsatisfactory to a large fraction, perhaps a majority, of ecologists. This dissatisfaction, expressed clearly by Reddingius (1971), Caswell (1978), Murdoch (1979), Connell and Sousa (1983), and Wiens (1984a), among others, does not hinge on the mere question of system stability, but on whether it is valid to define the existence of an equilibrium state at all, stable or unstable” (references found therein).

The mathematical intractability of global stability of multispecies systems means the equilibrium viewpoint has been the nucleus for theoretical study of ecosystem properties. However local stability analysis excludes the possibility of instability in the face of a large perturbation or the existence of non-equilibrium attractors (e.g. a periodic or chaotic attractor). The general consensus is that a more satisfactory definition of ecosystem stability is a global property called permanence, a test of species coexistence which requires only that densities of rare species tend to increase (Law and Blackford, 1992). While the permanence has its own restrictions, most seriously that demographic stochasticity could push trajectories which pass close to the boundary to extinction, its strength lies in asking basic globally qualitative questions of coexistence without dependence on understanding the complicated quantitative behaviour of the ecosystem dynamics:

> “There is a sense in which we have been asking more of our ecological models than may be necessary to predict the configurations of species that live together. The distinction between equilibrium and non-equilibrium dynamics is secondary to the question as to whether a set of species can live together in the first place. Arguably we would do better to find the configurations of species that cause the whole of boundary of the phase space to repel orbits that are not on the boundary, for it is at the boundary that questions of coexistence have ultimately to be settled. Informal ideas along these lines were suggested by Lewontin (1969), Maynard Smith (1969), Holling (1973), and Connell and Sousa (1983), and in recent years the notion has been given formal definition and extensively studied by mathematicians (reviewed by Hofbauer and Sigmund 1988)” Law & Blackford (1992, references found therein).

Yet despite these advances, the relationship between permanence and ecosystem complexity has only been addressed in a single paper (Chen and Cohen, 2001). In **Chapter 3** I present the second study on permanence-complexity relationships. Chen and Cohen

(2001) found permanence decreased with complexity just as did the early theoretical models using local stability analysis – but then they were explored in a similarly general framework. This opens up the question of how local and global stability are correlated, and the important question of 'how much confidence should we have in a theoretical ecology based on asymptotic [local] stability analysis?' (Anderson et al., 1992). By measuring the probability of local stability alongside permanence, I am able to study locally stable systems which are unstable in the face of a large perturbation (which I term 'fragile') and systems at non-equilibrium attractors (e.g. a periodic or chaotic attractor) and how they correlate with aspects of complexity.

Periodic fluctuations in the numbers of mountain hares

In the bridging paragraph between Robert May's (1973) book chapter on stability - complexity relationships and his chapter on stable limit cycles in few species models, May wrote:

> "In the models just considered, all the interactions between and within species were either represented by grossly simple equations or else summarised in the vicinity of equilibrium… It is difficult to effect any multispecies discussion otherwise. In this chapter, attention is restricted to models with but a few species, and considerably more detail is put into the description of the dynamical interactions between populations".

Over 35 years later this paragraph sums up the same transition I have taken from studying mathematical mechanisms of stability in general, large model ecosystems (Chapters 2 and 3) into the use of lower dimensional models to study the specific biological mechanisms that cause cyclic dynamics in Scottish populations of the mountain hare (Chapters 4 to 6). The hare system is simply a low dimensional subset of a higher dimensional system, yet I am forced to make the sharp transition from community ecology to population ecology, from a discipline which is strongly mathematical and data poor to one which is more empirical and data rich.

The reasons for cyclic dynamics in Scottish mountain hares are unclear, and this is the first attempt at using modelling to explore possible causes. Below I intertwine some historical context of population cycle research with justifications of the three modelling approaches I have taken. The first model (Chapter 4) is a simple ordinary differential equation (ODE) model of two interacting species. The framework is mathematically elegant and allows ecologists to employ mathematical concepts for analysis of the dynamic properties of the inter-specific interaction, but the model is biologically naïve and cannot incorporate potentially important detail. The second model is therefore the antipode, an individual based model steeped in biological reality that can only be studied by simulation (Chapter 5). The third model explores the influence of adding a spatial dimension to the simple ODE model (Chapter 6).

A fundamental mathematical contribution to the understanding of population cycles is the notion that persistent patterns of reasonably regular oscillations in natural ecosystems are stable limit cycles (May, 1973, May, 1972a). Limit cycles are closed loop trajectories with a fixed amplitude and period around an unstable equilibrium point and, as with a point attractor if it is stable, trajectories in the neighbourhood are attracted towards it. While this behaviour is qualitatively distinct from other types of dynamics in a deterministic setting, damped cycles can also be stochastically sustained. The mathematical causes of deterministic stable limit cycles are easily obtainable from any text on nonlinear dynamics (e.g. Hilborn, 2000): they are not possible with a single linear dynamic equation, but (at minimum and is not guaranteed) require the addition of non-linearity in the form of a time delay e.g. delay-differential equation or difference equation (although this is then not strictly a one-dimensional system (Hilborn, 2000)) or by adding a coupled interacting variable. The implication for ecologists is that for populations to exhibit stable limit cycles requires dependence of the current species density either on (1) an earlier density of the same species or (2) the density of other species. These two factors are often described in the ecological literature as ‘intrinsic’ and ‘extrinsic’ drivers of population cycles. Both types of factor have been implicated as the drivers of cyclic populations of an upland UK bird species, the red grouse (*lagopus lagopus*): the interaction with a parasite which reduces fecundity and increases mortality (extrinsic) (Dobson and Hudson, 1992b, Hudson et al., 1998, Hudson et al., 1992); and delayed density dependent changes in aggression and rate of young male recruitment (intrinsic) (Moss et al., 1996).

The work on red grouse has been successful in taking a synthetic approach to the study of population cycles, by using a combination of time series analysis, experimentation and mathematical modelling. Mountain hare cycles in Scotland have only really gained attention in the last few years with initiation of research by Scott Newey and Simon Thirgood at the Macaulay Institute in Aberdeen, although knowledge of the system has been greatly underpinned by many natural historical and specific population studies since the 1960s (e.g. Flux, 1962, Hewson, 1962). During this recent focus on cyclic dynamics in mountain hares, time series of hare shooting records from across Scotland have been analysed to statistically confirm that about half of populations are temporally cyclic, with a range of periods from 4 to 15 years and characteristically high amplitude with coefficients of variation of 0.39 to 1.80 (Newey et al., 2007b). Field experiments and surveys have been conducted (Newey et al., 2005, Newey and Thirgood, 2004, Newey et al., 2004) and the currently favoured explanation implicates an extrinsic driver of cycles - the interaction with a helminth parasite *Trichostrongylus retortaeformis* that reduces female fecundity (Newey et al., 2007a). Mathematical modelling has not yet been directed at this problem and, while this approach cannot directly test the parasitism hypothesis, modelling can assist in determining whether this interaction is capable of generating observed population dynamics. In **Chapter 4**, I use a simple ordinary differential equation (ODE) model of the interaction between a host and macroparasite (May and Anderson, 1978, Anderson and May, 1978) to test whether deterministic realistic hare stable limit cycles can be generated with parameters based on the best available empirical data.

Although density dependence is accepted as an important driver of population cycles, this has not always been the case. As with the relationship between ecological stability and complexity, it was Charles Elton who raised the challenge to ecologists to explain the phenomenon of population cycles. In his seminal paper (Elton, 1924) ‘Periodic fluctuations in the numbers of animals: their causes and effects’, which was based mainly on the periodic fluctuations of Norwegian lemmings and snowshoe hares, he argued that cycles must be driven by climatic fluctuations because of the synchrony of the fluctuations across huge areas. Despite theoretical interest in cyclic dynamics that pre-dates Elton’s paper (Lotka, 1925, Volterra, 1926), and Nicholson & Bailey’s (1935) account of both the mathematics and the biological mechanisms behind insect population cycles, mammal population cycles and models that were able to produce cyclic dynamics were studied largely independently: “the generality and importance of density dependent feedback mechanisms in creating fluctuations was not fully understood at that time” (Lindstrom et al., 2001). By the 1950s, a major cleavage split factions which, on one side, thought that cycles were driven by density independent processes which forced populations to obey environmental conditions, whilst the other side argued for density dependent processes which acted independently or tracked changes in the environmental conditions (Lindstrom et al., 2001). More recently there has been a growing realisation that both density-dependent processes and environmental variability shape real population dynamics (Lundberg et al., 2000), and there are numerous ways in which stochastic and deterministic processes can interact to generate regular fluctuations, even if they are not strictly stable limit cycles (Kaitala et al., 1996, Roughgarden, 1975, Lundberg et al., 2000, Bjornstad and Grenfell, 2001).

Related to this, there has also been a growing call for consideration and testing of multiple causes of cyclic dynamics. Single-factor hypotheses have been continually put forward since Elton’s (1924) paper, as expressed by Lindstrom et al. (2001): “one can expect a hypothesis to be raised approximately every four years” and for which they sceptically note that “different taxa or systems seem to have attracted different hypotheses…it is impossible to judge whether these taxonomic/system differences are real or simply reflect different emphases by research teams on different continents”. The ability to explore and contrast multiple factors may certainly depend on the scale and scope of studies, and there are few studies which have managed it. One important success has been the Klaune Boreal Forest Ecosystem Project, the largest ever terrestrial ecological experiment which ran from 1986 to 1996 in the south-western Yukon (Krebs et al., 2001b). Using a factorial experimental design the project disentangled the relative importance of some of the strongest candidates for control of the 10-year snowshoe hare cycles. Indeed, no one factor was singled out and instead food and predation were found to act together to drive the hare cycles. Furthermore, since the Kluane project, an intrinsic factor has been proposed to act synergistically with food and predation to drive cycles, based on striking differences in the reproductive output of captive female populations from low and high phases of the cycle (Sinclair et al., 2003, Krebs et al., 2001a). Similarly the most recent work on red grouse has synthesised the intrinsic and extrinsic factors into a multifactor hypothesis to offer the following explanation for their cycles: under conditions of high grouse density, elevated testosterone levels (and associated increases in male aggression) lead to suppression of the grouse immune system and thus increased parasitism (Mougeot et al., 2005, Redpath et al., 2006).

For modelling mountain hare population dynamics, the ODE model is general and strategic (Chapter 4) but it is also purely deterministic and ecologically naïve. It also considers only a single-factor hypothesis (parasitism) for cycles. There is substantial evidence from a range of mountain hare studies (Hewson, 1968, Flux, 1970, Iason, 1990 and Scott Newey pers. comm.) that maternal ‘quality’ influences the birthdate of young which in turn influences offspring ‘quality’. Such maternal effects can generate delayed responses to density and thus can potentially drive population cycles (Inchausti and Ginzburg, 2009). While each of the flaws of the ODE model could be tackled individually by developing a suite of more complex mathematical models, instead I develop a highly tactical model that envelops much of the ecologically complexity (**Chapter 5**). Elements of the structure are systematically modified or removed to dissect out their dynamical influences. Demographic stochasticity is incorporated, increasing the realism of the model and permitting stochastically sustained stable limit cycles.

In **Chapter 6,** I consider a spatial extension to the ODE mountain hare-parasite interaction model of Chapter 4. The strategic models of classical, non-spatial population dynamics were adapted from the mathematics of physiochemical disciplines to tackle population dynamical problems. With this derivation came three fundamental assumptions which are sufficiently realistic in models of simple physiochemical systems but are often violated in the ecological context (Czárán, 1998). First, populations consist of large numbers of individuals. Second, all individuals of the same population are identical in every dynamically relevant respect. Third, the movement of the individuals is such that the population as a whole can be treated as a perfectly mixed system such that each individual experiences the same environment. Relaxing the assumptions can affect the stability of populations and coexistence of interacting species, and lead to spatial patterning (Hassell et al., 1991, Turing, 1952, Bascompte and Sole, 1995).

For the mountain hare – *T. retortaeformis* system, the initial aim is to study the impact of space on the ODE model dynamics without introducing population structure or specifying scale (and therefore only the third assumption of perfect mixing need be relaxed for our purposes). While space can be introduced implicitly, for example using metapopulation models (Levins, 1969), direct spatial extension of the classical non-spatial models is ideally suited for assessing the impact of space on population dynamics because it allows comparison of predictions with the non-spatial counterpart (Czárán, 1998). In spatially explicit models, density has a location and thus it is local rather than overall density which is influenced by (and influences) the dynamics. The spatial dimension can be introduced as a discrete variable using patch-abundance models (represented by an ODE for each patch) or continuous space using reaction-diffusion models (represented by partial differential equations (PDE)). The main theoretical advantage of continuous-space models is the deterministic and tractable nature as a means of providing theoretical insights and generic understanding of spatial dynamics (Keeling and Rohani, 2007). However the mathematics behind these formalisms is complex and often highly technical (Murray, 1993). Perhaps this is why, despite its widespread application in ecology, the simple host-parasite ODE model (May and Anderson, 1978) adopted in Chapter 4 has never been spatially extended in continuous time and the resulting spatial dynamics remain unexplored. During the course of my Ph.D candidacy I was approached by a mathematician, Dr. Steve Webb at the University of Strathclyde, with the proposal of co-developing a PDE model of the mountain hare – parasite system. This is presented and studied in Chapter 6.

Chapter 2. Species abundance distributions and model ecosystem resilience - interactivity relationships

Abstract

Despite the fact that the species abundance distribution is a fundamental measure of ecosystem structure and biodiversity, and the decades of debate over the relationship between ecosystem stability and complexity, the effect of inequity in species abundances on stability - complexity relationships has remained an open question. Rarely do models link a static property like the abundance distribution to the dynamical properties of ecosystems. Here, we review different approaches to ecosystem modelling using Lotka-Volterra equations, emphasising the different assumptions made in the way that Lotka and Volterra derived them. Then we synthesise analytical arguments with numerical results on the role of variance in abundance distributions on ecosystem stability - complexity relationships. The analytical approaches are two simple tools that couple resilience (the rate of return to a locally stable equilibrium post-perturbation) with complexity (measured as interactivity) of any ecosystem whose equilibrium dynamics are captured by a Jacobian matrix. The results show that the resilience of an ecosystem can increase with interactivity when the abundance distribution is characterized by a skew towards many rare species. Further, some natural distributions are more inequitable than others, and we found that more equitable ecosystems were on average more resilient than their less even counterparts. This study suggests that changes to the species abundance distribution are likely to alter the dynamical properties of a real ecosystem. We discuss further ways in which abundance distributions may influence stability - complexity relationships, and the limitations and extensions of the analytical approaches used.

1. Introduction

The stability of model ecosystems has traditionally been related to ecosystem structure via three forms of complexity: the number of links within the ecosystem, the strength of those links and species richness (May, 1972b). Species richness directly relates biodiversity to stability and enables the study of the effect of biodiversity loss and gain on stability (e.g. Borrvall et al., 2000, Dunne et al., 2002). The other key component of biodiversity is species abundance and its relative distribution is a widely adopted measure of ecosystem structure (Magurran, 2004). However, models that link the dynamic properties of ecosystems with the relative abundance of species are scarce (see Hubbell, 2001 ch3 for a review).

A variety of relative abundance distributions have been observed, from highly inequitable (e.g. a plant community in a subalpine forest) to relatively equitable (e.g. a bird community in a deciduous forest) (Whittaker, 1970). Models of species abundance envelop the full breadth of observed distributions, and are typically split into statistical models that describe patterns observed in real communities and biological models that reference an ecological process in order to explain natural distributions (Magurran, 2004). However, most of these models are criticised for being static because they omit any clear link to population dynamics (Hubbell, 2001), leaving obvious questions that remain poorly addressed.

Classical dynamical theory in community ecology, largely based on Lotka-Volterra equations (LVE), offers a means of exploring relationships between dynamic properties of ecosystems and relative abundance distributions. Yet despite the LVE having comprised the core approach to the theoretical study of ecosystem properties for decades, these relationships remain poorly understood. Recently, Wilson and colleagues (2003, 2006) developed a framework, by extension of the LVE, for predicting the abundance distribution and other ecosystem properties. However, this theory is not yet fully linked with ecosystem stability. The primary aim of this chapter is to use the LVE to address the question of how ecosystem stability - complexity relationships depend on the equitability of relative species abundances.

In this chapter we refer to model ecosystems with locally stable equilibria as stable, and compare the relative stability of ecosystems by measuring their resilience to a perturbation from equilibrium. Even though global stability is a more satisfactory definition of ecosystem stability (Jansen and Sigmund, 1998, Law and Blackford, 1992), the tractability of local stability analysis of linear (or linearised) differential equation models has advanced the theoretical study of ecosystem properties. This chapter reviews, synthesises and advances some aspects of that groundwork.

Reasoning that stability - complexity relationships may be affected by the relative commonness and rarity of species takes us back to the origins of the stability - complexity debate. A paradox at the centre of ecology was started by reports of negative relationships between the probability of local stability and complexity in randomly filled Jacobian matrices (May, 1972b, May, 1971), an observation that challenged the conventional intuitive arguments developed by ecologists (Elton, 1958, MacArthur, 1955, Odum, 1953). However these Jacobians were not as general as proclaimed because all diagonals of the Jacobian matrix had an identical value, thereby assuming no difference in intraspecific interactions within species. Led by the patterns found in real webs, equilibrium dynamical theory has explored the stabilising effects of non-random interactions between species (Haydon, 2000, Rozdilsky and Stone, 2001) and their distribution (Emmerson and Yearsley, 2004, Neutel et al., 2002, Jansen and Kokkoris, 2003, Kokkoris et al., 2002), rather than the stabilising effects of interactions within species. Intraspecific interactions are self-regulatory processes generated through direct density-dependent processes, and under some conditions indirect feedback loops, that contribute to self-regulation which can confer stability not only to individual population dynamics but also to community dynamics (Yodzis, 1980, Saunders, 1978, Saunders and Bazin, 1975). If variation in the diagonal elements of the Jacobian is permitted, stability can increase with complexity (Haydon, 2000).

Interspecific variability in density dependence arises naturally under at least two rationales: if some species are considered strongly self-regulating compared to others e.g. autotrophs vs. heterotrophs (McCann, 2000), and if there is variation in species abundances. Positive stability - complexity relationships can result when variance in intraspecific interactions stem from specifying autotrophs and heterotrophs (Haydon, 1994). However, the effect of variability in abundance has not been studied and, given the ubiquity of inequity in the relative abundance distribution of ecosystems (McGill et al., 2007), may also permit stability to increase with complexity. Haydon’s (1994) result, for reasons discussed in §3ai, applies to two types of complexity, the number of links within the ecosystem and the strength of those links, and therefore we restrict our investigation to these, and combine into a single term ‘interactivity’ (which we define precisely in §3ai of the chapter).

There are at least two reasons why studies of this link between relative abundance of species and model ecosystem stability have not been closely explored. First, species abundances also feature in the interspecific interaction terms of the LVE where their distribution affects the variance and covariance structure of the Jacobian with their own potential effects on stability (Emmerson and Yearsley, 2004, Jansen and Kokkoris, 2003, Kokkoris et al., 2002). Second, the LVE can generate a wide range of abundance distributions depending on the detailed distributions of the underlying parameters that describe the nature of species interactions (Wilson et al., 2003) thus making it difficult to control variance in the abundances. In this study we also encountered this problem and apply a solution: a method that permits direct assignment of the equilibrium relative abundance distribution. This method has been adopted in a handful of previous studies but they have either assumed all species abundances were identical and omitted to check the plausibility of intrinsic growth rates (Chen and Cohen, 2001), or have applied it to a very limited set of trophic relations (Emmerson and Yearsley, 2004, Pimm and Lawton, 1978). Here we explore the resilience - interactivity relationships of more generally structured ecosystems with plausible species intrinsic growth rates.

In this chapter we offer an analytical synthesis supported by numerical results on the role of variance in the relative abundance distributions on stability-interactivity relationships of ecosystems modelled using the LVE. Firstly (§2), we clearly define how we modelled our ecosystems, emphasising the distinction between Lotka and Volterra's view of the LVE and how we measured feasibility and ecosystem stability (following calls for clarity in community modelling (Fowler and Lindstrom, 2002)). Then we ask our primary question in §3: do equitable ecosystems have different stability-interactivity relationships to inequitable? Using numerical and analytical approaches we show that they do. In §3a*i*, we revisit the analytical argument put forward by Haydon (1994). In §3a*ii*, we present a novel analytical argument that shows stability can increase with interactivity if the diagonal elements of the Jacobian are not identical. In §3b, we show numerically that variance in the diagonals of Jacobian matrices can generate positive relationships between average stability and interactivity. These results re-emphasise that assuming identical values is unjustified and can potentially result in misleading conclusions. In §3c we present positive stability-interactivity relationships for ecosystems with variance in their equilibrium relative abundance distribution. Finally, the discussion (§4) is split into two parts. In §4a we discuss how the species abundance distribution influences stability - complexity relationships, and in §4b we discuss the limitations and extensions of the analytical approaches used here for studying stability - complexity relationships.

2. Modelling ecosystems using the Lotka-Volterra equations (LVE)

(2A) LOTKA VS. VOLTERRA: GENERALITY VS. ECOLOGICAL TRANSPARENCY

Randomly constructed model ecosystems (Gardner and Ashby, 1970, May, 1972b) were embraced as a starting point and a simple mathematical framework for investigating the organisational constraints within real ecosystems that may contribute to an association between complexity and stability (Lawlor, 1978, McNaughton, 1978). Soon after their inception, fundamental ecological realities which they lacked were highlighted (Lawlor, 1978), most critically the feasibility of the equilibrium point i.e. positive equilibrium abundances (Roberts, 1974). In order to impose the restriction of feasibility, a specific set of equations had to be defined.

Although the formulations of Lotka (1925) and Volterra (1926) share an identical mathematical structure for the population dynamics of n species in an ecosystem,

$$\frac{dN_i}{dt} = N_i\left(b_i + \sum_{j=1}^{n} a_{ij}N_j\right) \qquad \text{for } i = 1,\ldots,n, \qquad \text{Eqn 2.1}$$

they were derived independently using two fundamentally different sets of assumptions (Haydon and Lloyd, 1999, Pimm, 1982, Real and Levin, 1991). The application and interpretation of the LVE depends on whose view is adopted: the model can either represent the linearization of the per capita growth rates of each species at a non-trivial equilibrium (Lotka's) or they are the globally applicable dynamic equations (Volterra's). Lotka's formulation has the often underappreciated feature of generality: any system of equations (not even the variables need to be specified, although here we assume N_i to be relative species abundance) can be approximated (using Taylor expansion) around a desired point. The drawback is that the parameters b_i and a_{ij} are functions of derivatives evaluated at a particular equilibrium; they are not system-wide and therefore cannot be provided with any clear ecological interpretation. Volterra, however, formulated the global dynamics of an ecosystem as a set of non-linear equations, leading to parameters with clear ecological meaning (a_{ij} per capita interaction strengths, b_i intrinsic growth rates) and with which the whole state space dynamics could be explored. Assuming a particular form for the dynamics within the full state space is of course likely to be a gross oversimplification of reality. In the same spirit as Emmerson & Yearsley (2004), in this chapter the LVE are applied to question the real world rather than emulate it.

(2B) MODEL FORMULATION

(2bi) Lotka's formulation

The stability properties of the equilibrium point ($\mathbf{N}^*$) follow from the eigenvalues of the Jacobian matrix $\mathbf{G}$. For dynamics given by the expression

$$\frac{dN_i}{dt} = N_i F_i(\underline{N})$$

where the F_i are the per capita rates of increase for each species, the elements of **G** are the partial derivatives of $d\mathbf{N}/dt$ with respect to N_j $\left(g_{ij} = \partial(N_i F_i)/\partial N_j \big|_{N_j = N_j^*} \right)$,

$$\mathbf{G} = \begin{bmatrix} g_{11} & g_{12} & \cdots & g_{1n} \\ g_{21} & g_{22} & \cdots & g_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ g_{n1} & g_{n2} & \cdots & g_{nn} \end{bmatrix}.$$

For Lotka's ecosystems, the functions describing the per capita rates of increase are unspecified, allowing us to specify the elements of the Jacobian directly. Without F_i the equilibrium point is indeterminate and cannot be checked for feasibility ($N_i^* > 0$).

Lotka's ecosystems were used to conduct a numerical study of the effect of variance in the Jacobian diagonal elements on resilience - interactivity relationships (§3b). Ecosystem interactivity (see §3ai for a formal definition) was controlled by the number and magnitude of Jacobian off-diagonal elements, and ecosystem resilience is formally defined in §2bv.

(2bii) Volterra's formulation

Volterra's ecosystems were used to conduct a numerical study of the effect of variance in the equilibrium species abundances on resilience - interactivity relationships (§3c). In this formulation, the per capita growth rates (F_i) are specified in Eqn 2.1 and the Jacobian matrix takes the form:

$$\mathbf{G} = \begin{bmatrix} a_{11}N_1^* & a_{12}N_1^* & \cdots & a_{1n}N_1^* \\ a_{21}N_2^* & a_{22}N_2^* & \cdots & a_{2n}N_2^* \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}N_1^* & a_{n2}N_n^* & \cdots & a_{nn}N_n^* \end{bmatrix}.$$

The equilibrium point is determined by setting Eqn 2.1 to zero (in matrix form, $\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{b}$, where **A** is the matrix of per-capita interaction strengths and **b** is the vector of intrinsic growth rates). Typically, the parameters, the elements of **A** and **b**, are assigned and the feasibility of the equilibrium abundances $\mathbf{N}^*$ checked. However, this approach does not permit control over variance in abundance. An alternative is to assign a feasible $\mathbf{N}^*$ and $\mathbf{A}$, and calculate $\mathbf{b}$ (Chen and Cohen, 2001, Emmerson and Yearsley, 2004, Emmerson and Raffaelli, 2004). By setting all per-capita intraspecific interactions (a_{ii}) to identical values (here -1) variance in the diagonal of the Jacobian is determined solely by the abundance distribution. This also controls for the potentially stabilising effect of variance in the distribution of a_{ii} values (Haydon, 1994).

We adopted this method but adapted it to permit control over interactivity as well as abundances, assigning the off-diagonals elements of the Jacobian (g_{ij}) rather than per-capita interspecific interactions (a_{ij}). The Jacobian matrix of our Volterra ecosystems therefore took the form:

$$\mathbf{G} = \begin{bmatrix} -N_1^* & g_{12} & \cdots & g_{1n} \\ g_{21} & -N_2^* & \cdots & g_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ g_{n1} & g_{n2} & \cdots & -N_n^* \end{bmatrix}.$$

The a_{ij} parameters were recovered by calculating the $\mathbf{A}$ matrix (= $[\mathrm{diag}(\mathbf{N}^*)]^{-1}\mathbf{G}$). The b_i values were then computed ($\mathbf{b} = -\mathbf{A}\mathbf{N}^*$) and checked for plausibility (autotroph $b_i > 0$, heterotroph $b_i < 0$: Pimm (1982); Emmerson & Yearsley (2004)).

(2biii) Model ecosystem size and structure

As a compromise between structural generality and computational tractability, ecosystems were modelled with ten species ($n = 10$). They contained paired interactions of consumer and resource species and a cascade trophic structure defined by no loops (Cohen and Newman, 1985) or discrete subwebs. The cascade trophic structure fits webs where body size tends to equal trophic level (Warren and Lawton, 1987, Cohen et al., 1993) and was constructed by placing negative effects of consumers on resource species above the diagonal of the Jacobian $\mathbf{G}$. The number of interactions between species divided by the number of topologically possible links (excluding cannibalism) gave the connectance C of the ecosystem. The binary connectance matrix $\mathbf{C}$ was checked for no discrete subwebs (all elements of the matrix $\mathbf{C}^{100}$ were non-zero). The strength of an interspecific interaction was measured as the magnitude of an off-diagonal element of the Jacobian $\left(|g_{ij}|_{i \neq j}\right)$. In the numerical studies, interactivity was varied by regulating connectance and mean absolute interspecific interaction strength ($\overline{|g_{ij}|_{i \neq j}}$, MAIIS for brevity).

(2biv) Species abundance distributions

Variance in the diagonal elements of the Jacobian (g_{ii}) for Lotka's ecosystems, and variance in relative equilibrium abundances for Volterra ecosystems, was generated using the beta probability density function (Fig 2.1). The beta distribution is continuous with a finite range between 0 and 1, and by varying one parameter we were able to generate distributions which were equitable (all identical), had low inequity (var = 0.008) or high inequity (var = 0.041). Assigning uneven distributions was undertaken hierarchically, such that species one in the model ecosystem was assigned the greatest abundance and species n the smallest. In this way, species which were more predatory than prey had a smaller Jacobian diagonal element or abundance.

(2bv) Ecosystem stability

The dynamic local stability of the equilibrium point is described by the n eigenvalues of the Jacobian **G**: stable if all real parts of the eigenvalues are negative. One of the long-standing issues in the stability - complexity debate has been over the correct sampling space for Jacobians (Haydon, 1994, Saunders, 1978, Saunders and Bazin, 1975). Here we sampled only those with stable equilibria and compared between samples (where some aspect of the structure was changed) using the real part of the dominant (most positive) eigenvalue ($\mathrm{Re}\,\lambda_d$). $\mathrm{Re}\,\lambda_d$ is related to the rate of return of the locally stable system to equilibrium following a (small) perturbation, defining the 'resilience' of an ecosystem (McCann, 2000). The more negative the dominant eigenvalue of the model ecosystem, the faster its return rate and therefore the more resilient it is to perturbation. Resilience is affected by a trade off between positivity and negativity in the real parts of all eigenvalues because the sum of the real parts of eigenvalues, and therefore the mean of the eigenvalues, is determined by the sum of the trace $\left(\sum_{i=1}^{n}\mathrm{Re}(\lambda_i)=\sum_{i=1}^{n}g_{ii}\right)$. We wanted the mean to stay the same for each Jacobian and therefore the trace was standardised to ensure its sum was always -1.

3. Do equitable ecosystems have different stability-interactivity relationships to inequitable?

(3A) ANALYTICAL STUDY OF THE EFFECT OF VARIANCE IN THE DIAGONAL ELEMENTS OF THE JACOBIAN ON RESILIENCE - INTERACTIVITY RELATIONSHIPS

We first looked at how resilience may be affected by variance in the diagonal elements of Jacobian matrices (var(g_{ii})). Here we describe two analytical results which show that when var(g_{ii}) > 0, the resilience of a complex system is able to increase with interactivity. The first is the well-established Geršgorin disc theory and we outline the relevant aspects of the theory. The second is the variance of the distribution of the real parts of eigenvalues, a novel approach based on an equation introduced by Levins (1975).

(3ai) Geršgorin disc theory

Geršgorin disc theory describes the distribution of eigenvalues in the complex (imaginary-real) plane (Geršgorin, 1931). It was developed in 1931 by Semyon Aranovich Geršgorin (1901 –1933), a Soviet (born in Belarus) mathematician, although only relatively recently applied to community ecology for the first time (Sugihara, 1983). Elements relevant to the study of stability - complexity relationships are revisited here (Haydon, 1994, Haydon, 2000), whilst proofs and other aspects of the theory can be found in Varga (2004) and Brualdi & Mellendorf (1994). For an *n x n* Jacobian matrix **G** there are *n* Geršgorin discs $D_1 \ldots . D_n$, one corresponding to each row. A Geršgorin disc is defined over the complex plane such that D_i is centred at the value of the diagonal element (g_{ii}) and has a radius (r_i) which is equal to the sum of the absolute values of the off-diagonal elements (g_{ij}) in the *i*th row:

$$r_i = \sum_{\substack{j=1 \\ j \neq i}}^{n} \left| g_{ij} \right| \qquad \text{Eqn 2.2}$$

Thus the positions of discs are set by the diagonal element whereas the radii of discs depend on the number and magnitude of off-diagonal elements (Fig 2.2a). We define the mean radius ($\overline{r_i}$) of Geršgorin discs as the interactivity of an ecosystem.

Three theorems shape the distribution of eigenvalues of the Jacobian matrix in the complex plane. The first is Geršgorin’s first circle theorem which states that every eigenvalue must lie within at least one of the Geršgorin discs. The second is Geršgorin’s second circle theorem which states that if *s* of the discs form an isolated connected domain then precisely *s* eigenvalues are found within this domain (Fig 2.2). Thus Geršgorin discs define an eigenvalue inclusion region. The third is that the sum of the real parts of the eigenvalues must equal the sum of the trace $\left(\sum_{i=1}^{n}\mathrm{Re}(\lambda_i)=\sum_{i=1}^{n}g_{ii}\right)$, which intuitively constrains the eigenvalues to balance about the centre of all discs with respect to the real axis. Thus, when the diagonal terms are identical (var(g_{ii}) = 0) and discs are centred in the same place, the dominant eigenvalue must be more positive than, or at most equal to, the diagonal value. However, when the discs are positioned differently (var(g_{ii}) > 0), the dominant eigenvalue can be more negative than the value of the most positive diagonal element. The Geršgorin discs provide bounds on how negative the dominant eigenvalue, and therefore how resilient the ecosystem, can be.

To usefully apply these theorems to eigenvalues of ecosystems with increasing interactivity requires the numerically supported assumption that the variance of the distribution of the eigenvalues within a disc is proportional to the radius of the disc (Haydon, 1994). In an ecosystem where species interact more strongly or with a greater number of other species, the Geršgorin discs will have larger radii. When the discs are centred in the same place (var(g_{ii}) = 0), as the radii of the discs increase, resilient systems can become less resilient but not more so. In contrast, when discs are centred at different points along the real axis (var(g_{ii}) > 0), the trade off between positivity and negativity in the real parts of eigenvalues allows the dominant real part to become more negative with increasing disc radius. In this way, ecosystem resilience can increase with ecosystem interactivity (Haydon, 2000).

(3aii) Variance in the distribution of real parts of eigenvalues

Levins (1975) presented a formula for the variance of the distribution of eigenvalues of a matrix (for derivation see Jorgensen et al., 2000), which we apply to the Jacobian matrix **G:**

$$\mathrm{var}(\lambda)=\mathrm{var}(g_{ii})+(n-1)\overline{g_{ij}g_{ji}} \quad \text{for } i,j = 1,\ldots,n \qquad \text{Eqn 2.3}$$

where n is the matrix order, g_{ii} are the diagonal elements, g_{ij} $(i \neq j)$ are the off-diagonal elements and λ is the spectrum (vector of eigenvalues) of **G**. Since eigenvalues can be complex numbers, imaginary parts can cause var(λ) to take negative values. However, it is the real part of the dominant eigenvalue that determines whether a system returns to equilibrium and Levins' formula can be modified (see Appendix for derivation) to give the variance in the real parts of the eigenvalues of **G**:

$$\mathrm{var}(\mathrm{Re}\,\lambda) = \mathrm{var}(g_{ii}) + (n-1)\overline{g_{ij}g_{ji}} + \overline{(\mathrm{Im}\,\lambda)^2} \quad \text{for } i,j = 1,....,n. \qquad \text{Eqn 2.4}$$

where Im λ are the imaginary parts of the eigenvalues. Intuitively, if the mean of the eigenvalues is fixed, we expect, in general, the real part of the dominant eigenvalue, and therefore ecosystem resilience, to decrease as var(Re λ) increases.

Using Eqn 2.4, we see that var(Re λ) cannot take a negative value, allowing clearer comprehension of how each of the terms contribute to the sum. The second term $\left((n-1)\overline{g_{ij}g_{ji}}\right)$ encapsulates all three traditional measures of complexity (the number of interacting species, the degree of connectance between species and the strength of these interactions), and will increase in magnitude with increases in any of them. The sign of this term depends on the types and strengths of interspecific interactions (g_{ij}). Competitive or mutualistic interactions will contribute positive values whilst consumer-resource interactions will contribute negative values. In the absence of the third term (i.e. if the eigenvalues are all real numbers) then increasing the number or strength of consumer-resource interactions provides a necessary and sufficient condition for positive resilience - complexity relationships. However when eigenvalues are complex, increasing consumer-resource interactions can only reduce variance in the real parts of eigenvalues if the associated increase in the third term, the mean of squared imaginary parts $\overline{(\mathrm{Im}\,\lambda)^2}$, is smaller than the decrease in the second term. It is not intuitive, or clear from Geršgorin disc theory, under which circumstances this would be true. We therefore employ a numerical study to investigate whether the behaviour of the eigenvalues can be readily understood in the ways suggested by these theorems. The imaginary parts render Eqn 2.4 a necessary but insufficient condition for increasing resilience with complexity of model ecosystems.

(3B) NUMERICAL STUDY OF THE EFFECT OF VARIANCE IN THE DIAGONAL ELEMENTS OF THE JACOBIAN ON RESILIENCE - INTERACTIVITY RELATIONSHIPS

Model ecosystems were generated using Lotka's formulation of the LVE (see §2bi). For different values of Jacobian diagonal variance and interactivity (MAIIS and connectance) we sampled 1000 stable Jacobians and recorded each vector of the real parts of eigenvalues (Re λ). We present these data in Fig 2.3 in three ways: Figs 2.3.*i-iii* (columns 1-3) show the distributions of real parts of the dominant eigenvalue ($\mathrm{Re}\,\lambda_d$) providing an impression of the range of resilience; in Figs 2.3.*iv* (column 4) these distributions are summarised by the average resilience, $\overline{\mathrm{Re}\,\lambda_d}$; Figs 2.3.*v* (column 5) show the mean variance in the full vector of the real parts of eigenvalues, $\overline{\mathrm{var}(\mathrm{Re}\,\lambda)}$.

The distributions of real parts of dominant eigenvalues (Figs 2.3.*i*-*iii*) confirmed the analytical result that when variance is present in the Jacobian diagonal, locally stable systems are able to be more resilient when interactivity is greater. Average resilience - interactivity relationships generally reflected this (Figs 2.3.*iv*). We also observed that average resilience tended to be higher when there was lower variance in the Jacobian diagonal (Figs 2.3.*iv*), and the variance in the real parts of eigenvalues showed qualitatively similar patterns to resilience (Figs 2.3.*v*).

There is clearly complexity in the results shown in Fig 2.3 which requires further consideration. First, in Figs 2.3.c.*iv* average resilience levelled-off to the same mean value as connectance was increased. This suggests the average eigenvalue behaviour was governed similarly in these systems. We noticed they shared the common feature of having large discs united as a single domain that extended over into the positive half of the complex plane (Table 2.1). As a result of sampling only stable Jacobians, this would restrict the most dominant eigenvalue to fall within a constant region of the real axis despite increasing connectance. This would also explain why we saw average resilience level-off for high var(g_{ii}) at high values of MAIIS (Table 2.1, Fig 2.3.a.*iv* circles).

Second, when MAIIS > 1, for var(g_{ii}) = 0 (Fig 2.3.a.*iv*, asterisks), we observed a positive resilience - interactivity relationship that conflicted with Geršgorin theory. As MAIIS was increased from 1 to 1000, the variance in the real parts of eigenvalues tended to zero (Fig 2.3.a.*v*) revealing that all real parts of eigenvalues converged on the diagonal elements (g_{ii} = -0.1). In Fig 2.3.c we set MAIIS equal to one to investigate further, and found that average resilience levelled-off as connectance increased (Fig 2.3.c.*iv*) and variance in the eigenvalues did not tend to zero (Fig 2.3.c.*v*). We deduce that the unexpected result was caused by an increase in strength rather than number of interactions, and return to discuss this finding in §4b.

(3C) NUMERICAL STUDY OF THE EFFECT OF VARIANCE IN THE RELATIVE ABUNDANCE DISTRIBUTION ON RESILIENCE - INTERACTIVITY RELATIONSHIPS

Model ecosystems were generated using Volterra's formulation of the LVE (see §2bii). As for Fig 2.3, for each measure of interactivity (connectance and MAIIS), the vectors of real parts are presented in three ways: Figs 2.4.*i*-*iii* (columns 1-3) show the full distributions of real parts of the dominant eigenvalue ($\mathrm{Re}\,\lambda_d$) providing an impression of the range of resilience; in Figs 2.4.*iv* (column 4) these full distributions are summarised by the average resilience, $\overline{\mathrm{Re}\,\lambda_d}$; Figs 2.4.*v* (column 5) show the mean variance, $\overline{\mathrm{var}(\mathrm{Re}\,\lambda)}$.

We did not find feasible ecosystems where var(g_{ii}) was zero or intermediate and interactivity was low (Fig 2.4a). (It is ironic that feasible systems with no variance in intraspecific interaction strengths, as assumed by May (1972b), are difficult to find at *low* levels of complexity.) The resilience - interactivity relationships for different relative abundance distributions (Fig 2.4) showed strong similarities to those found for varying the diagonal elements of Jacobians generated using Lotka's formulation of the LVE (Fig 2.3): the distributions of dominant real parts showed that variance in the abundance distribution can allow locally stable systems to become more resilient when interactivity is greater (Figs 2.4.*i*-*iii*); patterns in average resilience (Figs 2.4.*iv*) and the variance in the real parts of eigenvalues (Figs 2.4.*v*) generally reflected this; and average resilience tended to be higher when abundance distributions were more equitable (Fig 2.4.*iv*).

4. Discussion

(4A) THE SPECIES ABUNDANCE DISTRIBUTION AND STABILITY - COMPLEXITY RELATIONSHIPS

The main aim of this chapter was to explore how ecosystem stability - complexity relationships depended on the evenness of species abundances. Despite the fact that one of the universal laws of ecology is that ecosystems contain many rare and few common species (McGill et al., 2007), and the decades of debate over the relationship between ecosystem stability and complexity (McCann, 2000), the effect of inequity in species abundances on stability - complexity relationships has remained an open question. In this chapter we modelled interacting species using the classic LV equations, measured complexity as the ecosystem interactivity (connectance and mean interaction strength) and measured stability as the resilience of ecosystems to perturbation from a locally stable equilibrium. In LV model ecosystems, the equilibrium abundance distribution lies on the diagonal of the Jacobian matrix where it contributes to species self-regulation terms, and in the study of stability - complexity relationships, the diagonal elements have traditionally been assigned identically (Gardner and Ashby, 1970, May, 1972b). Firstly, we presented analytical arguments based on Geršgorin disc theory and variance of eigenvalues to show that resilience *can* increase with interactivity in the general case that the diagonal elements were inequitable. Secondly, we presented supporting numerical results which further showed that ecosystem resilience can *on average* increase with ecosystem interactivity. Then, we specifically attributed inequity in the diagonal elements to differences in equilibrium abundances and presented numerical results showing that ecosystems with even abundance distributions had different resilience - interactivity relationships to ecosystems with uneven distributions. We found that resilience increased with interactivity in LV model ecosystems where the abundance distribution was strongly skewed towards rare species.

Whilst variation in species abundances is ubiquitous across communities and ecosystems (McGill et al., 2007), there are different degrees of inequity. Although these differences may depend to a large extent on the sampling frame and definition of community (Loehle, 2006), empirical links between unevenness and various characteristics of communities are well documented. More even distributions have been linked to communities which are later in succession, less subjected to human disturbance and less open to immigration (McGill et al., 2007). The model ecosystems in this chapter were purposely constructed to allow stability to be directly comparable (see §2bv). We found that more equitable ecosystems were on average more resilient than their less even counterparts.

The species abundance distribution is typically studied as an emergent community-level property of the LV ecosystem model, like resilience in this work. We initially tried to study resilience - interactivity relationships this way, by generating a pool of ecosystems from randomly parameterised interaction strengths and intrinsic growth rates (see §2bii) and separating out the most equitable and inequitable ecosystems. This approach was abandoned because these ‘extremes’ were rarely encountered, and an alternative approach was adopted where variance in abundances could be controlled. Recently, however, Wilson and colleagues (2003, 2006) have made it possible to analytically approximate the mean and variance of the abundance distribution as a function of the statistical properties of interaction parameters (Wilson et al., 2003). Their equations link species abundance distributions to the interactivity of LV ecosystems. They have found that species abundance distributions were relatively insensitive to variation in per-capita interspecific interactions (a_{ij}) (Wilson et al., 2003), but that stronger mean per-capita interspecific interactions (a_{ij}) resulted in less even communities, whether these were competitive (Wilson et al., 2003) or resource-consumer communities (Wilson and Lundberg, 2006). The picture is complicated because their less equitable communities also contained fewer species, and species richness is an element of ecosystem complexity which has been shown to have strong effects on resilience (Ives and Carpenter, 2007, McCann, 2000). Nonetheless their results imply that interactivity not only affects resilience, as shown here, but also variance in the abundance distribution, which itself affects resilience and generates quantitatively (or even potentially qualitatively) different resilience - interactivity relationships.

When ecosystems are modelled using Lotka's local formulation of the LVE the only constraints placed on the Jacobian matrix are the distribution and structure of elements as directly assigned by the investigator, whereas, when using Volterra's global formulation the investigator is able to select Jacobians on the basis of feasibility of the equilibrium abundances and plausibility of intrinsic growth rates. We found that feasible, plausible Volterra-type Jacobians showed no difference in resilience - interactivity relationships from feasibly indeterminate Lotka-type Jacobians. This suggests that feasible, plausible Jacobians and feasibly indeterminate Jacobians had the same structure or, if their covariance structures were distinct, it did not seem to affect resilience - interactivity relationships.

(4B) LIMITATIONS AND EXTENSIONS OF THE ANALYTICAL APPROACHES FOR STUDYING STABILITY - COMPLEXITY RELATIONSHIPS

A question that arises with using Geršgorin disc theory to explore ecosystem stability is whether systems with non-zero variance in their Jacobian diagonals (var(g_{ii}) > 0) and large discs relative to this variance (r_i >> var(g_{ii})) (so that superficially they appear to be centred in the same place) have similar stability to systems with large discs which *are* centred in the same place (var(g_{ii}) = 0). This appeared to be the case when large discs were generated by increasing the number of interactions but not when large discs were generated by increasing the strength of interactions. We conjecture that this conflicting result may be explained because Jacobians with all diagonal elements identical and magnitudes smaller than off-diagonals (g_{ij}) are associated with eigenvalues that behave like those of skew symmetric matrices.

A matrix **M** is skew-symmetric (or antisymmetic) if all diagonal entries are zero and its transpose is also its negative, $\mathbf{M}^T = -\mathbf{M}$. The eigenvalues of skew-symmetric matrices are purely imaginary (or zero). This theory extends to diagonals that are all the same scalar value (k): if $\mathbf{G} = (\mathbf{M}+k\mathbf{I})$ then $\lambda(\mathbf{G}) = \lambda(\mathbf{M}) + \lambda(k\mathbf{I})$ where **I** is the identity matrix, and eigenvalues λ. Now the eigenvalues have a non-zero real part of value k. In our Jacobians there was a further difference that paired interspecific interactions (g_{ij}) were not of equal strength ($-g_{ij} \neq g_{ji}$). However, we found that a large difference in magnitude between the sum of the off-diagonal elements and k tended to reduce the variance in the real parts of the associated eigenvalues, in a similar fashion to the distribution of eigenvalues of a skew-symmetric matrix.

Although this finding has not been reported previously, its ecological relevance is questionable because ecosystems with identical intraspecific, and sign-symmetric interspecific, interaction strengths are not realistic. However, skew-symmetric matrices are shown here to exist in the model ecosystems generated by both Lotka and Volterra's formulations of the LVE which underpin much community dynamical theory. Further, Jacobian matrices that approach skew symmetry do not have eigenvalues that conform to the assumption that the variance of real parts of eigenvalues increase with Geršgorin disc radius. This is a critical assumption in the application of Geršgorin disc theory to the stability - complexity debate.

Geršgorin discs are an example of an eigenvalue inclusion set: they define an area in the complex plane in which the eigenvalues must lie. Brauer Cassini ovals (Brauer, 1947) are another eigenvalue inclusion set that have not yet been applied in an ecological context. The theorem has two parts. Part I: for any matrix $\mathbf{G} = \left[g_{ij}\right] \in \mathbb{C}^{nxn}$, $n \geq 2$, and any eigenvalue in the spectrum (vector of eigenvalues) of **G** ($\lambda \in spec(\mathbf{G})$),

$$(1)\ \lambda \in K_{ij}(\mathbf{G}) := \left\{ z \in \mathbb{C} : \left|z - g_{ii}\right| \cdot \left|z - g_{jj}\right| \leq r_i \cdot r_j \right\} \qquad \text{Eqn 2.5}$$

where K_{ij} is the called the (*i,j*)-th Brauer Cassini oval for the matrix **G**, g_{ii} and g_{jj} are the *i*th and *j*th diagonal elements and r_i and r_j are the sums of the absolute values of the off-diagonal elements in the *i*th and jth rows (equivalent to Geršgorin disc radius, Eqn 2.2). Part II: as Eqn 2.5 is true for each λ in *spec*(**G**), then

$$(2)\ spec(\mathbf{G}) \subseteq \mathcal{K}(\mathbf{G}) := \bigcup_{\substack{i,j \in N \\ i \neq j}} K_{ij}(\mathbf{G}),$$

where $\mathcal{K}$ is the Brauer set. The advantage of Brauer Cassini ovals is that they always define an area that is smaller than the Geršgorin discs (a simple example is given in Fig 2.5) and may offer novel qualitative insights. For example, K_{ij} can consist of two disjoint components (Brauer Cassini ovals may not be ovals) if $\left|g_{ii} - g_{jj}\right| > 2\sqrt{r_i \cdot r_j}$ (Varga, 2004). Thus when ecosystem interactivity is low and variance in intraspecific interactions is high, the trade off between positivity and negativity in the real parts of eigenvalues may be much more restricted, and therefore potential resilience much lower, than predicted by Geršgorin disc theory (Fig 2.5). The disadvantage is the calculation for large ecosystems is computationally expensive since there are $\binom{n}{2}$ Cassini ovals compared with n Geršgorin discs.

The equation for the variance in the distribution of real parts of eigenvalues (var($\operatorname{Re}\lambda$), Eqn 2.4) is a simple mathematical argument that says when variance in the intraspecific interaction strengths (var(g_{ii})) is greater than zero, the resilience of an ecosystem is able to increase with complexity. This holds not just for ecosystem complexity as measured by interactivity (connectance and mean interaction strength) but also for the third traditional measure of ecosystem complexity, species richness, although this has yet to be tested numerically. Eqn 2.4 also suggests how to modify the off-diagonal structure in order to minimize the value of the real part of the dominant eigenvalue (maximise resilience). Firstly, for a given set of interspecific interactions, resilience can be maximised by decreasing variance in the intraspecific interactions, var(g_{ii}). Secondly, conditional on a fixed value of var(g_{ii}), increasing the number or strength of competitive or mutualistic interactions will only decrease resilience whilst it is only by increasing the number and/or strength of consumer-resource interactions that resilience can be maximised.

We have presented two lines of analytical argument and supporting numerical results showing that the resilience of LV ecosystems can increase with their interactivity. The use of LV equations and measuring stability from an equilibrium viewpoint are open to criticism. Further, we have only considered one type of interaction between species that occur in ecosystems. (Interestingly, the analytical arguments conflict in their predictions of how different interaction types (mutualistic, competitive) should influence resilience - interactivity relationships and it would be interesting to reconcile these two theories.) Nonetheless, we have linked the stability of LV ecosystems with the equilibrium species abundance and shown that ecosystem resilience can increase with interactivity when the abundance distribution approximates the ubiquitous natural pattern, skew towards many rare species. This work suggests that changes to the species abundance distribution are likely to alter the dynamical properties of a real ecosystem. The LV framework could offer a means of exploring the loss of biodiversity, in terms of changes to abundance distributions, on ecosystem stability and its implications for conservation.

Table 2.1. Spillover and union in Geršgorin discs. Ranges of MAIIS over which: (A) there was union of discs into a single domain; (B) Geršgorin discs were large enough for one or more to spillover into the positive quadrant. Levels of $\overline{|g_{ij}|}_{i \neq j}$ were determined from Jacobians as sampled for Fig 2.3a and Fig 2.4a and therefore can be used in the interpretation of results presented in these figures. See Fig 2.2a for an example of spillover and Fig 2.2b for an example of union and spillover.

	Variance in Jacobian diagonal		
	0	*Intermediate (0.008)*	*High (0.041)*
(A) union	0.001-1000	0.1-1000	1-1000
(B) spillover	0.1-1000	0.01-1000	0.001-1000

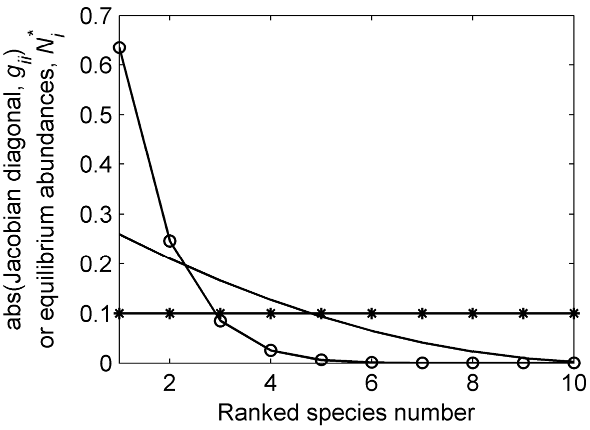


Figure 2.1. Equitable and inequitable relative distributions used to assign the absolute values of the Jacobian diagonal in §3b and equilibrium species abundances in §3c. Three levels of variance in these distributions were modelled: zero (asterisks); low (variance = 0.008, no marker) and high (variance = 0.041, open circles). Distributions were modelled using the beta probability density function (setting Z=1, W=1 for zero variance W=3 for low variance, W=10 for high variance).

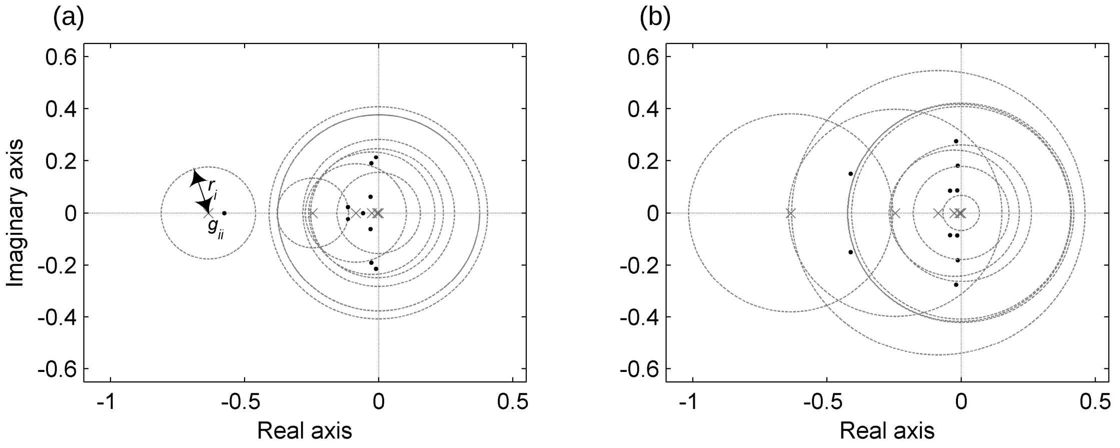


Figure 2.2. Geršgorin discs in the complex plane. (a) An example where discs are separated and form isolated domains. The isolated disc is annotated to illustrate that each disc D_i is centred at the diagonal element of the *i*th row in the Jacobian matrix (g_{ii}, crosses) and has a radius (r_i) equal to the sum of the absolute values of the off-diagonal elements in the *i*th row. If a disc does not overlap to form a connected domain, then the associated eigenvalue (dots) must lie within the disc, otherwise it could lie anywhere within the domain created by the overlapping discs. (b) An example of a connected domain with an empty disc. Jacobians were generated using Lotka's formulation with $\overline{|g_{ij}|}_{i \neq j} = 0.1$, $C = 0.3$, $\text{var}(g_{ii}) = 0.041$.

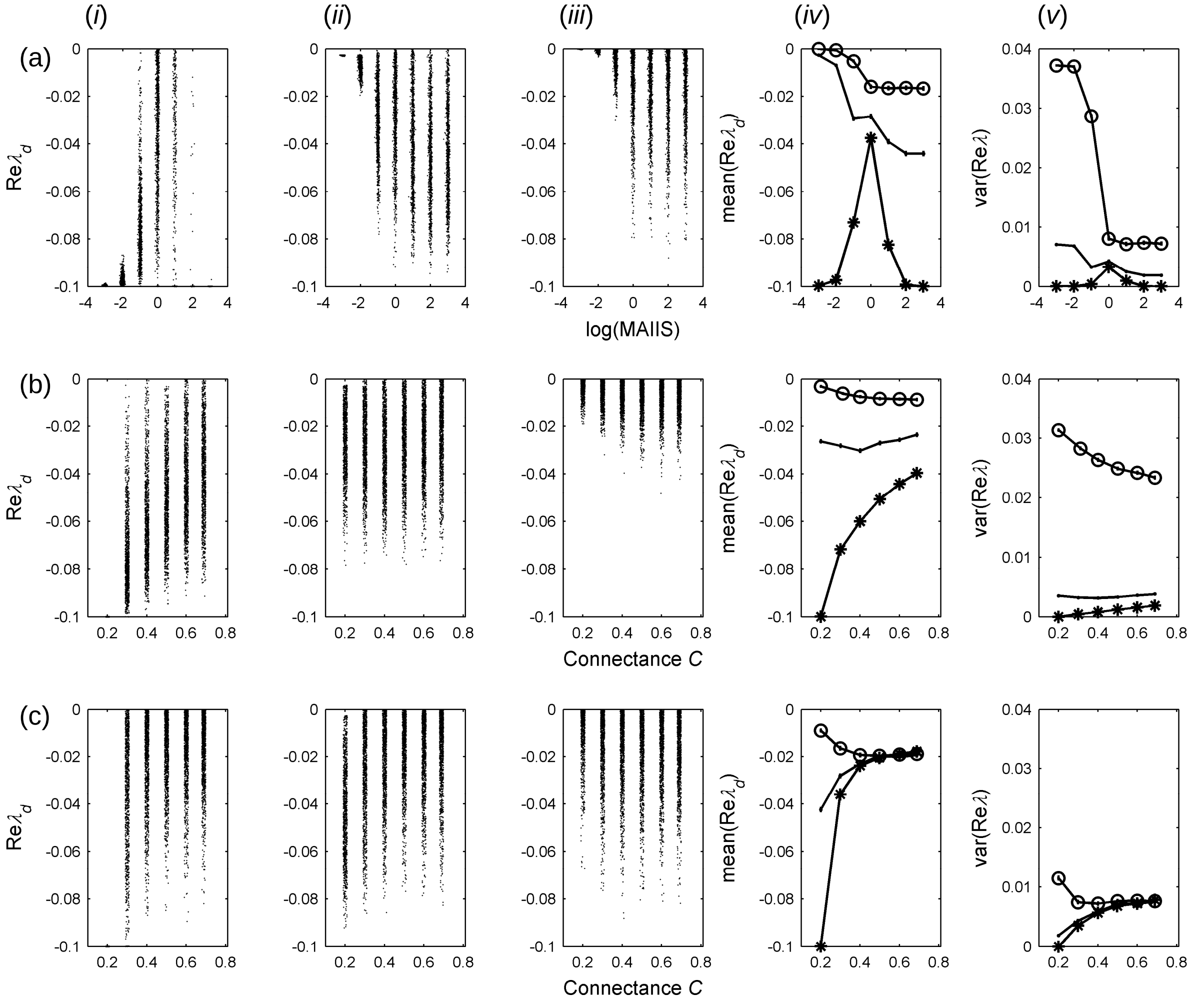


Figure 2.3. Effect of variance in the diagonal elements of stable Jacobians (var(g_{ii})) on the relationship between model ecosystem resilience ($\mathrm{Re}\,\lambda_d$) and interactivity as measured by: (a) MAIIS where $C = 0.3$; (b) connectance C where MAIIS=0.1 and (c) connectance C where MAIIS=1. (*i*-*iii*) Distributions of real parts of dominant eigenvalues ($\mathrm{Re}\,\lambda_d$) of 1000 stable Jacobians where: (*i*) var(g_{ii}) = 0; (*ii*) var(g_{ii}) = 0.008 and (*iii*) var(g_{ii}) = 0.041. (*iv*) Average stability ($\overline{\mathrm{Re}\lambda_d}$) measured as the mean (± SEM) of the distributions shown in (*i*-*iii*). (*v*) Mean variance (± SEM) of the real parts of all eigenvalues var($\mathrm{Re}\,\lambda$). Var(g_{ii}) = 0 (asterisks), var(g_{ii}) = 0.008 (no marker) and var(g_{ii}) = 0.041 (circles). SEMs are small and not clearly visible. An algorithm ensured the mean and variance of interaction strengths remained constant across connectance levels (Christianou and Kokkoris, 2008).

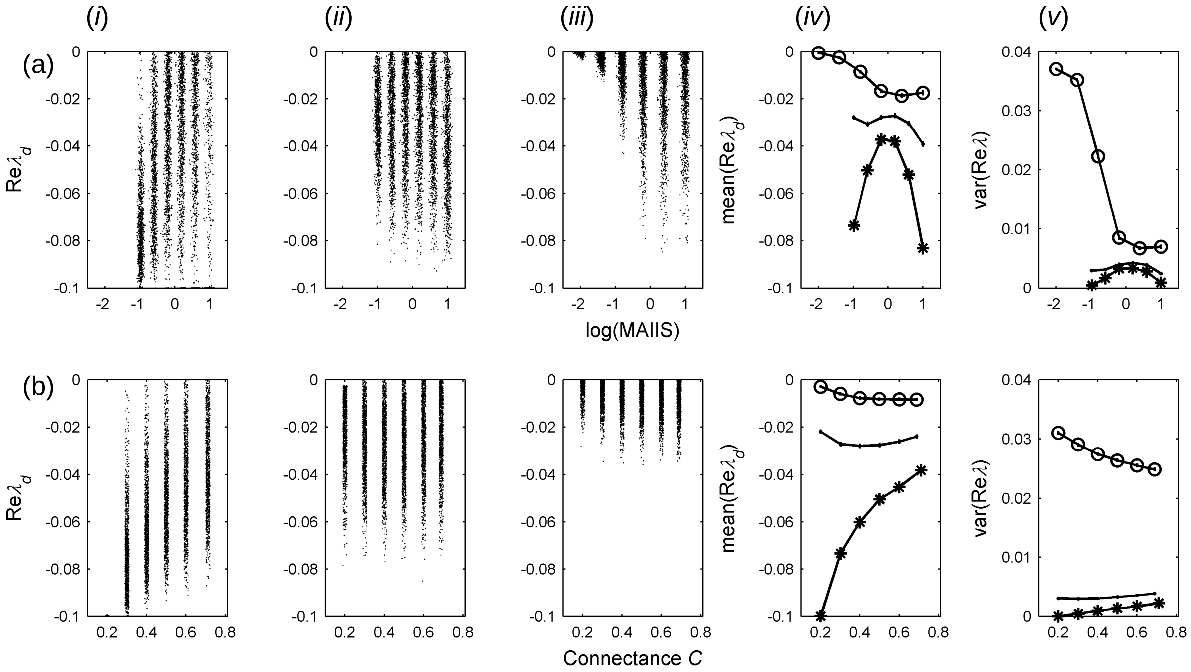


Figure 2.4. Effect of variance in the equilibrium relative abundance distribution ($\mathbf{N}^*$) on ecosystem stability at different levels of interactivity. (a) Interactivity measured as MAIIS with C = 0.3. For each x = [-2 -1 0 1 2] where MAIIS=10^x we searched up to 10000 candidate Jacobians for one that was stable, feasible and had a plausible **b** vector (see §2bii). This established the range over which we then sampled 1000 Jacobians at six intervals. (b) Interactivity measured as connectance where MAIIS=0.1. (*i*-*iii*) Distributions of real parts of dominant eigenvalues ($\mathrm{Re}\,\lambda_d$) of 1000 Jacobians where: (*i*) var($\mathbf{N}^*$) = 0; (*ii*) var($\mathbf{N}^*$) = 0.008, and (*iii*) var($\mathbf{N}^*$) = 0.041. (*iv*) Average stability ($\overline{\mathrm{Re}\lambda_d}$) measured as the mean (± SEM) of the distributions shown in (*i*-*iii*). (*v*) Mean variance (± SEM) of the real parts of all eigenvalues var($\mathrm{Re}\,\lambda$). Var($\mathbf{N}^*$) = 0 (asterisks), var($\mathbf{N}^*$) = 0.008 (no marker) and var($\mathbf{N}^*$) = 0.041 (circles). SEMs are small and not clearly visible. An algorithm ensured the mean and variance of interaction strengths remained constant across connectance levels (Christianou and Kokkoris, 2008). Initially for each level of interactivity we searched through up to 10000 model ecosystems looking for a plausible vector of intrinsic growth rates (**b**) with three autotrophs (b_i > 0) at the base of ecosystems. This established the range over which we then sampled 1000 Jacobians at six intervals and recorded each vector of the real parts of eigenvalues (Re λ).

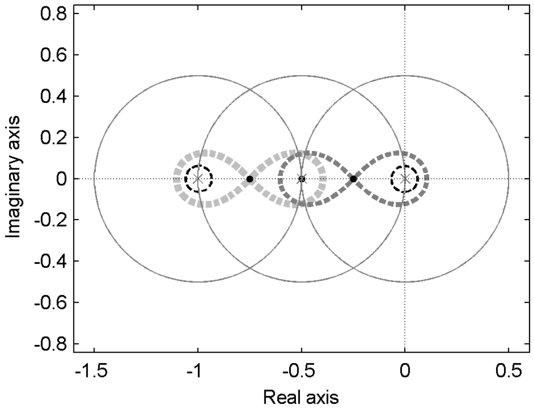


Figure 2.5. Brauer Cassini ovals (broken lines) and Geršgorin discs (solid lines) for the matrix $\begin{bmatrix} -1 & -0.25 & -0.25 \\ 0.25 & -0.5 & -0.25 \\ 0.25 & 0.25 & 0 \end{bmatrix}$. The eigenvalues (dots) were [-0.25 -0.5 -0.75]. The diagonals of the matrix are the centres of the discs and foci of the ovals (crosses). In this example each Brauer Cassini oval does not form an oval shape but two figure of eights and two small circles. The ovals form a smaller eigenvalue inclusion region than the Geršgorin discs. Ovals calculated with assistance from Gibson (2009).

Appendix: derivation of the variance of eigenvalues in terms of their real and imaginary parts

$$\operatorname{var}(\lambda) = \overline{\lambda^2} - \overline{\lambda}^2$$

(1) Finding the mean of eigenvalues

$$\overline{\lambda} = \frac{\sum \lambda_j}{n} = \frac{\lambda_1 + \lambda_2 + \ldots \lambda_n}{n} \qquad \text{for} \quad j = 1, 2 \ldots n$$

When adding complex numbers, the real parts are added separately from the imaginary parts:

$$\overline{\lambda} = \frac{(\operatorname{Re}\lambda_1 + \operatorname{Re}\lambda_2 + \ldots \operatorname{Re}\lambda_n) + (\operatorname{Im}\lambda_1 + \operatorname{Im}\lambda_2 + \ldots \operatorname{Im}\lambda_n)\, i}{n}$$

When dividing a complex number $\frac{a+bi}{c} = \frac{a}{c} + \frac{b}{c} i$, therefore

$$\overline{\lambda} = \frac{\left(\sum \operatorname{Re}\lambda\right)}{n} + \frac{\left(\sum \operatorname{Im}\lambda\right)}{n} i$$

If the complex variables are eigenvalues, then the complex eigenvalues will come in conjugate pairs. The mean of the imaginary parts of the eigenvalues $\left(\sum \operatorname{Im}\lambda / n\right) i$ will be zero, and therefore the mean eigenvalue will equal the mean real part:

$$\overline{\lambda} = \frac{\left(\sum \operatorname{Re}\lambda_j\right)}{n}.$$

(2) Finding the vector of squared eigenvalues

$$\lambda^2 = \frac{\sum (\lambda_j . \lambda_j)}{n}$$

If λ_j is a complex eigenvalue, it will have a conjugate λ_j^*. For any complex conjugate pair

$$\lambda_j{}^2 + \lambda_j^{*2} = 2(\operatorname{Re}\lambda_j)^2 - 2(\operatorname{Im}\lambda_j)^2$$

Therefore

$$\sum\left(\lambda_j{}^2\right) = \sum\left((\operatorname{Re}\lambda_j)^2\right) - \sum\left((\operatorname{Im}\lambda_j)^2\right)$$

$$\overline{\lambda^2} = \frac{\sum\left((\operatorname{Re}\lambda_j)^2\right)}{n} - \frac{\sum\left((\operatorname{Im}\lambda_j)^2\right)}{n}$$

(3) The variance of eigenvalues λ in terms of the variance of real parts and the mean of squared imaginary parts

$$\mathrm{var}(\lambda)=\frac{\sum(\mathrm{Re}\,\lambda)^2}{n}-\left(\frac{\sum\mathrm{Re}\,\lambda}{n}\right)^2-\frac{\sum(\mathrm{Im}\,\lambda)^2}{n},$$

$$\mathrm{var}(\lambda)=\mathrm{var}(\mathrm{Re}\,\lambda)-\overline{(\mathrm{Im}\,\lambda)^2}$$

(4) The variance of the real parts of eigenvalues

$\mathrm{var}(\lambda)=\mathrm{var}(g_{ii})+(n-1)\overline{(g_{ij}g_{ji})}$ (see Jorgensen {, 2000 #49} for derivation)

$$\mathrm{var}(\mathrm{Re}\,\lambda)=\mathrm{var}(\lambda)+\overline{(\mathrm{Im}\,\lambda)^2}$$

$$\mathrm{var}(\mathrm{Re}\,\lambda)=\mathrm{var}(g_{ii})+(n-1)\overline{(g_{ij}g_{ji})}+\overline{(\mathrm{Im}\,\lambda)^2}$$

Chapter 3. On the generality of stability - complexity relationships in Lotka-Volterra ecosystems

Abstract

Ecologists aim to understand how complexity persists in nature. In theoretical ecology, local stability is a widely used measure of ecosystem persistence and has made a major contribution to the ecosystem stability - complexity debate over the last few decades. However, permanence is coming to be regarded as a more satisfactory definition of ecosystem persistence and has relatively recently become available as a tool for assessing the global stability of Lotka-Volterra communities. Here we document positive relationships between permanence and Lotka-Volterra food web complexity and report a positive correlation between the probability of local stability and permanence. We investigate further the frequency of discrepancy (attributed to fragile systems that are locally stable but not permanent or locally unstable systems that are permanent and have cyclic or chaotic dynamics) and the causes of non-permanence at the boundary of the state-space and correlate them to aspects of complexity. We find that locally stable interior equilibria tend to have all locally unstable boundary equilibria. Since a locally stable boundary is inconsistent with permanent dynamics, this can explain the observed positive correlation between local interior stability and permanence. Our key finding is, at least in Lotka-Volterra ecosystems, that local stability may be a better measure of persistence than previously thought.

Introduction

Ecologists aim to understand the conditions under which a community of interacting species survives as a whole and in the long term. In practise, much of the research into the question of long term coexistence of species has regarded this as an equilibrium problem. From a theoretical perspective it has been the tractability of local (also known as asymptotic or neighbourhood) stability analysis that has ensured the pervasiveness of the equilibrium view point: ‘even if other definitions of stability are more attractive, if they are not tractable then the ecologist cannot adopt them with profit’ (Hutson and Schmitt, 1992). The deficiencies of local stability analysis are numerous and well known (Anderson et al., 1992, Haydon, 1994, Law and Blackford, 1992, Berlow et al., 2004) and there is little reason to believe that the natural world is in equilibrium. A more satisfactory definition of ecosystem stability is a global property called permanence, which requires only that densities of rare species tend to increase. The analysis of permanence was, however, intractable until recent attention from mathematicians (reviewed in Hofbauer and Sigmund, 1988) enabled Law and colleagues (Law and Blackford, 1992, Law and Morton, 1993, Law and Morton, 1996) to provide a non-technical description of a method for Lotka-Volterra (LV) communities that has made permanence analysis accessible as a tool to ecologists.

Despite permanence analysis being made tractable to ecologists for more than a decade, there are only a handful of theoretical community studies in which permanence has been used as well as, or in place of, local stability (Emmerson and Yearsley, 2004, Chen and Cohen, 2001, Vandermeer, 2006, Kristensen, 2008). One area where permanence will contribute to theoretical community ecology is in the ongoing debate over the relationship between stability and complexity of ecosystems. In the 1970s, theoreticians reported that three measures of complexity, species richness and the number and mean strength of interactions between species, decreased the probability of local stability in randomly parameterised large complex systems (May, 1972b, Gardner and Ashby, 1970). Recently, Chen & Cohen (2001) were the first to systematically explore permanence in a similarly general framework. They studied two of the measures of complexity, the number of interactions and species, and found that increases in both reduced the probability of permanence in ecosystem models. However, the theoretical ecology literature based on local stability has moved the stability - complexity debate on a great deal since the early 1970s, finding numerous conditions under which complexity can be locally stabilising as well as destabilising (Borrvall et al., 2000, Jansen and Kokkoris, 2003, Rozdilsky and Stone, 2001, Haydon, 1994, Haydon, 2000, Neutel et al., 2002). The aim of this chapter is to bring closer together the vast literature on local stability and the nascent use of permanence, which we attempt in three ways. First, we determine permanence-complexity relationships in model ecosystems of enhanced ecological plausibility (for example, Chen & Cohen (2001) assumed equal equilibrium species abundances and did not ensure the presence of autotrophs), and by studying the effect of species interaction strengths on permanence. Second, we investigate the match and discrepancy between predictions of local stability and permanence, and third, we study the reasons for non-permanence.

The mean interaction strength is a traditional measure of ecosystem complexity (May, 1972b) and we relate it here to permanence for the first time. However, taking the average neglects the natural variability of interaction strengths. In real ecosystems the range of interaction strengths can span nine orders of magnitude (Wootton, 1997) and the distribution is commonly observed to be skewed towards weak interactions (Fagan, 1997, Goldwasser and Roughgarden, 1993, Paine, 1992, Wootton, 1997, De Ruiter et al., 1995). Such variability has been identified as an important determinant of stability under some conditions. In competitive communities, greater variance in strengths of competitive interactions can increase the probability of stability (Jansen and Kokkoris, 2003). The non-random patterning of weak interactions in omnivorous loops increases local stability in empirical food webs (Neutel et al., 2002) and permanence in special sets of trophic relations (Emmerson and Yearsley, 2004). Further, non-equilibrium dynamics were stabilized when complexity was added via a species (consumer) with weak interactions (McCann et al., 1998). It is unclear however whether the skew towards weak interactions will influence permanence in more generally structured ecosystem models.

How much do predictions differ between local stability and permanence? Using two examples of simple communities Anderson et al. (1992) found the parameter space for community coexistence measured by local stability was substantially smaller than that under permanence. Permanent but locally unstable communities represent those which must have some form of non-equilibrium asymptotic behaviour e.g. cyclical or chaotic orbits. Here we characterise how the likelihood of non-equilibrium dynamics varies with ecosystem complexity. Communities may also admit locally stable behaviour in the absence of permanence (Chen and Cohen, 2001, Hofbauer and Sigmund, 1988). We characterise these as ‘fragile’ and study how the probability of encountering such fragility varies with ecosystem complexity. If the match and discrepancy between local stability and permanence can be understood, then we may be able to attempt to answer an important question for ecology which was posed by Anderson et al. (1992): ‘how much confidence should we have in a theoretical ecology based on asymptotic stability analysis?’.

In discussing complexity, we will examine the properties of the Jacobian matrix: order (species richness), number of elements (number of interactions between species) and magnitude of elements (strength of interactions). The Jacobian governs the local dynamics around a specified equilibrium point and thus we will use ecosystem complexity to refer to the properties of the Jacobian of the interior equilibrium. The criterion of permanence rests on the boundary: densities of rare species will tend to increase if the boundaries of the positive orthant repel the ecosystem dynamics away into the interior (Law & Blackford 1992). For clarity, we stress here the distinction between permanence and global asymptotic stability - permanence applies to all orbits and initial conditions where all species are present, but does not require that all orbits converge on the interior equilibrium point. However, since LV ecosystems have a unique equilibrium point, model ecosystems which are both permanent and locally stable must also be globally asymptotically stable. If an ecosystem is not permanent then there must be at least one attractor on the boundary. In this chapter we explore the way in which the probability of equilibrium and non-equilibrium attractors on the boundary changes with ecosystem complexity and relate this to the probability of permanence and local stability of the ecosystem.

The results presented in this chapter are arranged around three sets of questions. The first set of questions is on permanence-complexity relationships: (1.1) does relaxing assumptions made by Chen & Cohen (2001) affect complexity-permanence relationships? (1.2) what is the relationship between mean absolute interspecific interaction strength and permanence? and (1.3) what is the effect of skew towards weak interspecific interaction strengths on permanence? The second set is on local stability analysis and permanence: (2.1) are local stability and permanence correlated? (2.2) does the proportion of permanent ecosystems with non-equilibrium dynamics change with complexity? and (2.3) does the probability of fragility change with complexity? The third set is based on the boundary equilibria: (3.1) is non-permanence caused by equilibrium or non-equilibrium attractors on the boundary? and (3.2) does the probability of at least one locally stable boundary follow the same relationship with complexity as the probability of stability of the interior equilibrium?

Methods

MODEL ECOSYSTEMS

We constructed model ecosystems as Chen and Cohen (2001) did, using the familiar LV equations which describe the population dynamics of n interacting species,

$$\frac{dN_i}{dt} = N_i\left(b_i + \sum_{j=1}^{n} a_{ij}N_j\right) \qquad \text{for } i = 1,\ldots,n. \qquad \text{Eqn 3.1}$$

The equations were adopted as the global dynamics of the ecosystem *sensu* Volterra (1926), rather than the more general but locally applicable formulation of Lotka (1925). This means we can define the parameters in Eqn 3.1 with unambiguous ecological interpretations: b_i is the intrinsic growth rate of the ith species and a_{ij} is the per-capita effect of the jth species on the ith species and are the elements of the per-capita interaction matrix **A**. At the interior equilibrium point $\mathbf{AN}^* = -\mathbf{b}$, and the Jacobian matrix **G** has a simple form:

$$\mathbf{G} = \begin{bmatrix} a_{11}N_1^* & a_{12}N_1^* & \cdots & a_{1n}N_1^* \\ a_{21}N_2^* & a_{22}N_2^* & \cdots & a_{2n}N_2^* \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}N_n^* & a_{n2}N_n^* & \cdots & a_{nn}N_n^* \end{bmatrix}. \qquad \text{Eqn 3.2}$$

The elements of the diagonal of the Jacobian matrix (g_{ij} where $i = j$) represent intraspecific interaction strengths and the off-diagonal elements (g_{ij} where $i \neq j$) represent interspecific interaction strengths in the vicinity of the equilibrium point ($\mathbf{N}^*$). It is the off-diagonal elements of the Jacobian (g_{ij}), rather than the per-capita interactions (a_{ij}), which we refer to in the subsequent analyses as interspecific interaction strengths.

Model ecosystems were generated that contained paired interactions of consumer and resource species (Chen and Cohen (2001) also considered scenarios with unpaired interactions) with no discrete subwebs and a cascade trophic structure defined by no loops (Cohen and Newman, 1985). The cascade trophic structure was implemented by placing negative effects of consumers on resource species (g_{ij}) above the diagonal of the Jacobian matrix, and positive effects of resource species on consumers (g_{ji}) below. The complexity of each model ecosystem was defined by the properties of the Jacobian at the interior equilibrium point: species richness (n), connectance (C), which measures the proportion of actual interactions between species relative to all topologically possible interactions (excluding cannibalism), and mean absolute interspecific interaction strength ($\overline{|g_{ij}|}_{i\neq j}$, MAIIS for brevity).

There are two approaches to generating the Jacobian matrix at the interior equilibrium point under Volterra’s formulation of Eqn 3.1. Given the per-capita interaction matrix **A**, they differ by whether the equilibrium point ($\mathbf{N}^*$) or the intrinsic growth rates (**b**) are assigned. We followed Chen and Cohen (2001) by assigning $\mathbf{N}^*$, and calculating $\mathbf{b}$ (=-$\mathbf{AN}^*$). Chen and Cohen (2001) showed that the probability of an ecosystem being permanent decreased with increasing species richness and connectance. In their model ecosystems they assigned a unity equilibrium point (N_i^* = 1) and the non-zero elements of their per-capita interaction matrix **A** were drawn from a uniform random distribution in the interval (-1,0) for each a_{ii} and a_{ij} ($i < j$) and in the interval (0,1) for each a_{ij} ($i > j$).

Chen & Cohen (2001) made two ecologically unrealistic assumptions in their model ecosystems, the consequences of which we examine. They assumed all equilibrium abundances were equal and, by omitting to check the feasibility of intrinsic growth rates (**b** vector), they did not ensure the presence of autotrophs ($b_i > 0$). We constructed four sets of model ecosystems:.

1. The first set kept the assumptions and parameterisation of Chen & Cohen (2001), with the exception that we set equilibrium abundances (N_i^*) to be 0.5, for consistency with subsequent parameterisation.
2. The second set ensured feasibility of intrinsic growth rates by defining a quarter of all species as autotrophs ($b_i > 0$) and the remaining as heterotrophs ($b_i < 0$), with the autotrophs positioned at the base of the ecosystem.
3. The third set ensured the feasibility of intrinsic growth rates and relaxed the assumption of equal N_i^* by allowing the N_i^* to vary uniformly in the interval (0, 1). In this set the per-capita interactions were drawn from a uniform random distribution in the interval (-1,0) for each a_{ii}, (-2,0) for each a_{ij} ($i < j$) and (0,2) for each a_{ij} ($i > j$). The intervals were chosen to ensure the mean of the intraspecific ($\overline{g_{ii}}$) and interspecific interaction strengths ($\overline{|g_{ij}|}_{i \neq j}$) remained constant across all sets.
4. Modelling ecosystems by assigning $\mathbf{N}^*$ also permits specification of the off-diagonals elements of the Jacobian (g_{ij} where $i \neq j$) as independent random variates, allowing direct manipulation of the interspecific interaction strengths. Model ecosystem construction was equivalent to that for the third set as described above, except the interspecific interaction strengths ($|g_{ij}|_{i \neq j}$) were assigned using randomly distributed uniform values from the interval (-1,0) for each g_{ij} ($i < j$) and (0,1) for each g_{ij} ($i > j$).

STABILITY ANALYSES

Local stability of the equilibrium point is determined by the eigenvalues of the Jacobian matrix: stable if all real parts of the eigenvalues are negative. The Jacobians for the interior and boundary equilibria are calculated differently. For the interior equilibrium, the Jacobian elements are straightforward (Eqn 3.2). At each boundary at least one of the species has an abundance set to zero, therefore the abundances of the remaining subcommunity at the boundary equilibrium point (**M**) need to be determined and checked for feasibility ($M_i > 0$ for all i where $M_i \neq 0$). For the boundary equilibria, calculation of the diagonal elements of the Jacobian (see Appendix for further details) becomes,

$$g_{ii} = b_i + \sum_{\substack{j=1 \\ j \neq i}}^{n} a_{ij} M_j$$

if the ith species is missing ($M_i = 0$). The boundary at which all species abundances are zero ($M_i = 0 \;\; \forall i$) is the trivial equilibrium point. The Jacobian is a diagonal matrix containing only the intrinsic growth rates (**b**) and, since the eigenvalues of a diagonal matrix are the diagonal elements, its eigenvalues are the **b** vector. In all LV model ecosystems which contain any autotrophs ($b_i > 0$) the trivial point must therefore be unstable.

An ecosystem was defined as permanent if it satisfied two conditions: an average Lyapunov function existed near the boundary of the state space, and the system was dissipative (Law and Blackford, 1992). If an average Lyapunov function exists the boundary repels all trajectories into the positive orthant of state space, and if a system is dissipative then trajectories cannot tend to infinity. Therefore the system is permanent because it is bounded within the positive orthant. The dissipativity condition is satisfied here because our LV model ecosystems have all self-regulating species ($a_{ii} < 0$) and only consumer-resource interactions (Law and Blackford, 1992). To test our model ecosystems for the existence of an average Lyapunov function we used Jansen’s (1987) sufficient condition as laid out by Law & Blackford (1992), solved as a linear programming problem in MATLAB (version 7 release 14, The MathWorks Inc.).

Results

PERMANENCE-COMPLEXITY RELATIONSHIPS

Unless otherwise stated, the default construction of ecosystems was six species (n=6), for computational tractability, and a connectance (C=0.4) and mean absolute interspecific interaction strength (MAIIS=0.5), to match that of Chen & Cohen (2001).

1.1 The effect of relaxing assumptions made by Chen & Cohen (2001) on permanence-complexity relationships

Chen & Cohen (2001) assumed all equilibrium abundances were equal and did not ensure the presence of autotrophs ($b_i > 0$) in their model ecosystems. With these two assumptions intact we started by reconstructing Chen & Cohen's (2001) negative permanence-complexity relationships for species richness (Fig 3.1a line with circles) and connectance (Fig 3.1b line with circles). Ensuring the feasibility of intrinsic growth rates did not affect the qualitative results but did cause a small increase in the probability of permanence (Fig 3.1a, b lines with stars). Randomly generating the equilibrium abundances ($\mathbf{N}^*$) as well as ensuring the feasibility of intrinsic growth rates (Fig 3.1a, b dashed lines) generated results very close to those where the assumptions of Chen and Cohen (2001) were intact. We conclude that relaxing assumptions made by Chen & Cohen (2001) does not qualitatively affect permanence-complexity relationships. Subsequent analyses (sections 1.3-3.2, Figs 3.2-3.5) are based only on Jacobians with these relaxed assumptions.

Directly assigning the interspecific interactions (g_{ij} where $i \neq j$) had no qualitative and a small quantitative effect on the trends (Figs 3.1a, b solid line with no marker). Directly assigning the interspecific interactions had the advantage of permitting direct control over the interspecific interaction strengths (g_{ij} where $i \neq j$) and therefore was adopted for subsequent analyses (sections 1.3-3.2, Figs 3.2-3.5).

1.2 The relationship between mean absolute interspecific interaction strength (MAIIS) and the probability of permanence

For a connectance of 0.4, increasing MAIIS showed no clear effect on the probability of permanence, with all probabilities close to one. We tested whether this was true for a higher level of connectance of 0.9, and found a non-linear increase in the probability of permanence with MAIIS (Fig 3.1c).

1.3 The effect of skew towards weak interspecific interaction strengths on the probability of permanence

The distribution of interaction strengths in real ecosystems is skewed towards weak interactions (Berlow et al., 2004). Variance in absolute interspecific interaction strengths (VAIIS for brevity) was increased by skewing the distribution from which strengths were drawn towards small values (Fig 3.2a). Therefore the greater the VAIIS, the greater the skew towards weak interactions. The relationship between the probability of permanence and VAIIS depended on the level of VAIIS: at low VAIIS the relationship with the probability of permanence was negative, whilst at greater VAIIS the relationship with the probability of permanence was positive (Fig 3.2b). Thus the probability of permanence may increase with skew in ‘empirical-looking’ distributions of interaction strengths.

We examined the robustness of this u-shaped pattern across other values of complexity (Fig 3.2c-e). Increased species richness (Fig 3.2c) and connectance (Fig 3.2d) increased the depth of the u-shaped curve, whilst increased MAIIS increased the depth and shifted the trough of the u-shaped curve to greater VAIIS values (Fig 3.2e). The value of VAIIS at which the inversion from a negative to positive relationship occurred appeared to correspond approximately with MAIIS. We determined the inversion point for several values of MAIIS and found they were correlated but not in a simple way (Fig 3.2f).

PERMANENCE AND LOCAL STABILITY

2.1 Correlation between local stability and permanence

The probabilities that model ecosystems had a locally stable interior (dotted lines), were permanent (solid lines) and were both permanent and locally stable (dashed lines) with increasing complexity were all correlated (Fig 3.3) although there were differences in their probabilities (Fig 3.3). Not all ecosystems that were locally stable were permanent, and not all permanent ecosystems were locally stable. The difference between the dashed lines and the solid lines gave the probability that model ecosystems were globally but not locally stable (studied further in section 2.2). The difference between the dashed lines and the dotted lines gave the probability of finding model ecosystems which were locally stable but not permanent (studied further in section 2.3).

2.2 The relationship between the proportion of permanent ecosystems with non-equilibrium dynamics and ecosystem complexity

A permanent ecosystem with an unstable interior equilibrium has non-equilibrium dynamics. The relationship between the proportion of ecosystems with non-equilibrium dynamics and species richness depended on the level of species richness (Fig 3.4a solid line). For smaller ecosystems, the relationship was positive, whereas for larger ecosystems the relationship was negative with larger permanent ecosystems tending towards being locally stable. The relationship between connectance and the proportion of ecosystems with non-equilibrium dynamics was positive at relatively low connectance (below about ¾ connected) (Fig 3.4b solid line). At higher connectance levels and all values of MAIIS (Fig 3.4c solid line), the proportion stayed roughly constant. The relationship between the proportion of ecosystems with non-equilibrium dynamics and VAIIS depended on the level of VAIIS. When VAIIS was low, the relationship was positive, whereas when VAIIS was high the relationship was negative (Fig 3.4d, solid line).

2.3 The relationship between the probability of fragility and ecosystem complexity

Ecosystems which are locally stable but not permanent are unlikely to be robust to large perturbations, and described here as 'fragile'. However, it is necessary to bear in mind that the permanence method used here is only sufficient for systems with more than three species (Law and Blackford, 1992) and there may be undetected permanent ecosystems. Assuming, if there were undetected permanent ecosystems, that their proportion changed proportionally with changes in complexity, then the following observations hold. Larger ecosystems were increasingly likely to be fragile (Fig 3.4a dashed line), as were more connected ecosystems (Fig 3.4b dashed line). The probability of fragility stayed roughly constant with increasing MAIIS (Fig 3.4c dashed line) and did not show a consistent trend with VAIIS (Fig 3.4d dashed line).

THE BOUNDARY EQUILIBRIA AND PERMANENCE

3.1 Non-permanence and attractors on the boundary

Non-permanent ecosystems must result from attractors, either equilibrium or non-equilibrium, on the boundary. Both types of attractor were found to occur with non-permanence in our model ecosystems (Fig 3.5). The decrease in the probability of permanence with species richness and connectance (Fig 3.1a, b) was attributed to increases in both types of attractor on the boundary (Fig 3.5a, b). In contrast, the increase in the probability of permanence with increased MAIIS (Fig 3.1c) was attributed to a decreased probability of at least one locally stable boundary, since there was a roughly constant probability of non-equilibrium attractors on the boundary (Fig 3.5c). The probability of permanence decreased initially then increased with skew towards weak interspecific interaction strengths (measured as VAIIS, Fig 3.2b). The initial decrease was attributed to changes in both types of attractor on the boundary, while the increase was mostly attributed to a decrease in the probability of at least one locally stable boundary (Fig 3.5d).

3.2 The relationship between the probability of a locally stable boundary and ecosystem complexity

The probability of at least one locally stable boundary and the probability of a locally stable interior had opposite relationships with complexity of the interior equilibrium point (compare dashed line in Fig 3.3 with light grey shaded area in Fig 3.5). In the model ecosystems studied here (Figs 3.3-3.5) the mean probability of finding a locally stable ecosystem that had all locally unstable boundary equilibria was 0.94 (SD 0.04). Thus, locally stable ecosystems tended to have all locally unstable boundary equilibria. Since permanent ecosystems must have repelling boundary equilibria, local stability increased the probability that an ecosystem was also permanent.

Discussion

In this chapter we use permanence and local stability analysis as tools to examine three aspects of the ecosystem stability - complexity debate. The first explored permanence-complexity relationships in more ecologically plausible and generally structured ecosystems than previously. We showed that relaxing assumptions made by Chen and Cohen (2001) had no qualitative effect on permanence-species richness or permanence-connectance relationships, that increasing mean absolute interaction strength had a positive effect on permanence and that skew towards weak interactions may increase the probability that an ecosystem is permanent. The second considered how much predictions differed between local stability and permanence, what caused those differences and how they varied with complexity. We found that local stability and permanence were correlated and that discrepancy was attributable to both fragile (locally stable but not permanent) ecosystems and those which were permanent with non-equilibrium dynamics (permanent but locally unstable). The probability of finding these ecosystems changed with complexity, and did not show the same patterns. The third focused on the boundary of the state-space. We found that non-permanence was caused by both equilibrium and non-equilibrium attractors on the boundary, and that change in the probability of a locally stable boundary could not simply be attributed to change in boundary complexity. In fact, locally stable ecosystems tended to have all locally unstable boundary equilibria, meaning that local stability increased the probability of permanence. Below we discuss the implications of these findings and draw conclusions about their generality for theoretical ecology.

Permanence is an ecosystem property that confers global stability by requiring only that the densities of rare species must increase (Law and Blackford, 1992). The first systematic study of the permanence of ecosystems in relation to changes in ecosystem complexity was by Chen & Cohen (2001). They increased the complexity of ecosystems as measured by the species richness and connectance and found that the probability of permanence declined. We have shown that this pattern is robust to the inclusion of obligate autotrophs and variation in the equilibrium species abundances. It seems that larger, more connected ecosystems are generally less likely to be permanent than smaller, sparsely connected ecosystems.

A third long-standing measure of ecosystem complexity, the mean strength of interactions (abbreviated to MAIIS) between species (May, 1972b), had a positive effect on the probability of permanence. The probability of local stability behaved similarly, a result which is consistent with recently reported positive relationships across some mean values for LV competitive communities where the variance in interaction strengths were held constant (Jansen and Kokkoris, 2003), as was done here. This result is intriguing because it is contrary to analytical arguments based on the distribution of eigenvalues in the complex plane (Haydon, 1994, May, 1972b). One argument applies elements of Geršgorin disc theory (Geršgorin, 1931). Geršgorin discs are defined by the Jacobian matrix and exist in the complex (imaginary-real) plane where, in turn, they define the region in which the eigenvalues of the Jacobian must lie. If this region overlaps with the positive half of the complex plane then there is a greater than zero probability that the real part of the dominant (most positive) eigenvalue is positive and the system is locally unstable. The radius of the discs is determined by the sum of the absolute values of the interspecific interaction strengths. Therefore increasing MAIIS increases disc size and overlap with the positive half of complex plane, thus decreasing the probability of stability. (For a fuller introduction to the Geršgorin disc theory and proofs refer to Varga (2004) and for ecological application see Haydon (1994, 2000) and Chapter 2.) It appears that this analytical argument is challenged by our numerical results for increasing MAIIS. When a similar argument was applied to a different measure of ecosystem stability (relative local stability), numerical results have shown both predicted (Haydon, 1994) and unpredicted behaviour (Chapter 2). The unpredicted behaviour was attributed to the violation of a central assumption, that the variance of real parts of eigenvalues increases with Geršgorin disc radius, as a result of skew symmetry in the Jacobian matrix. It seems that this key assumption has also been violated here, but in this case by increasing the mean of interaction strengths whilst keeping the variance constant. Further investigation is required to link this particular Jacobian construction to restricted eigenvalue variance.

The patterning of relative interaction strengths has previously been shown to have profound effects on dynamical properties of ecosystems. For example, randomly permuting interaction strengths of modelled real webs has detrimental effects on local stability (Neutel et al., 2002, Emmerson and Raffaelli, 2004, Yodzis, 1981, De Ruiter et al., 1995). Further, theoretical studies suggest weak interactions can be stabilising if there are particular configurations of strong and weak interactions (Emmerson and Yearsley, 2004, Haydon, 2000, McCann et al., 1998, Neutel et al., 2002). We found that increasing the skew towards weak interactions initially decreased but then increased the probability of local stability and permanence, and this inversion point was dependent on the mean interaction strength. Our results agree with the analysis of LV competitive communities by Jansen & Kokkoris (2003) who also observed a u-shaped curve for the probability of local stability. As for Jansen & Kokkoris (2003), no patterning in the magnitudes of the interaction strengths was specified, suggesting that skew towards weak interactions can be stabilising (both locally and globally) in more generally structured ecosystems.

Returning to the question posed by Anderson et al. (1992): ‘how much confidence should we have in a theoretical ecology based on asymptotic stability analysis?’, we have found numerical results that provide good evidence that suggest ecologists should be confident in qualitative findings from local stability analysis of LV ecosystems. Our numerical results show the probability of local stability and permanence are strongly correlated. The quantitative correspondence was good at some parameterisations (e.g. few species, low connectance, low VAIIS), whilst at others it was poor (e.g. mid VAIIS). More importantly they showed the same qualitative changes with ecosystem complexity. The reason for the numerically-based correlation is as follows: if an ecosystem is locally stable then there is a high probability it has unstable boundaries (94% for the ecosystems studied here) and, since stable boundaries are detrimental to permanence, a locally stable ecosystem is a strong candidate for permanence.

However, local stability analysis did consistently classify some permanent ecosystems as unstable, and some locally stable ecosystems were not permanent. We examined further those ecosystems which possessed one form of stability but not both. Those that were locally stable but not permanent were characterised as fragile ecosystems. The probability of fragility was influenced by ecosystem species richness, connectance and variance of interaction strengths (Fig 3.4). In large LV ecosystems local stability may be less likely to imply permanence than in the smaller model ecosystems studied here because the probability of fragility increased linearly with species richness. Those ecosystems that were globally but not locally stable must have had non-equilibrium attractors e.g. limit cycles or chaotic attractors. Their probability was influenced by ecosystem species richness, connectance and variance of interaction strengths (Fig 3.4). Extrapolation of the results shown here for relatively small ecosystems (≤ 12 species) suggests that permanence implies local stability in large LV ecosystems.

As ecosystem complexity changes it may be expected that the complexity and number of boundary equilibria would be affected. If these changes result in an increase in the probability of at least one boundary being locally stable then this would be detrimental to permanence. If the changes in the complexity of boundary equilibria follow changes in ecosystem complexity then they would show similar local stability - complexity relationships. This line of reasoning predicts that permanence-complexity relationships should be opposite to local stability - complexity trends. We found that the converse is the case, that changes in local stability and permanence were correlated and the probability of a locally stable interior and probability of at least one locally stable boundary had opposite relationships with ecosystem complexity. We have explained this finding because locally stable equilibria have a high probability of having all locally unstable boundaries, but we have not explored how the complexity of boundary equilibria changed with complexity of the interior equilibrium. Further, it may also be expected that an increase in the number of boundaries would increase the probability of at least one boundary being locally stable and be detrimental to permanence. Although we did not explicitly study this, we observed that increasing the dimensionality (n) of ecosystems increased the number of boundary equilibria (since the number of boundary equilibria is $\sum \binom{n}{k}$ for $k = 1,\ldots,n$) yet the effect on stability was comparable to increasing the connectance where n was not changed. Our results suggest that there is little evidence for a strong effect of the number of boundaries on the probability of stability.

Permanence is a more satisfactory definition of ecosystem stability than local stability because it is a global criterion and is more empirically tractable than local stability (Anderson et al., 1992, Berlow et al., 2004). The adoption of permanence as a measure of ecosystem stability by both empiricists and theoreticians would facilitate the translation of data into model coefficients (Berlow et al., 2004) and aid alignment on the stability - complexity debate. However, the application of permanence in ecology is currently restricted to LV equations and only as a sufficient criterion when communities contain more than three species (Law and Blackford, 1992). Furthermore, all species modelled in LV equations are assumed to have a linear (type I) functional response. This special stipulation means LV communities have a unique equilibrium point. The introduction of plausible non-linearities may result in multiple interior equilibria and it is unclear how robust our findings would be to this form of increased generality. Nonetheless the LV framework underpins much community dynamical theory and this chapter has generalised results on permanence in LV ecosystems with increased ecological reality than previously and reports positive permanence-interaction strength relationships without citing special ecosystem architecture. Our key finding is numerical evidence that ecologists should be confident in qualitative findings from local stability analysis of LV ecosystems.

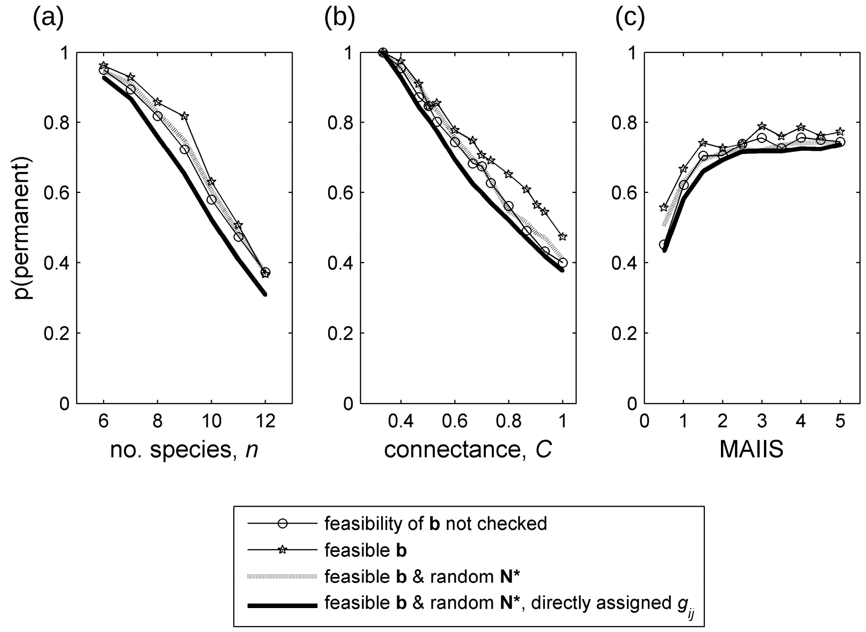


Figure 3.1. The probability of permanence with increasing complexity: (a) species richness n, (b) connectance C and (c) mean absolute interspecific interaction strength, MAIIS. In (c) C was fixed at 0.9 because when C=0.4 the probability of permanence across MAIIS values was ~1. Each point was based on at least 1000 ecosystems and where not varied or specified n=6, C=0.4, MAIIS=0.5 and variance in absolute interspecific interaction strengths (VAIIS) was 0.08. All Jacobians were not diagonally dominant. Circles represent Jacobians structured as in Chen & Cohen (2001) with equal equilibrium abundances (here $N_i^* = 0.5$) and no criteria on feasibility of intrinsic growth rates (**b** vector). Stars represent Jacobians with criteria on the feasibility of **b** included (the number of autotrophs was calculated as round(n/4)). Dashed lines represent Jacobians with a feasible **b** and randomly generated equilibrium abundances (N_i^*). Solid lines with no marker represent Jacobians with criteria on **b**, randomly generated equilibrium abundances (N_i^*) and directly assigned Jacobian off-diagonal elements (g_{ij} where $i \neq j$).

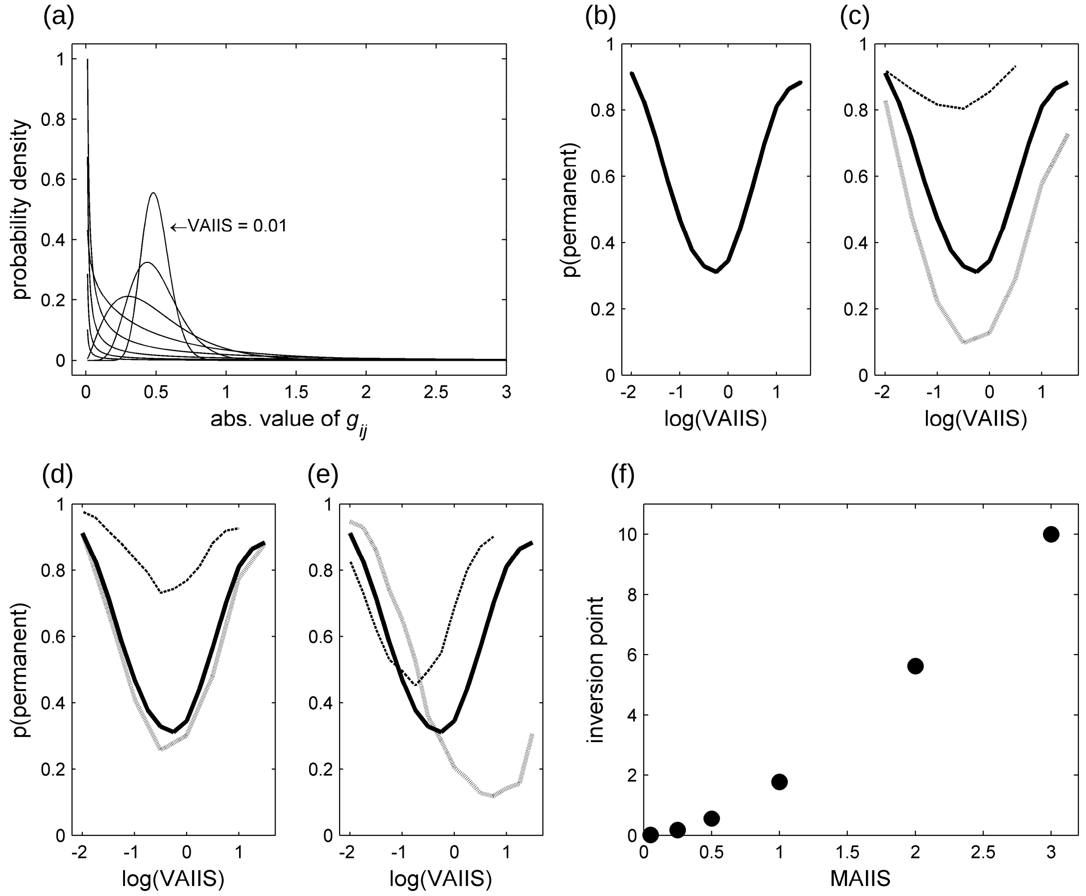


Figure 3.2. The probability that ecosystems were permanent as skew towards weak interactions was increased. (a) Probability densities of gamma distributions used to generate skew towards weak interaction strengths. Parameters of the gamma distribution were varied to generate a range of distributions with variances in interspecific interaction strengths (VAIIS) from 0.01 to 30 with a constant mean (MAIIS) of 0.5. (b) Probability of permanence in ecosystems with interspecific interactions assigned using the increasingly skewed distributions, where C=0.9 and n=6. We tested the generality of the u-shaped pattern for ranges of (c) species richness (n=4 dashed line, n=8 dotted line) (d) connectance (C=0.5 dashed line, C=1 dotted line) and (e) MAIIS (0.25 dashed line, 2 dotted line). (f) The relationship between MAIIS and the value of VAIIS (not logged) at which the inversion from a negative to positive permanence-VAIIS relationship occurred (trough in u-shaped curve). Each point in (b-f) was based on at least 1000 ecosystems, and where not varied or specified n=6, C=0.4 and MAIIS=0.5. No Jacobians were diagonally dominant.

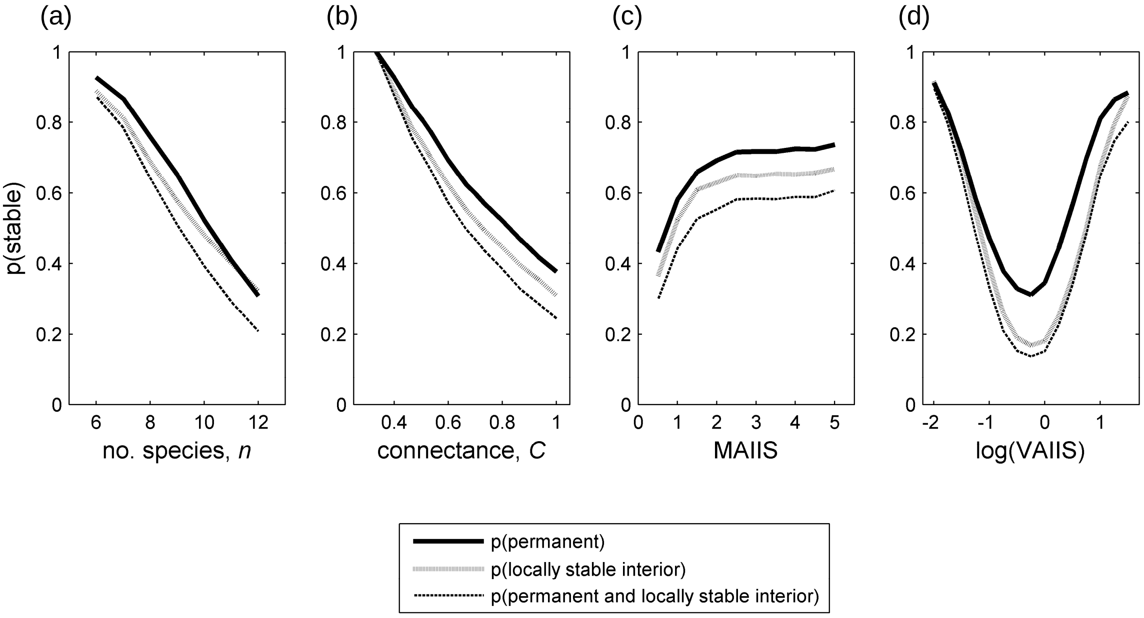


Figure 3.3. The probability that ecosystems were permanent, had a locally stable interior equilibrium point or were both permanent and locally stable, with increasing complexity. (a) species richness *n*, (b) connectance *C*, (c) mean absolute interspecific interaction strength (MAIIS) and (d) variance of absolute interspecific interaction strengths (VAIIS). Parameters as for Figs 3.1 and 3.2b. Each point was based on 10000 model ecosystems.

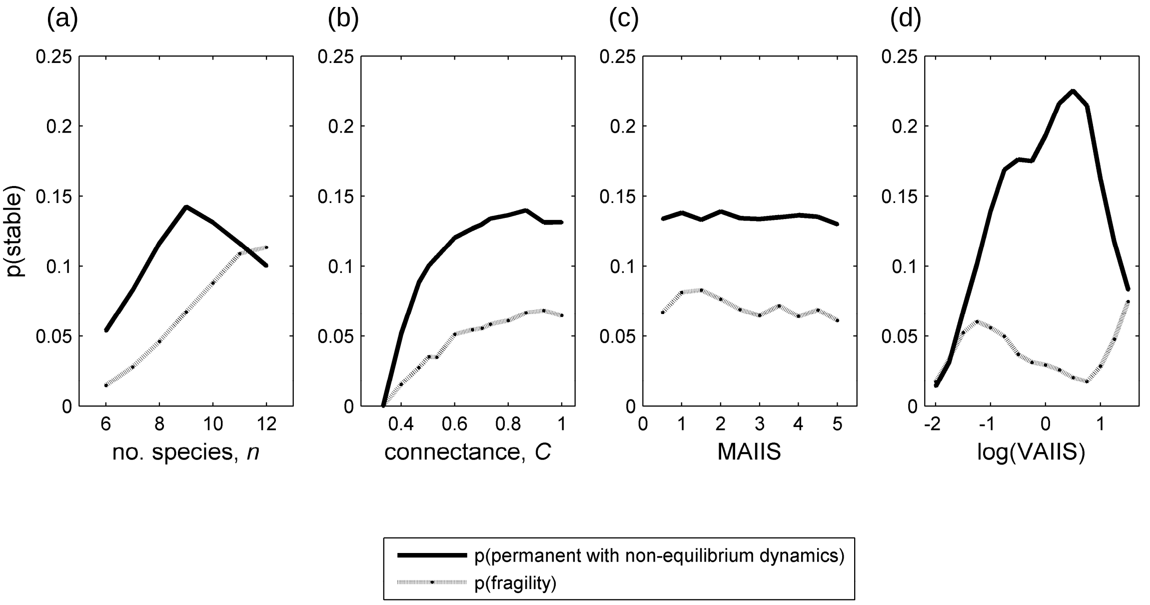


Figure 3.4. The probability an ecosystem was permanent but locally unstable and the probability an ecosystem was locally stable but not permanent with increasing complexity. (a) Species richness *n*, (b) connectance *C*, (c) mean absolute interspecific interaction strength (MAIIS) and (d) variance of absolute interspecific interaction strengths (VAIIS). Parameters as for Figs 3.1 and 3.2b. Each point was based on 10000 model ecosystems. Note scale on y-axis is different from other figures.

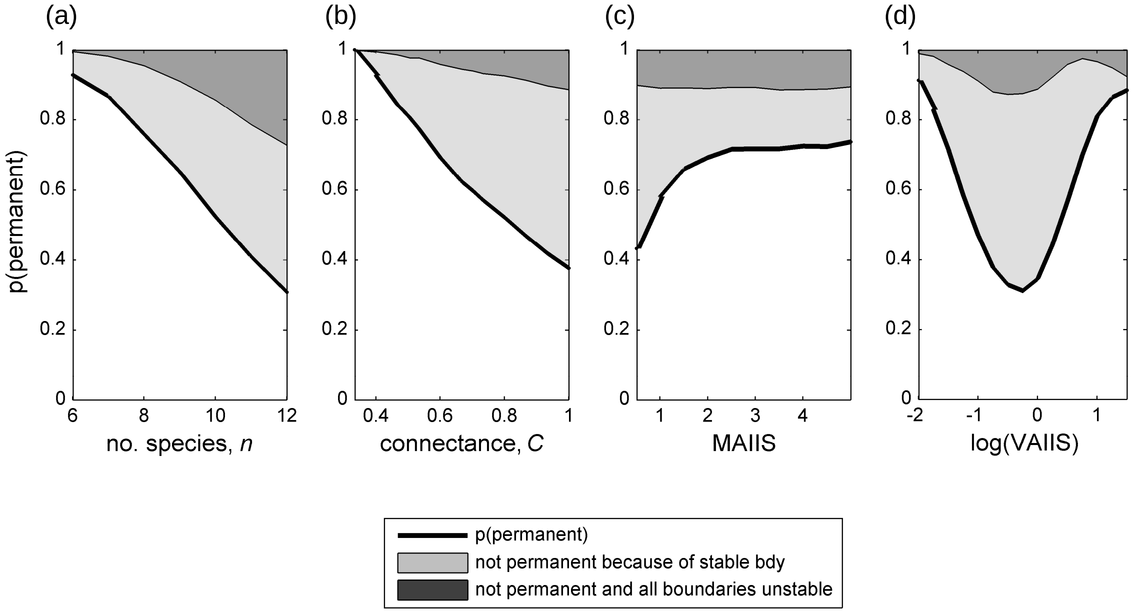


Figure 3.5. Attractors on the boundary that cause non-permanence. The probability of non-permanence is one minus the probability of permanence (solid line). The area above the line was shaded to indicate the likelihood that non-permanence was caused by one or more locally stable boundary equilibria (light gray area) or one or more non-equilibrium attractors on the boundary (dark gray area), as complexity was increased (a) species richness *n*, (b) connectance *C*, (c) mean absolute interspecific interaction strength (MAIIS) and (d) variance of absolute interspecific interaction strengths (VAIIS). Parameters as for Figs 3.1 and 3.2b. Each point was based on 10000 model ecosystems.

Appendix: Elements of the Jacobian matrix for interior and boundary equilibria of the Lokta-Volterra equations

The Lotka-Volterra equations (Eqn 3.1):

$$\frac{dN_i}{dt} = N_i(b_i + \sum_{j=1}^{n} a_{ij} N_j)$$

The off-diagonal elements of the Jacobian are the partial derivatives of the RHS of Eqn 3.1 with respect to N_j where $j \neq i$:

$$g_{ij} = \frac{\partial({}^{dN_i}\!/\!_{dt})}{\partial N_j} = \frac{\partial}{\partial N_j}(N_i(b_i + \sum_{j=1}^{n} a_{ij} N_j))$$
$$= a_{ij} N_i$$

This expression is the same for interior ($N_i = N_i^*$) or boundary equilibria ($N_i = M_i$), except $M_i = 0$ for boundaries where M_i is absent and thus $g_{ij} = 0$ $\forall$ $i \neq j$.

The diagonal elements of the Jacobian are the partial derivatives of the RHS of Eqn 3.1 with respect to N_i where now $j = i$:

$$g_{ii} = \frac{\partial({}^{dN_i}\!/\!_{dt})}{\partial N_i} = \frac{\partial}{\partial N_i}(N_i(b_i + \sum_{j=1}^{n} a_{ij} N_j))$$
$$= (b_i + \sum_{j=1}^{n} a_{ij} N_j) + N_i(a_{ii})$$
$$= b_i + \sum_{\substack{j=1 \\ j \neq i}}^{n} a_{ij} N_j + 2a_{ii} N_i$$

At the interior equilibrium ($\mathbf{N}^*$),

$$(b_i + \sum_{j=1}^{n} a_{ij} N_j^*) = 0$$
$$g_{ii} = a_{ii} N_i^*$$

If we have a boundary equilibrium (**M**) then $(b_i + \sum_{j=1}^{n} a_{ij} M_j)$ will not necessarily be zero. If $M_i = 0$ then,

$$g_{ii} = b_i + \sum_{\substack{j=1 \\ j \neq i}}^{n} a_{ij} M_j \ .$$

Chapter 4. Can parasites drive population cycles in mountain hares?

Abstract

Understanding the drivers of population fluctuations is a central goal of ecology. Although well-established theory suggests parasites can drive cyclic population fluctuations in their hosts, field evidence is lacking. Theory predicts that a parasite that loosely aggregates in the host population and has stronger impact on host fecundity than survival should induce cycling. The helminth *Trichostrongylus retortaeformis* in the UK's only native lagomorph, the mountain hare, has exactly these properties, and the hares exhibit strong population fluctuations. Here we use a host-parasite model parameterised using available empirical data to test this superficial concordance between theory and observation. In fact, through an innovative combination of sensitivity and stability analyses, we show that hare population cycles do not seem to be driven by the parasite. Potential limitations in our parameterisation and model formulation, together with possible secondary roles for parasites in determining hare demography are discussed. Improving our knowledge of leveret biology and the quantification of harvesting emerge as future research priorities. With the growing concern over the current management of mountain hares for disease control in Scotland, understanding their population drivers is an important pre-requisite for the effective management of this species.

Introduction

Understanding what drives population cycles is a central goal of ecology, yet despite more than 75 years of debate there is no clear consensus on their causation (Turchin, 2003). There is however a growing view that trophic interactions play an important role (Berryman, 2002). Whilst predator-prey and herbivore-plant systems have been well studied, the role of parasites has received less attention. Despite a strong theoretical basis that parasites can drive host cyclic dynamics (Anderson and May, 1978), empirical support is limited. While parasite mediated effects are thought to contribute to unstable dynamics in Soay sheep *Ovis aries* (Gulland, 1992) and Svalbard reindeer *Rangifer tarandus* (Albon et al., 2002), empirical evidence that parasites can drive cyclic dynamics in their wild host is currently limited to the red grouse - *Trichostrongylus tenuis* system (Hudson et al., 1998, but see Lambin et al., 1999).

The mountain hare is the only lagomorph species native to the UK with Scotland containing 99% of the UK population (McGradySteed et al., 1997). Mountain hares are believed to be under threat from habitat loss and fragmentation, local over-exploitation, hybridization and competition with the introduced brown hare and a growing concern over large-scale culls of mountain hares to control ticks and louping ill (Battersby, 2005, Kinrade et al., 2008, Macdonald et al., 1998, McGradySteed et al., 1997). Mountain hares are listed in Annex V of the EC Habitats Directive (1992) requiring the UK to ensure their conservation status and sustainable management. In response to growing concerns over the long term conservation status and current management of the species, in 2007 the mountain hare was made a UK Biodiversity Action Plan (BAP) species. The factors causing fluctuations and long term changes in the numbers and distribution of mountain hares remain unknown and complicate attempts to inform management through analysis of patterns in abundance. A greater understanding of the species population dynamics is essential for their sound management.

Scottish populations of mountain hares on grouse moorland are characterized by large amplitude fluctuations of variable regularity with a mean periodicity of 9.2 years (Newey et al., 2007b). The reasons for cyclic dynamics remain unclear (Newey et al., 2007a). Mountain hares are non-territorial and social interactions are not thought to be important (Flux, 1970, Hewson, 1976), and there is no evidence of food limitation (Keith, 1983). Mammalian and avian predators are controlled on moorland managed for red grouse in Scotland and therefore, unlike the situation in Scandinavia, predators are not thought to be important in driving mountain hare populations (Newey et al., 2007a). Hares are, however, susceptible to parasite infections, in particular the helminth *Trichostrongylus retortaeformis* and recent field studies have demonstrated that *T. retortaeformis* is loosely aggregated in the mountain hare population (Newey et al., 2005) and that parasite mediated effects on survival are small compared to parasite induced reductions in host fecundity (Newey and Thirgood, 2004, Newey et al., 2004). These features of the mountain hare - *T. retortaeformis* system are consistent with characteristics that analytical host-parasite models suggest can lead to instability and population cycles (May and Anderson, 1978).

Major advances in understanding causes of population dynamics have come from synthesising modelling and empirical work (Kendall et al., 1999, Turchin, 2003). Here we combine empirical field experiments, time-series analysis, and modelling to assess whether parasites can drive mountain hare population cycles. A range of observed dynamical patterns have been quantified from time series analysis, cross-sectional studies, and field experiments to generate a list of characteristic properties with which to compare with modelled population dynamics. Hare population densities fluctuate from 20-200 hares km^{-2} (Hewson, 1976, Watson et al., 1973), with a range of periods between four and 15 years (Newey et al., 2007b). *T. retortaeformis* burdens average approximately 2000 worms per individual (Newey et al., 2005). Our approach was to contrast these listed properties with equivalent characteristics in modelled mountain hare populations in order to: (a) test whether our current empirical understanding supports parasite driven hare dynamics; (b) in the case that it does not, identify plausible parameter changes which would lead to population dynamics with the observed properties; (c) determine whether small changes in parameters can account for the wide diversity of observed dynamics across Scottish populations; and (d) improve our understanding of the system and prioritise future empirical research activities.

Methods

We used a variant of the classic Anderson & May macroparasite model (Anderson and May, 1978, May and Anderson, 1978) introduced by Diekmann & Kretschmar (1991) which describes continuous growth equations for a host population of density, *H* which interacts with a parasite population, *P*:

$$\frac{dH}{dt} = -\alpha P - bH + aH\left(\frac{kH}{\delta P + kH}\right)^{k} \qquad \text{Eqn 4.1}$$

$$\frac{dP}{dt} = P\left[\frac{\lambda H}{H_o + H} - (\mu + \alpha + b) - \alpha\frac{P}{H}\left(\frac{k+1}{k}\right)\right] \qquad \text{Eqn 4.2}$$

Parameters are defined in Table 4.1. The structure of the model encapsulates important elements of the system that include: (a) the negative binomial distribution of parasites among hosts (Newey et al., 2005) described by the mean parasite load P/H and aggregation parameter k, (b) a transmission rate dependent on host density, and (c) host fecundity modelled through the use of a multiplicative term to avoid biologically meaningless negative host birth rates (Diekmann and Kretzschmar, 1991).

Point estimates and plausibility envelopes for parameterising Eqns 4.1 and 4.2 are given in Table 4.1. The data sources and methods of estimation are described in Appendix 4.1. Rather than strict confidence envelopes, plausible ranges of parameters were most practically based on the best available empirical information.

The dynamical properties of the parameterised model were derived using standard analytical techniques and numerical simulations (refer to the Appendix 4.2 for further details). Elasticity analyses were performed to compare the proportional effects of changing each parameter in Table 4.1 on dynamical properties of the model populations.

Results

MODEL PARAMETERISATION WITHIN EMPIRICALLY DEFINED PLAUSIBILITY ENVELOPE

Parameterising the model with the point estimates presented in Table 4.1 resulted in rapidly damped oscillations to a stable equilibrium point where parasite burdens were far greater than those found in mountain hare populations (Fig 4.1a, c). Elasticity analysis identified that: an increase in hare intrinsic mortality (b) or parasite-reduced hare fecundity (δ) or a decrease in hare intrinsic fecundity (a) would bring about a simultaneous reduction in both stability and parasite burdens. Increasing parasite-induced hare mortality (α) reduced parasite loads but was stabilizing while the parasite parameters (fecundity (λ), adult mortality (μ) and transmission inefficiency (H_0)) had little effect on equilibrium parasite load or stability. A new modified parameter set was identified by increasing the values of hare intrinsic mortality (b) and parasite-reduced hare fecundity (δ) and decreasing hare intrinsic fecundity (a) to empirically plausible limits (Table 4.1). The simulated population dynamics maintained a weakly stable equilibrium hare density characterized by weakly damped oscillations with a period within the observed range (Fig 4.1b, d). However, these changes could not bring parasite loads down sufficiently to be consistent with those found in mountain hares.

PARAMETER CHANGES WHICH GENERATE DYNAMICS WITH THE OBSERVED PROPERTIES

We reverse engineered changes to the modified parameter set that would reduce parasite loads whilst maintaining all other dynamical properties in the vicinity of those observed. Using elasticity analysis the key parameters in determining equilibrium parasite load were identified as hare intrinsic fecundity (a), parasite-reduced hare fecundity (δ), hare intrinsic mortality (b) and parasite-induced hare mortality (α) with some interactions also being important. Fig 4.2 shows the four parameters plotted pairwise revealing that to generate stable limit cycles with the observed properties requires either one of two possible parameter set modifications, both of which require increasing a parameter outside its plausibility envelope set by empirical data. To generate observed dynamics the effect of the parasite on hare fecundity (δ) can be increased by approximately ten fold. Alternatively hare intrinsic mortality (b) can be increased by about 0.8 adult hares per year (reducing mean hare life span by about 0.8 years) combined with a small increase in parasite-induced mortality (α) within the plausible envelope.

As we will discuss, we believe parasite-reduced fecundity (δ) and hare intrinsic mortality (b) may have been empirically underestimated. Increasing parasite-reduced fecundity (δ) from 0.0001 to 0.001 hare parasite^{-1} resulted in a qualitative change from a stable point to a stable limit cycle with a 15 year period (Fig 4.3a, d). Increasing hare intrinsic mortality (b) from 0.61 to 1.40 year^{-1} (annual survival of 0.25 - 0.54) resulted in a stable limit cycle with a period of 18 years. Subsequently increasing parasite-induced mortality (α) to 0.000014 reduced the period of the limit cycle to 15 years (Fig 4.3b, e). Increasing parasite-induced mortality (α) alone generated rapidly damped oscillations with a small period. It was not possible to obtain the observed population dynamics by changing hare intrinsic fecundity (a) alone.

For both sets of dynamics shown in Fig 4.3(a, d) and Fig 4.3(b, e) the peak parasite loads were unrealistically high (10^5) which, if we assume that the parasite load at the peak of the cycle corresponds to maximum parasite loads counted in the field, should be around 16,000 worms per hare. Parasite loads of a more realistic amplitude were obtained by increasing parasite-induced mortality (α) above 0.00004 (Fig 4.4a), which lies well within the plausibility envelope. Additionally, the simulated hare populations shown in Fig 4.3(a, d) and 4.3(b, e) spend most years at numbers much below the lower observed limit for hare density. Changes in parasite fecundity (λ) and transmission inefficiency (H_0) affected the amplitude of hare oscillations but not of parasite burdens (Fig 4.4b and c). Thus, a set of parameters was identified that produced realistic dynamics in both hare and parasite populations (Fig 4.3c, f).

CAN SMALL CHANGES IN PARAMETERS ACCOUNT FOR VARIABILITY IN DYNAMICAL PROPERTIES?

Scottish populations of mountain hares exhibit a wide diversity of observed dynamics. We used the model to look for parameters that may vary across Scotland and affect period of cycles and amplitude of limit cycles within plausibly small changes in their value. Fig 4.5 shows the sensitivity analysis of stability and period to small changes in individually varied parameters around the system which generated realistic dynamics (Fig 4.3c, f). Stable limit cycles occurred where the system crossed the boundary from stable to unstable, and amplitude increased with increasing instability. Variation in hare intrinsic fecundity (a), parasite-reduced hare fecundity (δ), parasite-induced hare mortality (α) and adult parasite mortality (μ) could account for the range of periods observed in natural populations. Variation in all parameters in Fig 4.5 except adult parasite mortality (μ) could account for variability in stability and amplitude that occur across the species range in Scotland. Finally, although the parasite transmission parameters (λ and H_0) were not found to influence stability or period, the amplitude of the hare density limit cycle was sensitive to small changes in their value (Fig 4.4).

Discussion

This model of the mountain hare - *T. retortaeformis* interaction cannot predict observed population dynamics of mountain hares with realistic parasite burdens within the broad-range of parameter space we judge to be plausible. We now discuss three possible interpretations of this observation. 1) Parasites are the main drivers of hare cycles, but the model, while including the key elements of the interaction, represents them insufficiently realistically. 2) Parasites are the main drivers of hare cycles and the model has altogether omitted important ways in which the parasites influence hare demography. 3) Parasites are indeed not the main drivers of hare cycles.

ARE KEY ELEMENTS OF THE INTERACTION REPRESENTED SUFFICIENTLY REALISTICALLY?

To represent the hare-parasite system sufficiently realistically requires both adequate model parameterisation and formulation. As several of our plausible parameter ranges were based on small sample sizes or indirect data sources, it is possible that our estimated parameter ranges are wrong. The key difficulty is to find a model where the dynamics are unstable and parasite loads realistic. Parasite burdens were particularly sensitive to the level of parasite-induced hare mortality (α), and our estimate was based on a single study (Newey and Thirgood, 2004). However, the study found almost no difference in survival between parasite-reduced and untreated hares (Newey and Thirgood, 2004) and increasing parasite-induced mortality (α) while lowering parasite burdens towards more realistic levels, has a strong stabilising influence on the resulting dynamics.

Parasite burdens were also sensitive to hare fecundity (a), parasite-reduced hare fecundity (δ) and hare mortality (b). Here, fecundity was used as the measure of recruitment and leveret pre and post-natal mortalities were not included because the effect on parasites at these stages is unknown (but see next section). Mountain hares are killed for sport, pest and disease control but this mortality is not included in the current analysis. The relationship between density and harvesting has not yet been studied in mountain hares (Newey et al., 2007a). Game harvesting bags are a good proxy for population abundance in red grouse (Cattadori et al., 2003) but there is likely to be more inconsistency across years in mountain hares. If, as suspected, the relationship between mountain hare density and harvesting is not density dependent, then the current model formulation holds and hare mortality rate (b) should be increased. Decreasing hare recruitment, strengthening parasite suppression of hare recruitment or higher hare mortality is destabilising and reduces parasite burdens, but to attain realistic dynamics a large parasite-induced mortality rate (α) is still required.

If our estimate of parasite-induced hare mortality (α) is reasonable then it seems unlikely that a key element of the parameterisation has been omitted, and now we query the formulation of our model. Hare recruitment and parasite development were represented as purely continuous processes. Time delays and seasonality are well-known to be destabilising to the population dynamics of infectious diseases (Altizer et al., 2006, Greenman et al., 2004), and both occur in mountain hares and the parasite *T. retortaeformis*. Mountain hares do not mature in their year of birth but in the following year, and the breeding season is restricted to about nine months of the year (Flux, 1970). *T. retortaeformis* is a direct life-cycle parasite; eggs voided in the host's faeces develop to an infective stage outside the host over a period of time which depends on climatic conditions (Crofton, 1948). Although it is well established that the developmental time lag has a destabilising influence on model host dynamics (May and Anderson, 1978) the current model does not incorporate a time delay in parasite recruitment. In favourable conditions development time is short and the assumption of negligible time delay in relation to changes in hare densities is reasonable. However development may last several months over winter. We have explored discrete-time formulations of our model which incorporated: a step function that restricted hare reproduction (at an accordingly increased rate) to a nine month breeding season; a delay in the maturation of leverets until the start of their first breeding season; and a simple delay (that ranged between one and 12 weeks) in parasite maturation that was constant across the year. With these alternative formulations damping times increase but we still don't recover sustained limit cycles within the plausible parameter ranges. However, we don't have to go as far outside these ranges as we do with the purely continuous time formulation.

ARE IMPORTANT WAYS IN WHICH THE PARASITES INFLUENCE HARE DEMOGRAPHY OMITTED?

The red grouse - *T. tenuis* system in Scotland has similar characteristic features as the mountain hare - *T. retortaeformis* system, such as low predation, greater parasite reduced fecundity than survival, and range of parasite burdens. Yet in applying a similar approach as here, Dobson & Hudson (1992b) were able to reproduce grouse cycles. A striking difference is that parasite effect sizes (α, δ) were estimated at around 30 times greater for grouse than those estimated here. As parasite effect on fecundity (δ) was calculated from seven week old brood sizes, we now discuss the possibility that parasites may affect aspects of hare recruitment other than the number of ova shed in females.

Parasites may have a larger impact on recruitment through influences on leveret survival, growth rate, or timing of breeding. The timing of breeding is important for reproductive success in mammals (e.g. Clutton-Brock et al., 1982) and is influenced by parasite infection in a range of species (Allander and Bennett, 1995, Feore et al., 1997, Mulvey et al., 1994). Time of first breeding in mountain hares is influenced by temperature, female age, size and weight with older, larger and heavier females attempting to breed earlier than those younger and smaller (Flux, 1970). Young born earlier in the year have a longer growing season, enter the winter heavier and larger than late born young and have higher over-winter survival and greater future fecundity (Iason, 1989a, Iason, 1990). Thus females may seek to breed earlier to produce more, higher quality young and we suggest future studies could profitably investigate a maternal effect of parasite load on the timing of breeding, survival and growth of leverets.

Maternal effects may destabilise population dynamics and promote cycles (Beckerman et al., 2002). To model this would require a new hare-parasite model formulation that could encapsulate: a maternal body size effect on the birthdate of young; a maternal parasite load effect on the birthdate of young; adult body sizes determined by birthdate; and adult hare mortality related to body size. This additional parasite-mediated effect may reduce the extent to which parameters need to deviate from our point estimates to generate realistic dynamics. However, they require a move from simple ordinary differential equation formulations of host-parasite dynamics to a partial differential equation model or individual based approach, which is beyond the scope of the current chapter.

Other forms of environmental variation that would lead to sufficiently large stochastic variation in the parameters of the host-parasite model at realistic frequencies could result in the generation of sustained limit cycles of a realistic magnitude from the damped oscillations predicted by the deterministic model. However, there is as yet no empirical data to inform the magnitude, covariation, or frequencies of these stochastic processes.

A SECONDARY ROLE FOR PARASITES?

If parasites are not the main driver of mountain hare cycles, could they still have a role in hare population dynamics? Parasitic nematodes of Soay sheep increase the depth of population crashes initiated by winter food shortage (Gulland et al., 1993). Similarly, reduction of parasitic nematodes from a red grouse population (Hudson et al., 1998) arguably does not remove a tendency to cycle (Lambin et al., 1999, Tompkins and Begon, 1999) but parasites might deepen the extent of grouse crashes rather than determine their frequency. This notion is supported by our analyses, which showed that hare cycle amplitude was very sensitive to parasite transmission parameters whereas period was relatively insensitive.

CONCLUSION

Despite the observation of large parasite burdens in mountain hares, and the perceived absence of predation and food-limitation, we have found limited support for parasite-driven hare cycles. The results of our sensitivity analysis suggest that lower recruitment rates, stronger parasite suppression of recruitment or raised adult hare mortality than currently realised, would allow a closer fit between model predictions and observed dynamics. Therefore we identify leveret biology and the quantification of harvesting of hares for sport, pest and disease control as research priorities. If parasites do drive hare cycles, the model presented here suggests that our understanding of the full effects of parasites on hare demography is importantly incomplete.

Table 4.1. Parameter estimates and plausible limits from field experiments and related host-parasite systems with which to parameterize the hare - *Trichostrongylus retortaeformis* model. Values in bold generate dynamics closest to those observed (modified parameter set).

Symbol	*Parameter*	*Unit*	*Lower plausible limit*	*Point estimate*	*Upper plausible limit*	*Data source*
a	Intrinsic fecundity of adult hares (in absence of parasites)	year^{-1}	**1.8**	2.3	2.8	Newey et al. (2004)
δ	Parasite-induced reduction in hare fecundity	hare parasite^{-1}	0	0.000016	**0.0001**	Newey & Thirgood (2004)
b	Intrinsic mortality of adult hares (in absence of parasites)	year^{-1}	0.08	0.35	**0.61**	Newey & Thirgood (2004)
α	Parasite-induced hare mortality	year^{-1}	0	**0.000008**	0.0001	Newey & Thirgood (2004)
λ	Parasite fecundity	year^{-1}	80	**1000**	2800	Hobbs unpublished, Flux (1970), see Appendix 4.1
H_0	Transmission inefficiency constant	hare	13500	**38200**	66800	Newey et al. (2005), Newey & Thirgood (2004), Newey et al. (2004)
μ	Adult parasite mortality	year^{-1}	0	**0** (0.1 for elasticity analysis)	1.2	Dobson & Hudson (1992), based on *T. tenuis.*
k	Negative binomial parameter/ degree of overdispersion		0.5	0.57 (**0.5** in model, see Appendix 4.2)	2	Newey et al. (2005)

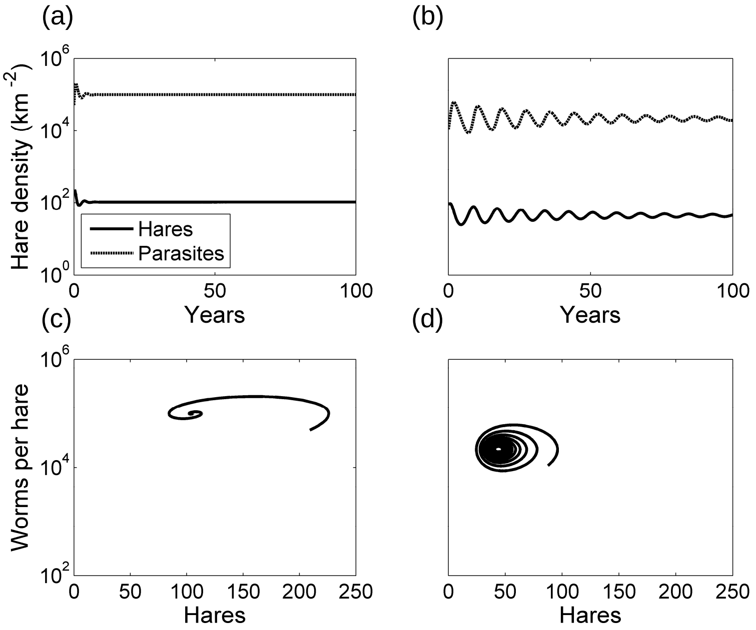


Figure 4.1. Simulated population dynamics based on the empirical information available on the hare-parasite interaction (Table 4.1). The model was parameterized in (a, c) using our point estimates and in (b, d) with the modified parameter set chosen to be the best fitting combination within the identified plausibility envelope. The time series are shown in the top row (a, b) where the solid line represents the hare population size (hares per km^2) and the dashed line is parasite load per hare. The dynamics in state space are shown in the bottom row (c, d).

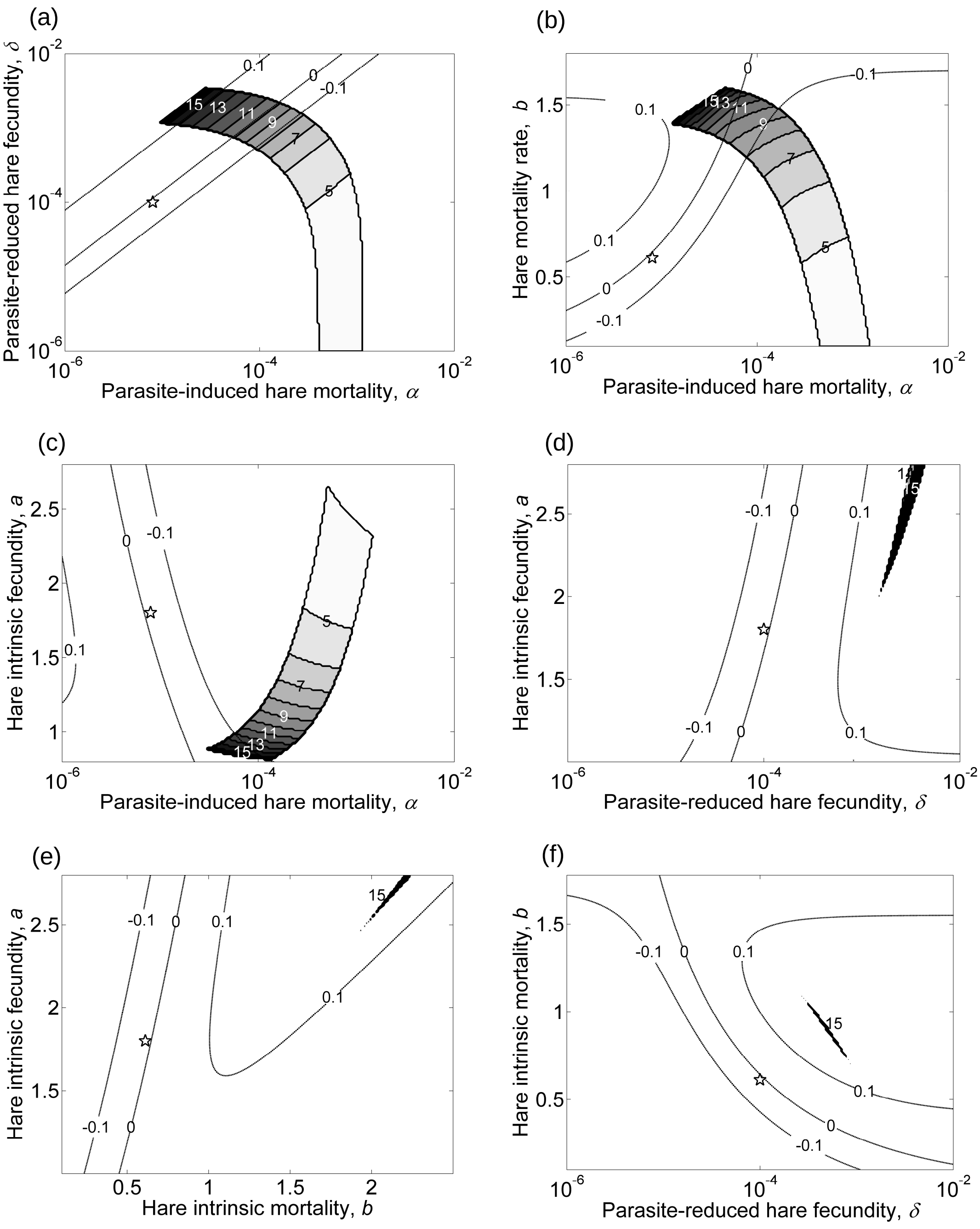


Figure 4.2. Parameter changes required to obtain dynamical properties observed in wild hare populations are given by the distance between the star and the polygon. The star is the position of the modified parameter set, the closest we get to observed dynamics within the empirically determined plausibility envelope, whilst the polygon represents the observed range of dynamics specified by the observed equilibrium hare densities (20-200 km^{-2}), equilibrium parasite load (1000-3000), and period of four to 15 years (period contours indicated). Stability contours are shown (dashed lines: value of real part of dominant eigenvalue -0.1 (stable), 0, and 0.1 (unstable)) with stable limit cycles occurring at low positive values. Other parameters were held constant at the modified values.

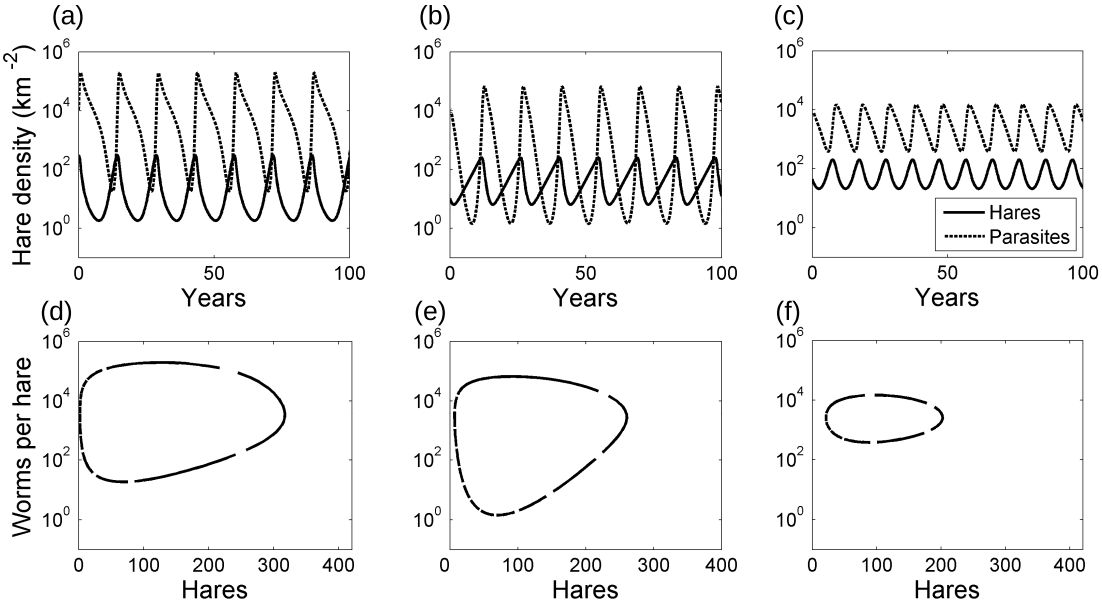


Figure 4.3. Simulated population dynamics after parameter changes to get closer to the observed dynamical properties. (a, d) Parasite-reduced hare fecundity, δ, increased from 0.0001 to 0.001 hare parasite^{-1}. (b, e) Hare intrinsic mortality, b, increased from 0.61 to 1.40 year^{-1} and parasite-induced mortality, α, from 0.000008 to 0.000014 year^{-1}. Both resulted in a stable limit cycle which passed through unrealistically high parasite and low hare numbers. (c, f) Realistic population dynamics generated using: a = 1.8; b = 0.61; δ = 0.001; α = 0.00004; λ = 600. For the time series (top row), the solid line represents the hare population size (hares per km^2) whilst the dashed line is parasite load per hare. For the limit cycles in state space (bottom row), the velocity within the limit cycle is indicated by the length of the dashes, one per year.

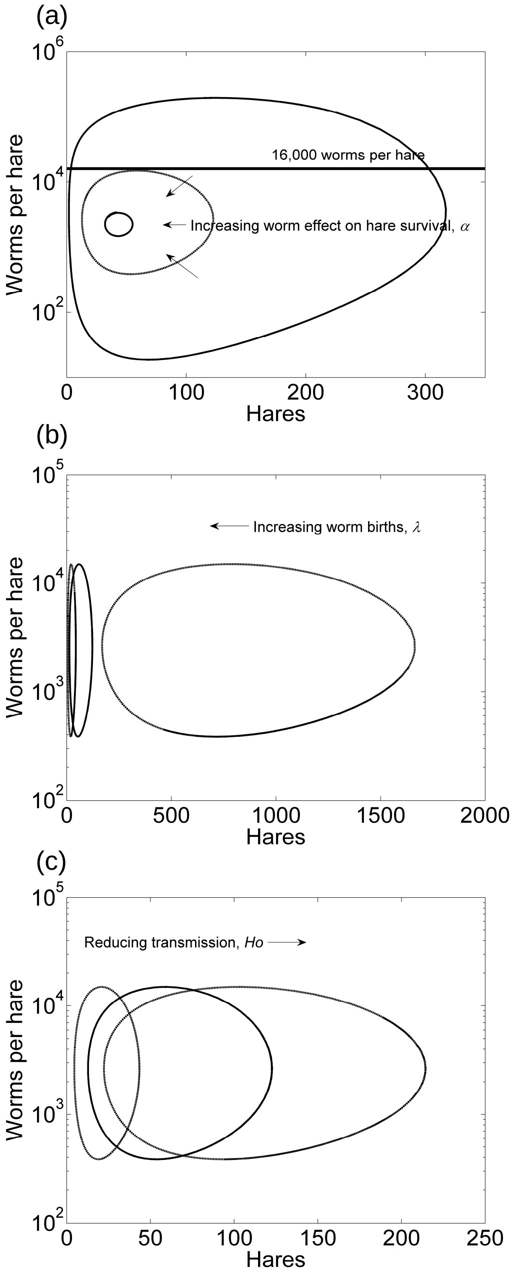


Figure 4.4. The effect of small, plausible changes in parameters on the amplitude of the limit cycles. (a) Increasing α from our point estimate of 0.000008 (largest limit cycle) to 0.00004 (medium limit cycle) reduces the parasite load oscillation to below 16,000 worms per hare (straight line). The cycle shrinks further as α is increased to its upper plausible limit of 0.000104 (smallest limit cycle). (b) Flexibility in λ and (c) H_0 controls the amplitude of the hare oscillation. Three limit cycles are presented in both (b) and (c) where the middle limit cycle was generated using point estimate values of λ or H_0, either side of limit cycles generated by setting λ or H_0 to their lower or upper plausible limit. Other parameters were kept constant: $a = 1.8$, $\delta = 0.001$, $b = 0.61$, $\alpha = 0.00004$, $\mu = 0$, $k = ½$.

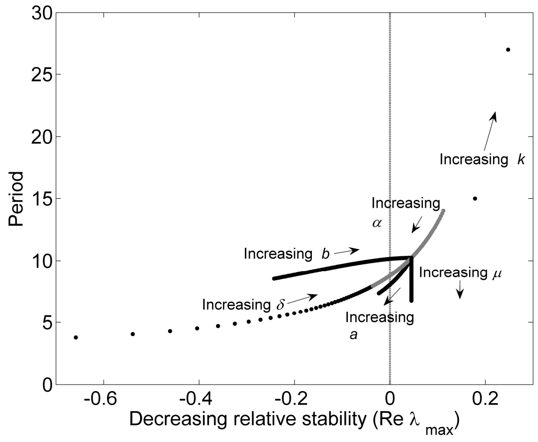


Figure 4.5. The effect of small, plausible changes in parameters on stability and period. One parameter was varied at a time, while others were held at values for the system which generated realistic dynamics (Fig 4.3c, f): parasite-induced hare mortality (α) was varied from its point estimate to upper plausible limit; hare intrinsic fecundity (a), hare intrinsic mortality (b) and adult parasite mortality (μ) were varied from lower to upper plausible limits; degree of overdispersion (k) values ½, 1, 2; Parasite-reduced fecundity (δ) was varied from its point estimate to 0.001 hare parasite^{-1} and follows the opposite path to α. The vertical line at $Re\lambda_{max} = 0$ marks the boundary between a stable (negative) and unstable (positive) equilibrium.

Appendix 4.1: Parameter estimation

Where possible, field data from mountain hares in Scotland were used, otherwise data were drawn from closely related systems. Both males and females were included in the model population because both sexes are hosts to the parasite population.

a, Intrinsic fecundity of hares (in absence of parasite) (year^{-1})

Data from hares for which parasite burdens were measured at the end of the breeding season (Newey et al., 2004) were used to estimate annual fecundity. We regressed estimated annual fecundity against parasite burden for the female hares and extrapolated back to zero parasites. The estimate was halved to account for males in the population at an assumed ratio of 1:1. Thus *a* was set at 2.3 with a 95% confidence interval of 1.8 – 2.8.

δ, Parasite-induced reduction in hare fecundity (hare parasite^{-1})

Data from hares which were treated for parasites prior to the breeding season showed treated hares had significantly lower parasite loads and higher fecundity (Newey and Thirgood, 2004). The same data was reanalysed by directly relating parasite burden and fecundity to estimate the effect of an individual parasite on fecundity. The effect was estimated from the absolute value of the (negative) slope of the regression line between fecundity and parasite burden as 0.000031 hares per worm per year, although the link between parasite load and fecundity when analysed in this way was not statistically significant ($F_{1,31}$ = 0.15, p = 0.703). The estimate was halved to account for males in the population at an assumed ratio of 1:1. The lower plausible limit was taken as zero and the upper 95% confidence limit was 0.0001 hares per worm per year.

b, Intrinsic hare mortality (in absence of parasite) (year^{-1})

Survival of adult hares was recorded over the duration of a parasite reduction experiment where adult female mortality (n = 13) of parasite reduced hares was 0.23 (SE 0.10) over eight months (Newey and Thirgood, 2004). Converting this to annual mortality results in an estimate of 0.35 hares per year (95% CI 0.08-0.61). Death of around one third of hares per year is consistent with the average life expectancy of hares of three years (Hewson, 1976).

a, Parasite-induced adult hare mortality (year^{-1})

In the parasite treatment experiment carried out by Newey et al. (2004) almost no difference in adult hare mortality was found between the treated (0.23 with SE 0.10, n = 13) and untreated groups (0.24 with SE 0.09, n = 11). However, there was a difference in the mean parasite load between groups, so that each parasite added over the treated mean parasite load (1125 worms per hare) could contribute to the death of as much as 0.0001 of a hare per worm. The mean estimate was 0.000008 hares per worm, which translates into an unrealistic burden of 125000 worms required to kill a single hare.

λ, Parasite birth rate (year^{-1})

Parasite birth rate is specified here as the number of eggs produced per adult worm per year. In the absence of data on *T. retortaeformis* in hare hosts, we estimated this parameter from a combination of sources on closely related host systems.

Parasite egg production was estimated from a small dataset kindly provided by R. Hobbs (unpublished) on *T. retortaeformis* in the wild European rabbit (*Oryctolagus cuniculu*s (L.)). The slope of the regression line between the number of adult worms and corresponding egg production per gram of faeces estimated per worm as 0.05 eggs worm^{-1} gram^{-1} (95% CI 0.01-0.09) and was significantly different from zero ($F_{1,12} = 7.01$, $p = 0.021$). To calculate per worm daily egg production, egg numbers per faecal gram were multiplied by daily production of hard faeces in hares. Daily hard faecal production has been quantified at approximately 58g (range 25-89 Flux (1970)). Annual egg production was thus approximated at 1000 eggs per worm per year (empirically estimated range 80-2800). Our measure of egg production for *T. retortaeformis* in hares is much lower compared to *T. tenuis* in grouse which can shed up to 40000 eggs per gram of faeces (Shaw et al., 1989).

H_0, Transmission efficiency constant (hare)

This parameter reflects the proportion of eggs that do not go on to complete their life cycle and re-enter the host. During the part of the life cycle from parasite egg to adult there are many sources of mortality. These are hard to identify and measure. H_0 removes the need to quantify survival at each stage by clumping them all together, and simply estimating the proportion which are lost and do not reach adulthood.

The method used here provides a crude estimate of H_0 and is based on Eqn 4.2. We assume that there is no hypobiosis (arrested development of larvae in the host) so that during the early stages of reinfection parasite densities are small, such that terms 2 and 3 in Eqn 4.2 are negligible. This gives an equation for the reinfection rate per host post-treatment (ε):

$$\varepsilon = \frac{1}{H}\frac{dP}{dt}$$

$$\varepsilon = P\left(\frac{\lambda}{H_0 + H}\right)$$

which can be rearranged to isolate H_0:

$$H_0 = \frac{\lambda P - \varepsilon H}{\varepsilon} \qquad \text{Eqn 4.3}$$

The parasite reduction experiments (Newey and Thirgood, 2004, Newey et al., 2004) provided estimates of post-treatment reinfection rates for three different years and two different seasons. Hare densities for these sites were estimated using distance sampling. The mean parasite load for adult hares was calculated from a cross sectional study of 587 hares across 30 central Scotland estates (Newey et al., 2005). Yearly loss of parasites was averaged over the sites to give a mean H_0 of 38200 with empirically estimated range 13500 to 66800.

μ, Adult parasite mortality (year^{-1})

Nematode gut parasites of the genus *Trichostrongylus* have similar life cycles (Olsen, 1986). In the related host-parasite system of red grouse and *T. tenuis*, worms are thought to live as long as their grouse hosts (Hudson et al. 1992). In absence of data for *T. retortaeformis* in hares we assume that adult worms only die when the host dies, and set $\mu = 0$.

k, Negative binomial parameter, measure of parasite aggregation among hosts

The parasite is negatively binomially distributed among hosts (Newey et al., 2005). The degree of aggregation is described by the parameter k of the distribution, estimated to be 0.57 in adult hares (both male and female) with monthly estimates available for individual months from December to May giving a range around this mean of 0.37 to 2.26. These values suggest the parasite is mildly aggregated among hares when compared with a range of wildlife host-parasite systems (Shaw et al., 1998). The structure of the model (Eqns 4.1-4.2) places k as an exponent in the hare growth equation. Mathematical analysis is greatly facilitated by assuming k might range between 0.5 and 2.

Appendix 4.2: Analysis

This section describes how the dynamical properties of the parameterized model were derived using analytical techniques and numerical simulations.

EQUILIBRIUM HARE AND PARASITE DENSITY

Mean density is assumed to correspond to the interior equilibrium density. To solve for the interior equilibrium density, the derivatives in Eqns 4.1-4.2 are set to zero and a solution for *H* and *P* sought. However, manipulation of Eqn 4.1 was required before being able to achieve this. Firstly, Eqn 4.1 was divided by *H*:

$$\frac{dH}{dt} = H\left\{-\alpha\left(\frac{P}{H}\right) - b + a\left(\frac{k}{\delta\left(\frac{P}{H}\right)+k}\right)^{k}\right\}$$

Therefore at equilibrium:

$$0 = -\alpha x - b + a\left(\frac{k}{\delta x + k}\right)^{k}$$

where *x* is the parasite load at equilibrium:

$$x = \frac{P*}{H*} \qquad \text{Eqn 4.4}$$

Analytical solutions for the interior equilibrium point can now be obtained by substituting *x* into *dH/dt* = 0. This is straightforward for the special cases *k* = ½, 1 and 2, which sufficiently covers the range of empirical *k* values (see above). Setting *k* = ½ and rearranging *dH/dt* = 0 results in a cubic equation in *x*:

$$0 = (2\alpha^2\delta)x^3 + (4b\alpha\delta + \alpha^2)x^2 + (2b^2\delta + 2b\alpha)x + b^2 - a^2\,,$$

for *k* = 1,

$$0 = (\alpha\delta)x^2 + (b\delta + \alpha)x + b - a\,,$$

while for $k = 2$,

$$0 = (\alpha\delta^2)x^3 + (4\alpha\delta + b\delta^2)x^2 + (4\alpha + 4b\delta)x + 4b - 4a\,,$$

and x is recovered as the only positive, real solution. Now the equilibrium hare density can be isolated in terms of the constant x:

$$H^* = \frac{(\mu + b + \alpha)H_0 + \alpha\left(\frac{k+1}{k}\right)H_0 x}{\lambda - (\mu + b + \alpha) - \alpha\left(\frac{k+1}{k}\right)x}$$

and from Eqn 4.4, $P^*=xH^*$. The host-parasite equilibrium point was termed feasible if hare and parasite population sizes were greater than zero ($H^* > 0$, $P^* > 0$).

STABILITY

Linear equilibrium stability analysis was used to infer the stability of the modelled dynamics. In a two dimensional system, populations bounded from both extinction and growth to infinity must have a stable dynamical structure which, in this case, is either a stable equilibrium point or stable limit cycle (Diekmann and Kretzschmar, 1991). We rejected those regions of parameter space in which the populations either go extinct or grow to infinity. Stability of the interior equilibrium point was determined by constructing the Jacobian matrix (**J**) which contains the growth equations differentiated with respect to each of the host and parasite:

$$\mathbf{J} = \begin{bmatrix} \frac{\partial \dot{H}}{\partial H} & \frac{\partial \dot{H}}{\partial P} \\ \frac{\partial \dot{P}}{\partial H} & \frac{\partial \dot{P}}{\partial P} \end{bmatrix}$$

where

$$\frac{\partial \dot{H}}{\partial H} = -b + a\left(\frac{kH^*}{\delta P^* + kH^*)}\right)^k + a\delta\frac{P^*}{H^*}\left(\frac{kH^*}{\delta P^* + kH^*}\right)^{k+1}$$

$$\frac{\partial \dot{H}}{\partial P} = -\alpha - a\delta\left(\frac{kH^*}{\delta P^* + kH^*}\right)^{k+1}$$

$$\frac{\partial \dot{P}}{\partial H} = \lambda P^*\left(\frac{H_0}{\left(H_0 + H^*\right)^2}\right) + \alpha\left(\frac{k+1}{k}\right)\frac{P^{*2}}{H^{*2}}$$

$$\frac{\partial \dot{P}}{\partial P} = \frac{\lambda H^*}{H_0 + H^*} - (\mu + \alpha + b) - 2\alpha\left(\frac{k+1}{k}\right)\frac{P^*}{H^*}$$

From **J** the eigenvalues associated with the equilibrium states can be calculated and the dominant (most positive) eigenvalue indicates the local stability of the equilibrium point. A negative dominant eigenvalue denotes a stable point and the magnitude determines the rate of damping to equilibrium. Growth equations that produce oscillatory dynamics will have complex conjugate eigenvalues. Where a pair of complex eigenvalues cross the imaginary axis of the complex plane we can expect to see a stable limit cycle with an increase in amplitude as the eigenvalues move deeper into the positive real half of the complex plane. Close to the bifurcation the period of the oscillations can be approximated from the natural frequency (e.g. James, 2001), given by the imaginary part of the dominant eigenvalue (ω): Period = $2\pi / \omega$. More accurate estimation of the period of oscillatory systems far from the bifurcation and the amplitude of stable limit cycles were determined by numerical simulation.

ELASTICITY ANALYSIS

Elasticity analysis was used to compare the proportional effects of each parameter in Table 4.1 on dynamical properties of the model populations. This permitted identification of key parameters in determining each property. Elasticity analysis considers only linear perturbations and therefore is only valid within the local vicinity of a specified point in the multidimensional parameter space. Thus elasticity was recalculated when the parameters were changed. In the analyses, parameter space was sampled between $\pm 10\%$ of parameter values using a Sobol’ sequence (Sobol' (1967), C++ code by J. Burkhardt http://people.scs.fsu.edu/~burkardt/index.html). The Sobol’ sequence is a quasi-random sampling method, which permits more uniform sampling of multidimensional parameter space than uncorrelated random points (Press et al., 1992).

Chapter 5. Dissecting the drivers of population cycles: interactions between parasites and mountain hare demography

Abstract

There is growing awareness that the cyclic population dynamics in vertebrate species are driven by a complex set of interactions rather than a single causal factor. For the mountain hare, population cycles have been characterised throughout much of its circumpolar distribution but the reasons for this dynamical behaviour remain unknown. Empirical research in the Scottish uplands demonstrates that macroparasitism, maternal effects on the vital rates of offspring, and a seasonal environment, are potentially important ecological processes in this system, and all these processes can theoretically increase the propensity for cyclic dynamics. Here we incorporate these ecological details into an individual-based model (IBM) of a mountain hare population infected by a gut nematode, *Trichostronglyus retortaeformis*. First, we establish a model that captures mean characteristics of observed mountain hare time series and parasite intensities. Second, by systematically removing model structure we dissect out dynamical influences of maternal effects. The model allows delayed responses to life history by linking maternal body size and parasite infection to the future survival and fecundity of offspring. We found that these delayed life history effects (DLHEs) were weakly destabilising and allowed parameters to be closer to empirical estimates in order to generate observed hare population cycles. We therefore suggest DLHEs could be important processes in host-parasite systems. Third, by modifying model structure we investigated the dynamical influence of the mechanism of parasite transmission. We found that the mechanism had a strong influence on host population stability. We identify a 'best fit' mechanism and discuss the implications for parasite aggregation mechanisms, host movement and natural geographical variation in host population dynamics.

Introduction

In order to break down complexity and understand process drivers, theoretical ecologists use abstractions of ecological processes. A process which has captured the attention of ecologists since inception of the field is cyclic population dynamics (Elton, 1924), yet despite the intervening 85 years of research there is still no clear consensus as to what processes drive cyclic dynamics (Turchin, 2003). The causes of population cycles can include trophic interactions, individual variability, environmental variation and the complex interplay between these factors and population demography (Bjornstad and Grenfell, 2001, Lundberg et al., 2000, Sutherland, 1996, Beckerman et al., 2002).

Simple mathematical models show that direct effects of macroparasites can potentially drive population cycles (Anderson and May, 1978, May and Anderson, 1978), although empirical support for their role in destabilising host populations is limited to a few species (Svalbard reindeer: Albon et al., 2002, Soay sheep: Gulland, 1992, Gulland and Fox, 1992, red grouse: Hudson et al., 1998, Hudson et al., 1992). The parasitic nematode *Trichostrongylus retortaeformis* has been implicated as a driver of cyclic population dynamics in a small mammal found in the Scottish uplands, the mountain hare *Lepus timidus* (Newey and Thirgood, 2004). However, a simple model implies the parasite effect is too weak to account for sustained hare cycles and realistic parasite intensities (Townsend et al., 2009, Chapter 4).

Trophic interactions are considered to play an important role in driving population cycles (Turchin, 2003, Berryman, 2002). The effects of trophic interactions may manifest themselves at the population level either directly or indirectly as a function of immediate and delayed responses to either density or to life history effects (Beckerman et al., 2002). While an immediate life history effect is a change in population demography in response to the current environment, a delayed life history effect (DLHE) occurs in the future, changing future population demography as the result of the current environment. Thus maternal effects, which transmit individual life-history responses between generations, can give rise to DLHEs (Beckerman et al., 2002). DLHEs can generate individual variability, or a lag in the density dependence (delayed density dependence), with significant effects on the stability of population dynamics (Beckerman et al., 2002, Benton et al., 2001, Lindstrom and Kokko, 2002).

Observations suggest that delayed life history effects (DLHEs) may play a role in mountain hare population dynamics, and the seasonal environment that characterises the Scottish uplands is echoed in patterns of mountain hare and parasite demography. In the next section we give details of the empirical evidence that DLHEs and seasonality are important structural elements of the system.

ECOLOGY OF THE MOUNTAIN HARE – T. RETORTAEFORMIS SYSTEM

In a wide variety of organisms, the life-history traits of offspring, such as growth rate, survival, size, age at first reproduction and offspring fecundity, depend on maternal condition and provisioning (Benton et al., 2001 and references therein). In mountain hares, the timing of breeding is important for reproductive success, as it is for many vertebrate species (e.g. Clutton-Brock, Guinness & Albon, 1982). Mountain hares in Scotland begin breeding in February (Flux, 1970; Hewson, 1976) and the timing of first breeding is determined by winter temperature, female age, size and weight with older, larger and heavier females attempting to breed earlier (Hewson, 1968; Flux, 1970). Young born earlier in the year have a longer growing season, enter the winter heavier and larger than late born young and therefore have a higher chance of over-winter survival and greater future fecundity when they enter the breeding population in the following year (Hewson, 1968; Iason, 1989a, 1989b, 1990). Females may seek to breed earlier in the year to produce young with greater survival and reproductive potential.

Although it has not been studied for mountain hares, parasitic infections are an important influence on the timing of breeding in a range of vertebrates (Allander and Bennett, 1995, Feore et al., 1997, Mulvey et al., 1994). While parasite reduction experiments suggest that female mountain hares with high parasite infections early in the breeding season shed fewer ova (Newey and Thirgood, 2004), this direct parasite effect has been shown, using a simple analytical model of the hare - *T. retortaeformis* system, unlikely to be strong enough to account for sustained hare cycles and realistic parasite intensities (Townsend et al., 2009, Chapter 4). However, if maternal parasite infection also delayed the timing of breeding, the resulting maternal effect would constitute an additional 'indirect' parasite effect that may increase the overall impact of parasites on hares. Since the level of nematode infections are thought to be dependent on host densities because of an increase in transmission rates (Arneberg et al., 1998), the result would be a delayed density dependent effect of the parasite on the host, with a tendency to destabilise population dynamics (Turchin, 2003). In this chapter we explicitly include maternal effects by making the timing of first breeding in a model mountain hare population dependent on female body size and level of parasite infection, and the timing of breeding a determinant of offspring body size, which in turn influences adult survival and fecundity (Fig 5.1a). We examine the model population for the presence of DLHEs via their dynamical impact.

In host-parasite systems seasonal variation in host demographics and parasite transmission can destabilise the population dynamics and increase the likelihood of cycles (Altizer et al., 2006, Greenman et al., 2004). In mountain hare populations, reproduction is restricted to nine months of the year and seasonal patterns have been recorded in host vital rates. Adult mortality peaks in late winter – early spring (Iason, 1989b, Flux, 1970), pregnancies peak in spring (Flux, 1970, Hewson, 1970), and mortality in leverets peaks with the onset of winter (Iason, 1989b, Flux, 1970). Transmission of *T. retortaeformis*, as with most direct life-cycle intestinal parasites, depends on the production of and host encounters with parasite infective stages in the environment and decay rate of external life history stages (Altizer et al., 2006). For species of the family *Trichostrongylidae*, infective stage development and survival depends critically on temperature and humidity (Olsen, 1986). For *T. retortaeformis* in Scotland, eggs mostly survive the winter resulting in a mass hatching in spring (Crofton, 1948). Large numbers are maintained throughout the summer because the rapid rate of hatching more than compensates for the increased death rate due to higher temperatures and desiccation of larval stages (Crofton, 1948). Susceptibility of the population to infection is also expected to increase in spring and summer as a result of raised testosterone levels in males, naïve immune systems of juveniles and a combination of the periparturient rise in females with shared foraging habitat with juveniles (Cattadori et al., 2005). We incorporate seasonality via a hare breeding season and pulses of hare mortality, recruitment and parasite transmission.

A TACTICAL APPROACH

Here we adopt an individual based modelling (IBM) framework to develop a tactical highly detailed model that encompasses a large degree of ecological detail. This approach allows us to incorporate leveret biology, suspected DLHEs and seasonality An IBM approach requires being explicit about parasite transmission mechanisms. One of the key features of parasitic infection, especially of nematodes with a direct life cycle, is the aggregated distribution of parasites between hosts, such that a few hosts harbour the majority of parasites (Shaw et al., 1998). Several effects are thought to contribute to aggregation: host heterogeneities, clumping of infection events and the positive feedback of the reinfection process (Rosa and Pugliese, 2002, Shaw and Dobson, 1995). In the Anderson & May analytical framework (Anderson and May, 1978, May and Anderson, 1978), the effect of aggregation is accounted for by assuming a negative binomial distribution of parasites between hosts. In an IBM, however, the infection status of each host must be tracked explicitly. Although Crofton (1948) carried out intensive studies in Scottish grasslands on the availability of infective larvae of *T. retortaeformis* to hosts, no study has looked at transmission within and between its mountain hare host. We devise three parasite transmission mechanisms and test the impact on hare population dynamics.

The first task of this chapter is to present a mountain hare - *T. retortaeformis* model which is able to generate realistic mountain hare population cycles and parasite intensities. Rather than reproduce the dynamics of a particular hare population, we judge model fit based on characteristic dynamical properties identified for Scottish populations (Newey et al., 2005, Newey et al., 2007b). The second task is to study the dynamical effect of removing or modifying structure in this base model. The results are focused around four specific questions about how parasites may drive hare cycles and the diversity in dynamics we observe: a) does making the timing of breeding dependent on maternal body size and parasite burden generate DLHEs? b) Do DLHEs reduce the strength of direct parasite effects necessary to reproduce observed dynamics? c) How do different parasite transmission mechanisms affect the dynamics? d) Can the wide geographical diversity of observed dynamics across Scottish populations be recovered?

Methods

THE MODEL

Fig 5.1b is a schematic outline of the IBM showing the chronological order of events in the time step of one year. The fine details of the model are provided in the supplementary material, and model parameters are summarized in Table 5.1. The model runs on an annual cycle of eight principal steps with the chronological order of events chosen to reflect the natural sequence of identified seasonal pulses in hare adult mortality, reproduction, juvenile mortality, recruitment and parasite transmission. Reproduction takes place within a breeding season such that leverets can be born only between 7th March and 31st September. Hare and parasite populations are "censused" once a year after adult mortality was imposed but before the start of the breeding season, close enough to harvesting time (often in December after the close of the grouse season (Hewson, 1970)) to be comparable to hare bag data used in the time-series analysis of Newey et al. (2007b).

The model links individual hare attributes to their survival, fecundity, time of breeding and vital rates of offspring (Fig 5.1a). An adult hare with few parasites and a large body size was more likely to survive the winter (Fig 5.1a, links G and H, details in Appendix 5.4) and reproduce earlier in the year (links B & C, see Appendix 5.2). Females could have up to three litters and the birthdates of second and third litters depended on the gestation period and a randomly determined inter-litter period (see Appendix 5.2). Females with fewer parasites tended to have more offspring (link D, see Appendix 5.3 and Supplemental Fig 5.1) but having larger litters early in the year reduced the size of later litters (link E, see Appendix 5.3).

Leverets born earlier in the breeding season had longer to grow before winter and attained a larger size (link A, details in Appendix 5.1). However, leveret survival was calculated as an accumulation of daily survival rates and therefore earlier born leverets had a lower chance of surviving to the onset of winter (link F). Therefore a female that began breeding had smaller leverets, she was able to have larger litters later in the year with a higher chance of surviving to the onset of winter. As data were lacking on leveret biology, the value for daily survival rate (*DLS*) was reverse engineered as part of the model selection process.

Parasite transmission was controlled by parasite fecundity (λ), transmission inefficiency (H_0) (details in Appendix 5.5) and the mechanism of transmission, of which we devised three alternatives (see ‘Structural changes to the best fit model’).

CHARACTERISING REAL HARE TIME SERIES AND PARASITE BURDENS

We summarised the dynamics of hare and parasite populations in Scotland using the mean and range of four characteristics: the period of hare cycles, the amplitude of hare cycles, mean parasite infection and the extent of statistical over-dispersion in the distribution of parasites between hares (as summarized by the relevant parameter of the negative binomial distribution, *k*) (Table 5.2). Empirical estimates for period and amplitude were taken from analyses by Newey et al. (2007b) of hare game bag time series (n = 56, median length = 37 years). For statistics on parasites, we compiled a dataset of burdens for 654 hares sampled over 4 years from cross-sectional surveys conducted on 29 estates (Newey et al., 2005) and data presented in Boag and Iason (1986). The burden distribution from each of the 29 estates was fitted with a negative binomial distribution, the parameters of which are mean burden and *k*. By assuming that different estates have separate hare populations and their parasite infections are not synchronised, the mean and range of mean burdens and *k* for the 29 estates should provide an idea of the variation in Scottish populations.

CHARACTERISING SIMULATED HARE TIME SERIES AND PARASITE BURDENS

Characteristics of simulated hare time series and parasite burdens were estimated as for empirical data. Where variation in empirical and simulated data characteristics were compared, mean parasite infection and dispersion (*k*) were estimated by sampling an individual year within a time series. Otherwise time series were characterised from more than just a single sample year, with estimates taken at five yearly intervals. Time series simulations ran for 37 years (after a minimum burn-in of 50 years in simulations to remove transient dynamics), the mean and range for period and amplitude was estimated from 56 simulated time series and the mean and range of mean burden and parasite dispersion (*k*) from 29 time series.

Simulations of model mountain hare populations could, however, also be classified as implausible. Given that the observed maximum hare density is 200 km^{-2} (Watson et al., 1973, Hewson, 1976), simulations which reached hare densities of greater than 400 hares km^{-2} were considered implausible. Extinction resulting from demographic stochasticity was prevented by permitting some immigration, but simulations which exhibited near annual extinction frequencies were judged implausible. A transition from equilibrium dynamics to sustained cycles or as an increase in the amplitude of sustained cycles was regarded as a reduction in stability.

MODEL PERFORMANCE

Model performance was judged on the fit of the simulated population dynamics to the four observed characteristic properties of hare time series and parasite burdens. The model with the ‘best fit’ structure and parameters was selected on the basis of match to mean observed values. This took into account demographic stochasticity by running the model 200 times to quantify the 95% confidence interval for each characteristic estimated from the simulated data. The mean observed values were required to fall within these intervals. The best fit model was also required to exhibit sustained cycles and have realistic mean annual values of hare mortality rate, hare recruitment rate, juvenile burdens and litter sizes.

STRUCTURAL CHANGES TO THE BEST FIT MODEL

We investigated the DLHEs on model mountain hare population dynamics in three ways. First, by comparing the best fit model with models where the links between female body size and parasite burden and timing of breeding were removed. Removal of the body size-timing link (B in Fig 5.1a) would leave an indirect effect of parasite burden on size (through links C-A) which could complicate interpretation of results, therefore we investigated models where the burden-timing link (C) was removed and where both links were removed (see Appendix 5.2 for how birthdate was calculated). Second, we measured the increase in the overall parasite effect on fecundity (δ) that was required to recover observed dynamics. δ was estimated from the simulated data as the slope of the relationship between parasite burden and ova shed, and was increased by manipulating the direct parasite effect on fecundity (link D in Fig 5.1a) via the burden thresholds for allocating ova shed in the second litter (see Supplemental Fig 5.2). Third, by comparing the best fit model with a model without burden thresholds for ova shed (removed link D), thus leaving only the DLHEs to impact female hare fecundity (link E).

Three transmission mechanisms were devised for the model (see Appendix 5.5 for details) and their dynamical effects compared. In the first mechanism, parasite recruits entered a pool from which they were allocated among the whole hare population (‘global’) in each transmission pulse. The second mechanism represented local transmission, recognising that hares maintain home ranges (Flux, 1970) and therefore new parasites may be more likely to reinfect the same host, or the offspring they produce. In the third mechanism, hares were given a lifetime dose of parasites as leverets rather than annual augmentation of infection. This was considered a plausible governing mechanism because hares only live for three years on average (Hewson, 1976) and added infections after the first year may be relatively low in fertility (Skorping et al., 1991).

CHANGES TO THE PARAMETERISATION OF MODELS

The characteristics of hare time series and parasite burdens from the best fit model and models with structural changes were examined across the plausible ranges of parameters (Table 5.1). Parameter combinations were generated using a Sobol’ sequence (Sobol', 1967) because this technique allowed us to sample parameter space more uniformly than if samples were taken at random (Press et al. 1992). This was particularly important given the small numbers of samples (n=29 for calculation of parasite burden statistics and n=56 for calculation of hare time series statistics).

Elasticity analysis was performed on the best fit model to compare the proportional effects of changing parameters on the characteristic properties of simulated hare time series and parasite burdens. Given the large number of parameters in the model, the analysis was conducted on a select few parameters of interest: direct parasite effect on mortality (α) and overall parasite effect on fecundity (δ), parasite transmission parameters (λ, H_0) and leveret survival *LS* (*DLS* multiplied by the length of the breeding season). Parameters were sampled from empirically determined plausibility ranges (Table 5.1) except for the empirically unquantified *DLS* which was explored across the range 0.990-0.998 and δ which was an emergent parameter from the model.

Results

The structure and parameterisation of the best fit model (in which all DLHE links are enabled) are reported in Table 5.1. Fig 5.2 is a simulated hare and parasite time series showing sustained cycles. The dynamical characteristics for 200 such time series are summarised in Fig 5.3. The mean values of period, amplitude, mean burden, parasite dispersion from real hare and parasite data fell within the 95% confidence intervals of the simulated data characteristics (Fig 5.3), and corresponded well to the mean simulated values (Table 5.2). Mean simulated values for the period of hare cycles was 9.5 years, with amplitude 0.77, parasite burdens of 2759 and parasite dispersion of 0.75.

DOES MAKING THE TIMING OF BREEDING DEPENDENT ON MATERNAL BODY SIZE AND PARASITE BURDEN GENERATE DELAYED LIFE HISTORY EFFECTS (DLHES)?

Simulations of hare and parasite population dynamics with the parasite infection-timing of breeding link (Fig 5.1a, link C) removed reduces the amplitude of hare density fluctuations (amplitude =0.73, Fig 5.4a). Further removing the body size-timing link (Fig 5.1a, link B) reduces the amplitude further (amplitude = 0.63, Fig 5.4b). The distributions of dynamical characteristics for simulations where parameters were sampled across plausible parameter space suggest that, compared to the best fit model, when links were removed amplitudes tended to be smaller (Fig 5.5b) and parasites were more dispersed (Fig 5.5d), while parasite burdens (Fig 5.5c) and period (Fig 5.5a) tended to be larger. Exploring the effects of structural changes on the plausibility of simulated dynamics and the propensity of cyclic dynamics we found no major differences between the best fit model and models where the links were removed (Table 5.3). These results suggest that the links between maternal body size and parasite burden generated DLHEs that had similar weak destabilising effects on the model hare population dynamics.

DO DLHES REDUCE THE STRENGTH OF DIRECT PARASITE EFFECTS NECESSARY TO REPRODUCE OBSERVED DYNAMICS?

The relationship between hare cycle amplitude and overall parasite effect on fecundity (δ) for simulations where DLHEs were removed is shown in Fig 5.6. With the burden-timing link removed, increasing hare cycle amplitude from 0.73 (as estimated in the absence of this link, Fig 5.4a) to the observed mean 0.81 required an increase in δ of 0.00006 year^{-1}, whilst in the absence of both links δ was required to be increased by almost twice this amount (0.00011 year^{-1}) to increase amplitude from 0.63 (estimated in the absence of both these links, Fig 5.4b) to 0.81.

A simulation in which the direct effect of parasites on female fecundity was removed and only DLHEs affected fecundity showed hare density fluctuating close to equilibrium (Fig 5.4c). Sampling across parameter space, more time series were plausible and the highest percentage for all models (10%) were non-cyclic (Table 5.3). All time series exhibited amplitudes below the mean observed value (Fig 5.5b) and mean burdens were mostly higher than the observed mean (Fig 5.5c), thus lowering the overall fit to real characteristics of hare time series and parasite burdens (Table 5.3). These results suggest that the direct parasite effect on fecundity had a strongly destabilising effect on hare population dynamics, in contrast to the weaker indirect parasite effects on fecundity caused by the DLHEs.

HOW DO DIFFERENT TRANSMISSION MECHANISMS AFFECT THE DYNAMICS?

The best fit model allocated 90% of parasites locally (self-infection or within family) and 10% on a population-wide (‘global’) scale (Table 5.1). A simulation where parasite recruits were allocated to hares solely on a global scale fluctuated around a relatively small equilibrium hare density and ranged from non-cyclic to small amplitude ten year period cyclic dynamics (Fig 5.4d). In contrast, when parameters were allowed to vary within plausible limits, amplitudes ranged widely (Fig 5.5b). However, 95% of runs generated plausible dynamics compared to 77% for the best fit model (Table 5.3), suggesting that global distribution of parasites generally had a stabilising effect on model hare dynamics. The poor fit to observed characteristics (Table 5.3) was caused by a tendency towards long periods and large burdens (Fig 5.5a, c).

A model with locally distributed parasites generated time series that varied from non-cyclic to high amplitude ten year cycles (Fig 5.4e). When parameters were allowed to vary within plausible limits, the lowest percentage of time series were plausible (45%, Table 5.3) and parasites were more strongly overdispersed (lower *k*) than the mean observed value (Fig 5.5d). These results suggest local transmission tended to have a destabilising effect on hare dynamics.

A model developed to allocate lifetime burdens to leverets generated dynamics that were starkly different from other models considered. When parameterized with best fit parameters, the model exhibited non-cyclic dynamics at a high equilibrium hare density (Fig 5.4f). In contrast, across parameter space, dynamics were generally found to be cyclic (Table 5.3, although they appeared more irregular than the smooth cycles seen for other model structures) with periods and mean burdens above the upper observed limits (Fig 5.5a, c) and amplitudes below the lower observed limit (Fig 5.5b). This structural modification resulted in the lowest fit to observed dynamical characteristics (Table 5.3).

CAN THE WIDE GEOGRAPHICAL DIVERSITY OF OBSERVED DYNAMICS ACROSS SCOTTISH POPULATIONS BE RECOVERED?

Although the characteristics of the best fit model adequately captured the mean empirically determined values (Fig 5.3), we investigated whether the model could reflect the observed geographical diversity in hare dynamics. Variation generated by demographic stochasticity in repeated simulations matched reasonably well the observed range in hare cycle amplitudes and mean burdens (Table 5.2). Variation generated by changing parameters widened the range for all characteristics, improving the match to real ranges of period, amplitude and parasite dispersion (Table 5.2). Given that variability in period is a distinctive feature of Scottish mountain hare population dynamics (Newey et al., 2007b), our analyses suggest that period was particularly sensitive to leveret survival and the direct parasite effects on hare fecundity and survival (Table 5.4). Variation generated by changing parameters worsened the match to the observed range of mean burdens with unrealistically high numbers of 10^5 being reached (Table 5.2). We found that poor leveret survival and strong parasite-induced hare mortality were associated with more realistic burden levels (Table 5.4). Realistic mean burdens were also associated with the local parasite transmission mechanism and the presence of DLHEs (Fig 5.5c).

The best fit model did not generate sufficient variation in k, the dispersion of parasites amongst hares (Table 5.2). The structurally changed models also failed to reproduce the observed range (Fig 5.5d). Large k (well dispersed parasites) was most strongly associated with a strong parasite effect on hare mortality (α) and parasite transmission parameters (λ, H_0), as would be expected (Table 5.4). It is therefore possible that the variation in k was restricted in the simulated data because the real variation in α, λ and H_0 was based on small, under-representative sample sizes (Townsend et al., 2009, Chapter 4).

Discussion

We explored the direct and delayed effects of a macroparasite on host population dynamics using the host-parasite interaction between mountain hares and *T. retortaeformis* as a model system. We developed an IBM of an infected host population which could reproduce host time series and distribution of parasite intensities with mean characteristics taken from empirical studies of mountain hares in Scotland. The model was structured to allow delayed responses to life history by linking maternal body size and parasite infection to the future survival and fecundity of offspring. We found these maternal effects could generate DLHEs that had a weak destabilising effect on hare population dynamics. The nature of individual based modelling required formulating explicit mechanisms of parasite transmission. As this was unknown, we devised and compared three different mechanisms and found the best fit was a combination of local and population-wide transmission. While the best fit model was able to reproduce the mean dynamical behaviour, an adequate model of mountain hare population dynamics should also be capable of replicating the natural diverse array of behaviours. We found that, with realistic variation in parameter values, the best fit model could capture the observed variation in three of the four studied dynamical characteristics.

DLHEs can increase the propensity for complex dynamics by generating delayed density dependence and individual variability (Beckerman et al., 2002). In simple dynamic models, the transmission via maternal inheritance of average individual 'quality' has been shown to be a plausible cause of forest lepidopteran cycles (Ginzburg and Taneyhill, 1994) and microtine rodent cycles (Inchausti and Ginzburg, 1998) by causing delayed density dependence. Delayed density dependence is detectable using time series analysis and has been identified in cyclic Scottish mountain hare time series (Newey et al., 2007b). However, delayed density dependence has many potential sources: it is classically associated with endogenous factors including direct effects of trophic interactions (Turchin, 2003), but can also be generated by temporally autocorrelated environmental noise (Lundberg et al., 2000). It is currently almost impossible for time series analysis to distinguish among competing potential causes (Beckerman et al., 2002). While this work does not prove that DLHEs are acting in mountain hare populations, we found that DLHEs could have a destabilising effect on the dynamics. A previous model required an increase in the direct effect of parasites on fecundity outside of the empirically estimated envelope to generate hare population cycles (Townsend et al., 2009, Chapter 4), while the presence of DLHEs reduced the increase in this parameter necessary to generate realistic dynamics. The reduction in this required increase was approximately $1\text{x}10^{-4}$ year^{-1}, a large amount given the 'combined' parasite effect on fecundity (δ) has been empirically estimated in the order of 10^{-4} to 10^{-5} year^{-1} (Townsend et al., 2009, Chapter 4, Newey and Thirgood, 2004). DLHEs allowed parameters to be closer to empirical estimates in order to generate observed hare population cycles, and could be important processes in host-parasite systems.

The DLHEs could have a stronger effect on the propensity for cyclic dynamics than estimated here. In comparison to the direct parasite effect on fecundity, the DLHEs had a relatively weak destabilising impact. We note, however, that their impact may have been greater if the effect on time of breeding was made more sensitive to female fitness through a more biologically realistic mechanism. In the IBM, the timing of litters subsequent to the first was determined by an inter-litter period which was drawn from a uniform random distribution of between 1 and 60 days. While in principal postpartum oestrus allows female hares to copulate within just a few hours of parturition (Höglund, 1957), the 60 day upper limit was reverse engineered to generate distributions of pregnancies and birthdates that were realistically spread across the breeding season (Flux, 1970, Hewson, 1970). While some variability is expected in inter-litter period, making it strongly stochastic may have effectively decoupled the impact of timing of the first litter on the timing of subsequent litters.

It is common practice in the theoretical investigation of the complex population dynamics to compare the match of modelled to real time series using dynamical characteristics. This method of goodness of fit is open to criticism (Kendall et al., 1999), especially where just a single aspect of the time series, such as the period (Dobson and Hudson, 1992a), is abstracted. We have taken this approach but used two characteristics of hare populations, period and amplitude of cycles, and two characteristics of parasite distributions between hares, mean infection and level of aggregation. We have generally found during our investigations that, while it is relatively easy to obtain realistic periods, it is most difficult to capture realistic mean infection levels. Both the elasticity analysis performed here and on a previous analytical model (Townsend et al., 2009, Chapter 4) agree that intensity of parasite infection is strongly affected by the parasite's effect on host mortality, but experimental studies do not support a strong effect (Newey and Thirgood, 2004). The IBM introduced leveret survival and identified it as a potentially important determinant of parasite intensity in adult hares. This suggests that host age-structure may be an important aspect of this host-parasite system and future models should separate leveret and adult demography.

Host population dynamics depend on the mechanism causing aggregation in parasites between hosts (Rosa and Pugliese, 2002). Aggregation is a characteristic feature of macroparasites distributions (Shaw et al., 1998) and a pattern which is likely to result from several factors, most notably host heterogeneities, clumping of infection events and the positive feedback of the reinfection process (Rosa and Pugliese, 2002, Shaw and Dobson, 1995). Here, we explicitly modelled mechanisms of parasite transmission. A population-wide ('global') mechanism was the IBM equivalent of the multiple infections term in the model of Pugliese et al. (1998), while the local transmission mechanism combined all three aggregation factors to some degree. A previous study has compared the effect of host heterogeneity (in immunity) and clumped infections and found the model with clumped infections tended to be less stable (Rosa and Pugliese, 2002). We have found that the model which included more aggregation effects tended to have more aggregated parasites between hosts and less stable host population dynamics.

We found a mixture of local and population-wide parasite transmission was optimal, and this could have interesting implications for the effects of host movement on population dynamics. The best fit model for the mountain hare - *T. retortaeformis* system used a mix of predominately local transmission with a small percentage (10%) of population-wide transmission. The predominance of local transmission suggests the observed distribution of burdens arises largely from individual differences between hosts, their local environment and/or infection pressure. This corresponds reasonably well to what is known about the local movements of mountain hares – they maintain home ranges but these are not exclusive and they often feed alongside other hares (Flux, 1970). In fact, any factors influencing host heterogeneities, hare movement or the longevity of *T. retortaeformis* free-living stages could result in variation in the balance of local-global transmission. Varying degrees of locally and globally distributed infections between mountain hare populations in the UK, or within or across years in the same population, is a plausible mechanism for generating the wide range of hare population dynamics observed.

In contrast, allocating lifetime parasite infections to newborn hosts gained limited support as the governing mechanism of transmission in the mountain hare-parasite system. Since each cohort had a different mean parasite burden according to parasite availability in their year of birth, this transmission mechanism generated a cohort effect where each generation had similar life histories in terms of fecundity and survival. One of the consequences for the population dynamics was reduced host cycle amplitude compared to the other models. In deterministic analytical models, the introduction of a cohort effect increases individual variability and this is destabilising when the underlying deterministic dynamics are stable and stabilising to non-equilibrium deterministic dynamics (Lindstrom and Kokko, 2002). However, in an IBM, a cohort effect presumably aggregates individual variability from more idiosyncratic variation. Further, we do not have a deterministic counterpart making it difficult to determine what effect on stability should be expected, but the reduction in individual variability in parasite burdens appears to contrast with analytical model results – tending to reduce the amplitude of cyclic dynamics. The lifetime burden allocation mechanism was proposed because of the short average lifespan of hares and the lower fertility of more recently acquired parasites (Hewson, 1976, Skorping et al., 1991). The unrealistic dynamics resulting from this transmission mechanism suggests that the additional infections picked up by adult hares through their lifetime are important to the parasite population.

The model presented here captured mean characteristics of real mountain hare time series and the level of infection of the nematode parasite *T. retortaeformis*, and much of the empirically observed diversity in these characteristics. Further natural variation could be accounted for by population differences in the balance of local and population-wide parasite transmission. The model included direct parasite effects on the fecundity and survival, links between maternal body size and parasite burden on the timing of breeding, leveret biology, seasonality in hare reproduction, recruitment, mortality and parasite transmission, and modelled mechanisms for parasite transmission. As has been shown for red grouse, snowshoe hares, Soay sheep and Svalbard Reindeer (Gulland et al., 1993, Ives and Murray, 1997, Albon et al., 2002, Mougeot et al., 2003, Krebs et al., 2001a), the effect of parasites on mountain hares likely forms part of a complex set of interactions that lead to population cycles. Further work is needed to provide better parameter estimates and to provide empirical estimates for important life-cycle stages, for example, we included immigration in the model to prevent stochastic extinctions, although this was not based on dispersal data. Mountain hare populations in Scotland are harvested for sport and increasingly to attempt to control tick-borne disease. Dispersal, harvesting and population control likely have significant effects on hare populations and ongoing field and modelling work are exploring these issues.

Table 5.1. Individual based model parameter values and their plausible ranges used in model analyses. Where possible, parameters were estimated from empirical data sources, otherwise parameters were reverse engineered during the best fit model selection process.

Parameter	*Units*	*Value used in best fit model*	*Reverse engineer-ed?*	*Plausible range*	*Source*
Model population site area	km^2	20			
Min. hare body size (hindfoot length)	mm	115			unpublished data
Max. hare body size (hindfoot length)	mm	150			unpublished data
Min. adult hare mortality in absence of parasites	year^{-1}	0.08			Townsend et al. (2009), Chapter 4
Max. adult hare mortality in absence of parasites	year^{-1}	0.61			Townsend et al. (2009), Chapter 4
Max. hare lifespan	years	10			Macdonald, Mace & Rushton (1998)
Earliest recorded birth date of the year		7th March			Hewson (1970)
Latest birthdate for 1st litter		14th May			Flux (1970)
Latest birthdate of the year		31st Sept			Flux (1970)
Length of breeding season	days	203			
Gestation period	days	50			Borg, Höglund & Notini (1952), Höglund (1957)
Minimum inter-litter gap	days	1			Höglund (1957)
Added variation in inter-litter gap	days	round(unif) ~(0,59)	Yes		
Size of 1st litter	leverets	1 - 2			Based on Flux (1970), Iason (1990) and Hewson (1976)
Size of 2nd litter	leverets	0 - 6			
Size of 3rd litter	leverets	0 - 6			
Pre-natal mortality in 2nd litter	ova or embryos	8%			Iason (1990)
Pre-natal mortality in 3rd litter	ova or embryos	2%			Iason (1990)
Date after which litters were affected by preceding litter sizes		8th June			Iason (1990)
Reduction in proceeding litters for each leveret born in 1st litter	ova or embryos	0.7			Iason (1990)
Reduction in 3rd litter for each leveret born in 2nd litter	ova or embryos	0.5			Iason (1990)
Daily leveret survival rate (*DLS*)	day^{-1}	0.994	Yes	0.990-0.998	Upper limit on annual survival 50% from Hewson (1976)
Parasite burden threshold below which two ova shed in 1st litter	parasites	500	Yes		
Method for setting burden thresholds for ova shed in 2nd litter (see Supp. Fig 5.1)		Increasing per-parasite effect on ova shed with burden	Yes		
Proportion of parasites distributed locally		0.9	Yes		
Parasite-induced hare mortality (α)	year^{-1}	0.00005	Yes	0-0.0001	
Parasite fecundity in spring pulse (λ_{spring})	year^{-1}	440		30-1230	Townsend et al. (2009), Chapter 4
Parasite fecundity in autumn pulse (λ_{autumn})	year^{-1}	560		40-1540	
Transmission inefficiency in spring pulse (Ho_{spring})	hare	60000	Yes	13500-66800	
Transmission inefficiency in autumn pulse (Ho_{autumn})	hare	20000	Yes	13500-66800	

Table 5.2. Mean (and range) of four characteristic properties of real and simulated mountain hare time series and parasite burdens. In order to assess whether the best fit model could capture the mean observed values and Scottish geographical diversity in the characteristic properties, the table presents the mean and range of these properties from (i) empirical sources, (ii) repeated simulations of the best fit model with best fit parameterisation (Fig 5.3) and (iii) simulations of the best fit model where parameters were varied within plausible ranges (Fig 5.5).

		Observed time series		*Simulated time series from best fit model*	
Property	*Units*	*(i) Empirical estimate*	*Source*	*(ii) Stochastically generated variation*	*(iii) Parameter generated variation*
Period of hare cycles	years	9.2 (4-15)	Newey et al. (2007b)	9.5 (9-13)	12.3 (7-24)
Amplitude of hare cycles (coefficient of variation)		0.81 (0.39-1.80)	Newey et al. (2007b)	0.77 (0.58-1.41)	0.79 (0.05-1.72)
Mean annual adult hare burden of *T. retortaeformis*	hare^{-1}	1936 (190-4957)	Based on reanalysis of datasets described in Newey et al. (2005) and Boag and Iason (1986). See Methods.	2759 (42-7705)	20186 (140-164460)
Parasite dispersion (k)		1.16 (0.19-5.55)		0.75 (0.46-1.26)	0.60 (0.28-1.36)

Table 5.3. The effect of structural changes on the stability of modelled dynamics and fit to four characteristic properties of observed mountain hare time series and parasite burdens. For each model, time series were generated until 56 plausible (did not go extinct or reach implausible hare densities) runs were obtained. (i) The % of total runs collected that were implausible. (ii) The % of total runs that were plausible and non-cyclic according to an ACF correlelogram (see text). (iii) The % of total runs that were plausible and cyclic according to an ACF correlelogram. (iv) The % of plausible runs whose characteristics fell within the observed ranges of period, mean burden and parasite dispersion. Amplitude was omitted to acknowledge that random exogenous forcing can cause dampened oscillations to persist as regular fluctuations (Kaitala et al., 1996). (v) The % of plausible runs whose characteristics fell within the observed ranges of period, mean burden, parasite dispersion and amplitude. Model structures abbreviate as: best fit (Best), parasite burden-timing link removed (-BT), burden-timing and size-timing links both removed (-BTST), direct parasite effect on fecundity removed (DPF=0), population-wide parasite transmission (Global), local transmission (Local), burdens allocated once during lifetime (Once). Fit to observed was based on the period (for cyclic time series) and amplitude of full 37 year time series and mean values of parasite dispersion and mean burden from five yearly estimates to avoid autocorrelation between estimates in consecutive years. Parameters that were not varied as part of the perturbations were kept at values set for the best fit model.

Model	No. series	Dynamical stability (% of total runs)			Fit to observed (% of plausible runs)	
		(i) Implausible	*(ii) Non-cyclic*	*(iii) Cyclic*	*(iv) Exc. amplitude*	*(v) Inc. amplitude*
Best	79	16	6	77	32	15
-BT	82	33	2	65	40	13
-BTST	71	21	1	77	43	13
DPF=0	60	7	10	83	25	0
Global	59	5	3	92	20	0
Local	124	55	5	40	46	9
Once	77	23	9	68	3	0

Table 5.4. Elasticity analysis showing the proportional effect of changes in parameters of the best fit model on four characteristic properties of mountain hare time series and parasite burdens. Only the three coefficients with the largest absolute values are shown. The overall parasite effect on fecundity (δ) was negative, therefore to ease interpretation the strength (magnitude) of the effect was used in the analysis. Period and amplitude were estimated from the full 37 year time series, whilst parasite dispersion and mean burden were mean values of five yearly estimates (five yearly basis used to avoid autocorrelation between estimates in consecutive years). The analysis was based on 305 plausible runs of the best fit model.

	Period	*Amplitude (CV)*	*Mean burden*	*Parasite dispersion (k)*
Controlled parameters				
Leveret survival (LS)	-0.5	0.3	11.4	
Parasite-induced adult hare mortality (α)	-0.7	-1.0	-6.3	0.2
Spring parasite fecundity (λ_{spring})				
Spring transmission inefficiency (Ho_{spring})			3.0	0.1
Autumn parasite fecundity (λ_{autumn})				0.1
Autumn transmission inefficiency (Ho_{autumn})				
Emergent parameter				
Strength of overall parasite effect on hare fecundity (δ)	0.2	0.3		

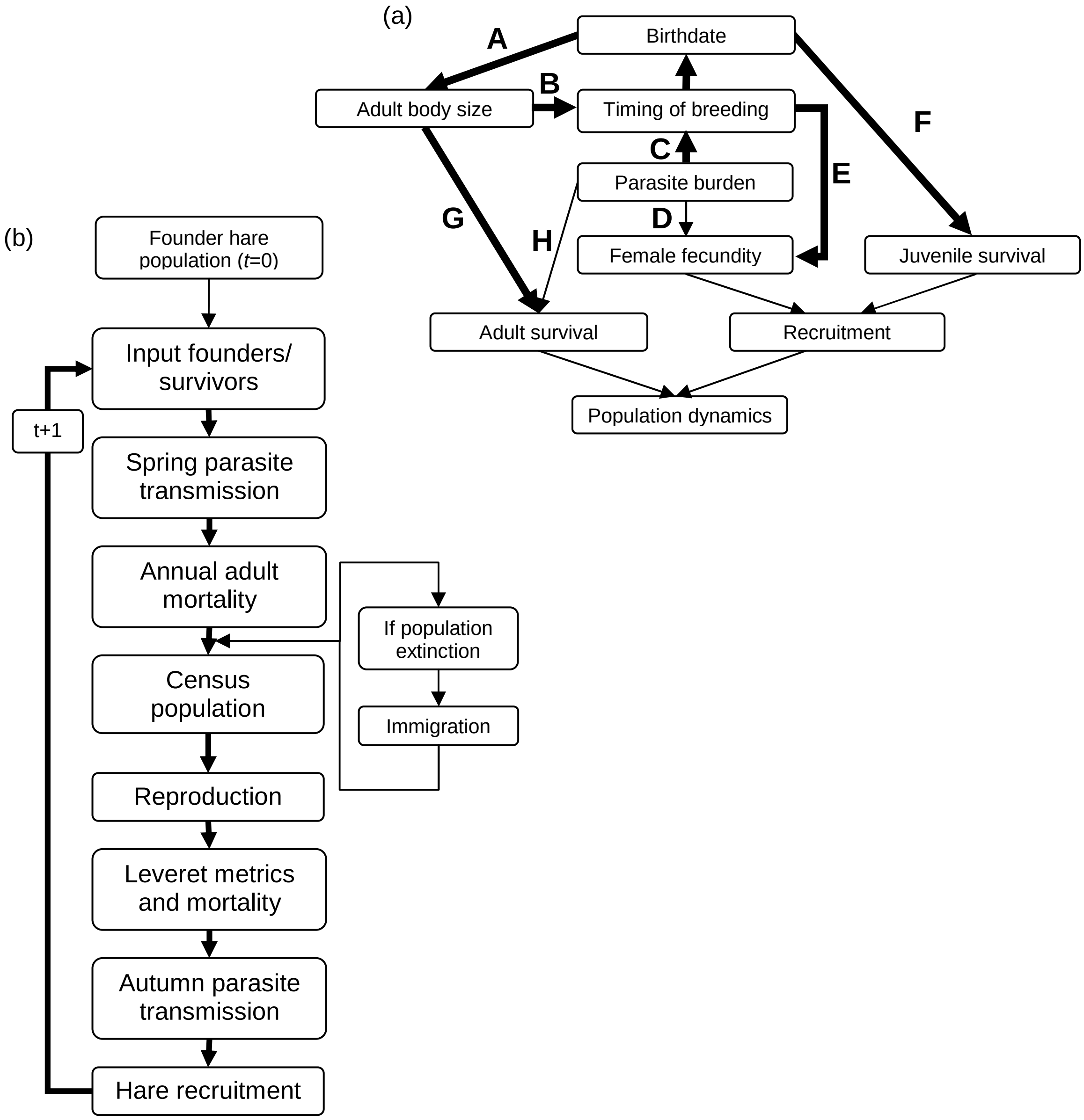


Figure 5.1. Schematic diagrams showing structure in the model. (a) Modelled links between individual hare attributes and hare population dynamics. Thin arrows constitute a model which does not contain any maternal effects on survival and fecundity. (b) Outline of the order of events that the hare population experiences over a year in the IBM.

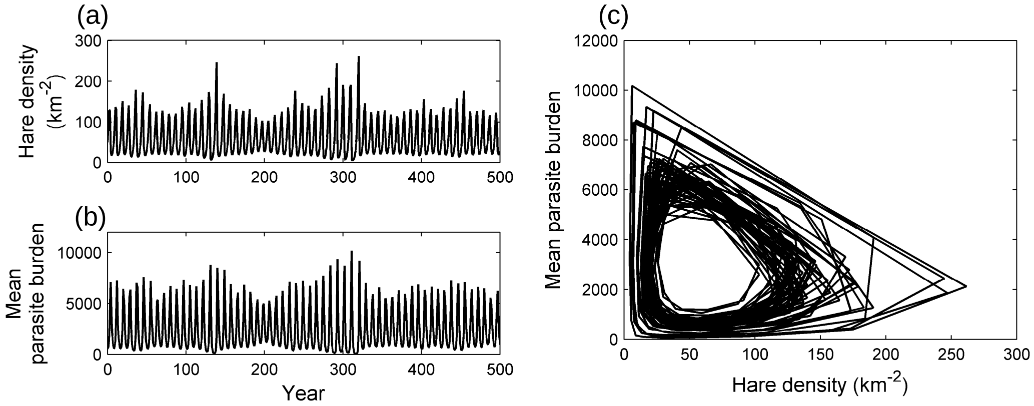


Figure 5.2. Simulated population dynamics from a single run of the best fit model of (a) hares and (b) parasites. (c) The sustained cycles in state space. Hares cycled with a ten year period and amplitude of 0.79. Parasites were distributed between hares with a mean of 2400 worms and *k* of 0.80.

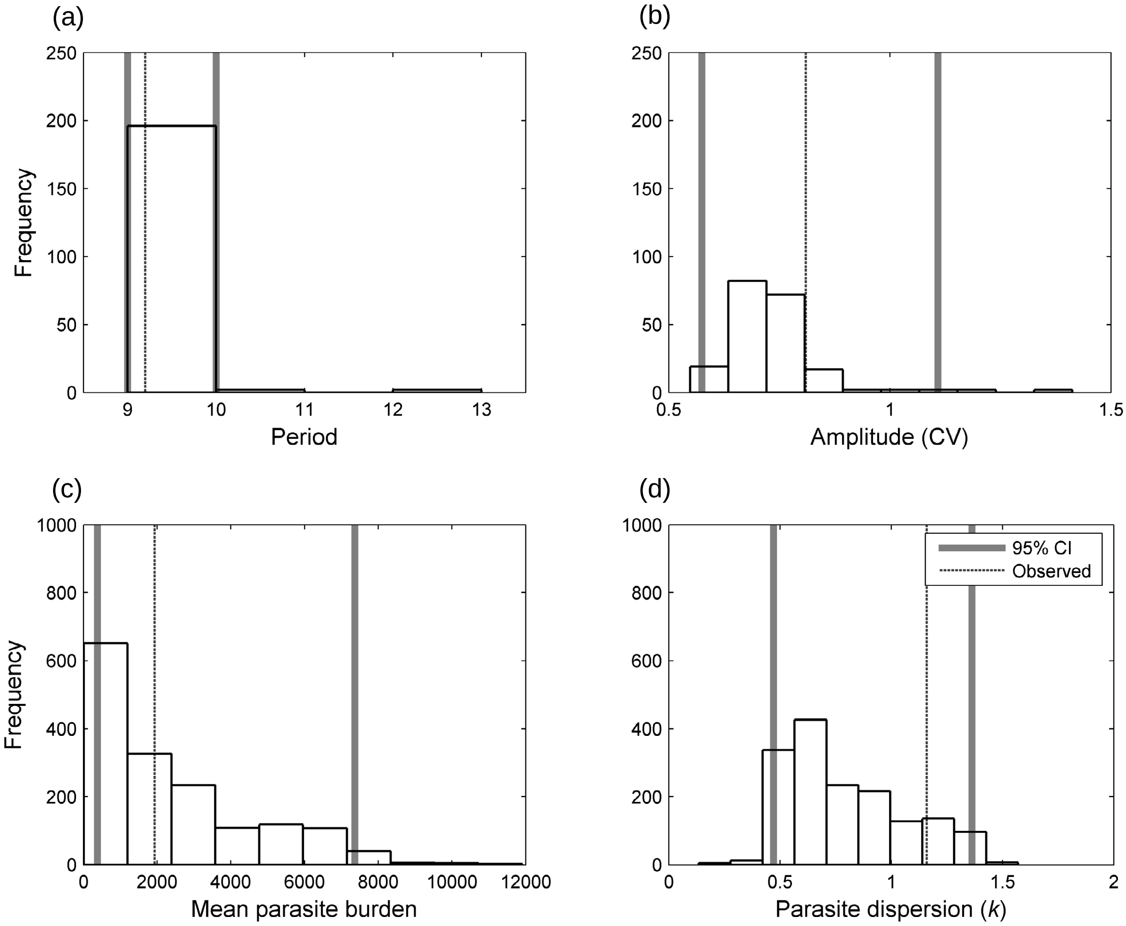


Figure 5.3. Summary statistics for four characteristic properties of mountain hare time series and parasite burdens: (a) period of hare cycles, (b) amplitude of hare cycles (measured as the CV of the time-series), (c) mean parasite burden and (d) parasite dispersion *k*. Frequency histograms were generated from 200 simulations of the best fit model. For each distribution the 95% percentile interval is shown (thick grey lines), and the mean observed value (dotted line). In (a, b) each estimate was based on the full 37 year time series, whereas in (c) and (d) annual estimates were taken every five years to avoid autocorrelation between estimates in consecutive years.

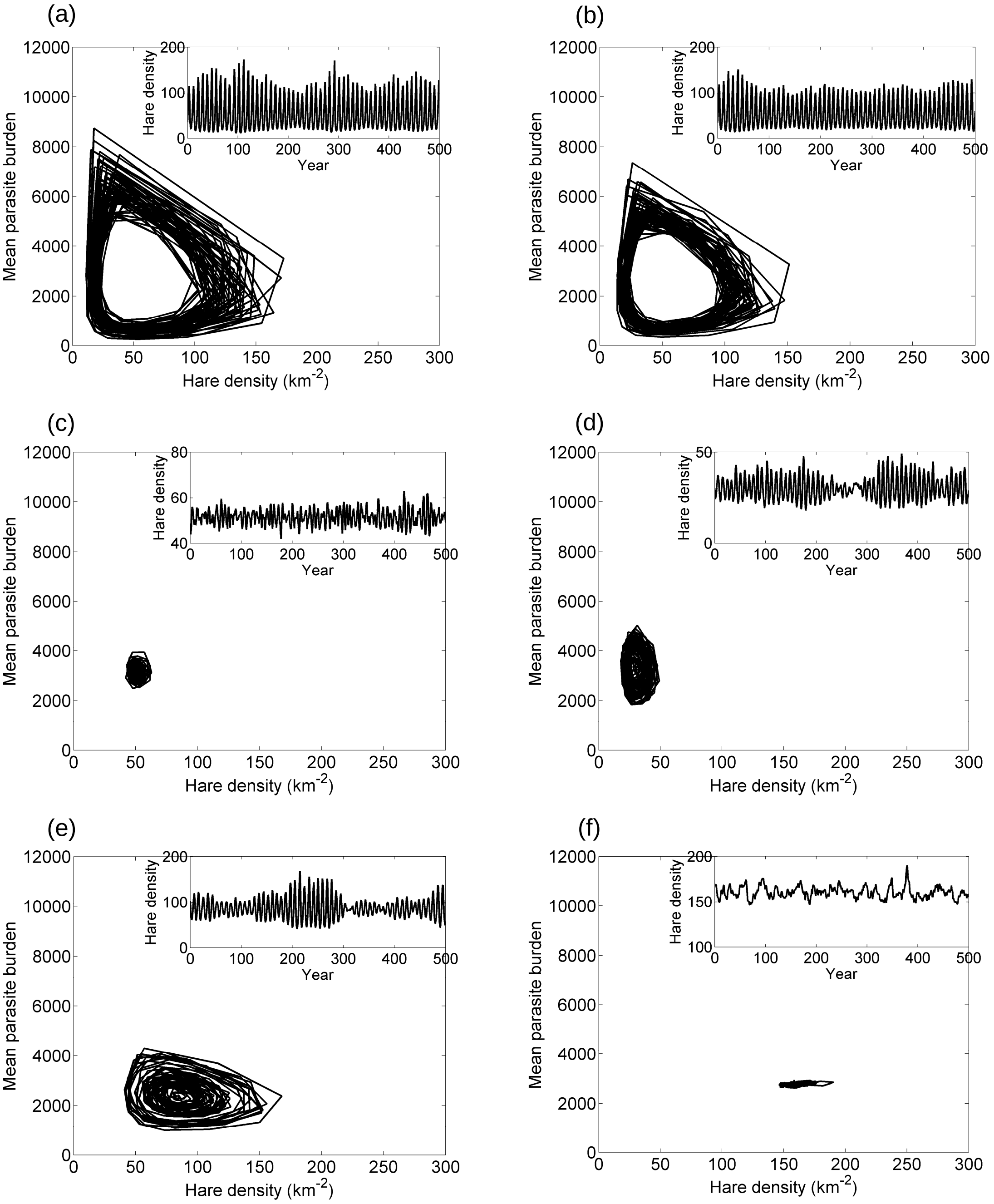


Figure 5.4. Simulated hare and parasite population dynamics following structural changes to the best fit model: (a) burden-timing link removed; (b) both the burden-timing and size-timing links removed; (c) the direct effect of parasites on fecundity removed; (d) parasite recruits globally distributed across the whole hare population; (e) parasite recruits distributed locally within hare families; (f) burdens allocated once during a hare's lifetime. Hare time series shown in the insets, note different scales. Parameters that were not varied as part of the perturbations were kept at values set for the best fit model (Table 5.1).

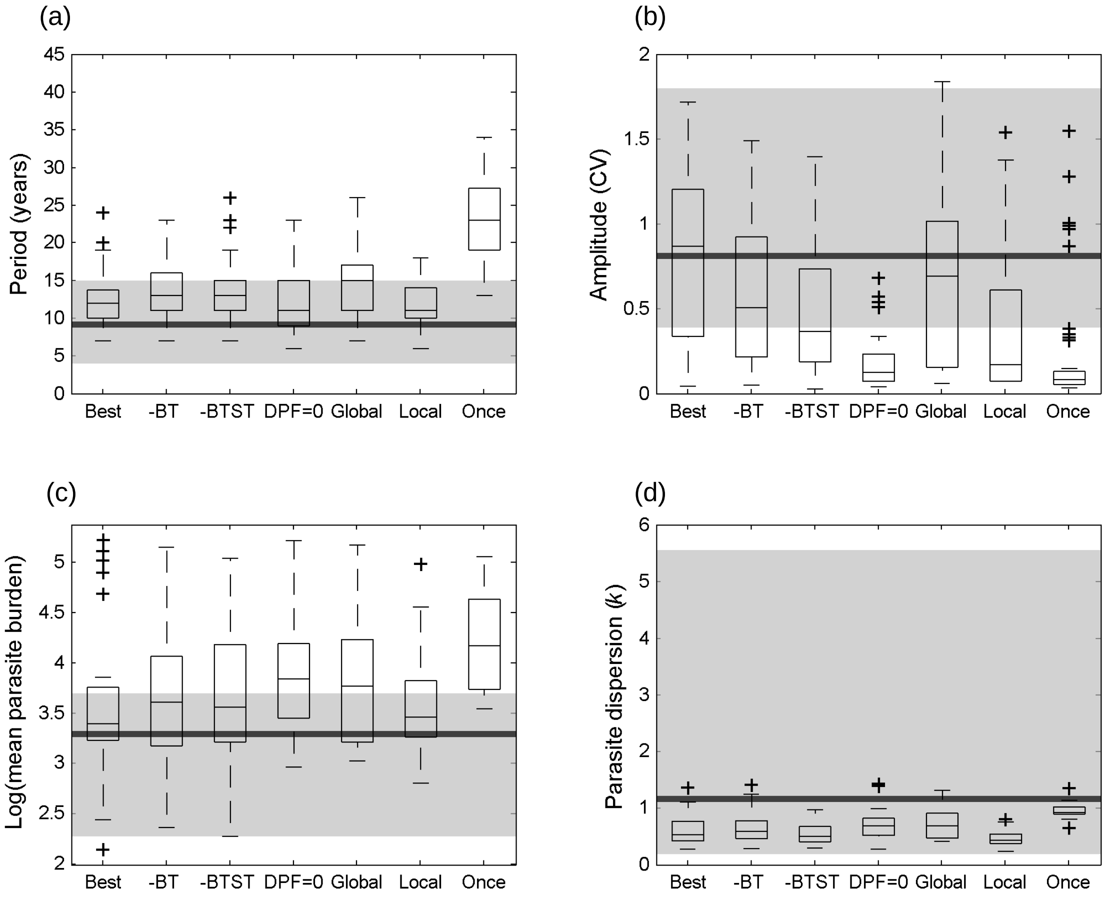


Figure 5.5. Comparing variation in four characteristic properties of mountain hare time series and parasite burdens across different models and to the observed variation (range covered by light grey boxes, mean marked with dark grey line). Parameters were varied within the plausible parameter envelope. The characteristics are (a) period (for cyclic time series), (b) amplitude of hare cycles, (c) mean burden and (d) parasite dispersion *k*. Model structures abbreviate as: best fit (Best), parasite burden-timing link removed (-BT), burden-timing and size-timing links both removed (-BTST), direct parasite effect on fecundity removed (DPF=0), population-wide parasite transmission (Global), local transmission (Local), burdens allocated once during lifetime (Once). Parameters that were not varied as part of the perturbations were kept at values set for the best fit model.

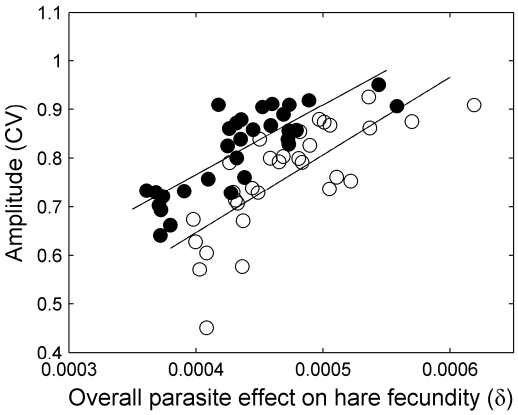


Figure 5.6. The relationship between the amplitude of hare cycles and the ‘overall’ parasite effect on hare fecundity when maternal effects on leveret birthdate were removed from the best fit model. Parasite-reduced fecundity (δ) takes a negative value, therefore to ease interpretation the strength (magnitude) of the effect is graphed. When the burden-timing link was removed (filled circles) the regression coefficient for the slope was -1428 year ($t_{2,29}$=-7.61, p<<0.001) and intercept 0.195 ($t_{2,29}$=-2.37, p=0.03). When both the burden-timing and size-timing links were removed (open circles) the regression coefficient for the slope -1598 year ($t_{2,29}$=-6.26, p<<0.001) and the intercept was not significantly different from zero.

Appendix 5.1: Body size

The adult size a juvenile attained was determined by birthdate. Since late born leverets show some compensatory growth (Iason, 1989a), a curvilinear relationship was used to link birthdate (days after $B_{earliest}$, x, see Appendix 5.2) and end of season juvenile size:

$$HFL = HFL_{\max} - \frac{HFL_{\text{int}}}{(\text{Length of breeding season})^2}.x^2$$

where HFL_{int} is the difference between HFL_{max} and HFL_{min}, and the breeding season lasted for 203 days (latest birthdates estimated at around 31st September (Flux, 1970)).

Appendix 5.2: Birthdate

All females had a first litter. The timing of the first litter lay between the earliest recorded birth date of the year ($B_{earliest}$) 7th March (Hewson, 1970) and the latest for a first litter of the breeding season ($B_{1,latest}$) 14th May (Flux, 1970). The number of days after $B_{earliest}$ when a female gave birth (x) was related to her body size HFL_i and parasite load P_i (Fig 5.1a) according to:

$$x = \begin{cases} \left(\frac{P_i}{P_{\max}} + \frac{HFL_{\max} - HFL_i}{HFL_{\text{int}}}\right).\left(\frac{B_{1,latest} - B_{earliest}}{2}\right) & \text{if } P_i < P_{\max} \\ \left(1 + \frac{HFL_{\max} - HFL_i}{HFL_{\text{int}}}\right).\left(\frac{B_{1,latest} - B_{earliest}}{2}\right) & \text{if } P_i \geq P_{\max} \end{cases} \qquad \text{Eqn. 5.1}$$

where P_{max} is 16,000 the maximum parasite burden recorded in the field (dataset described in Newey et al. (2005)), and HFL_{int} is the difference between HFL_{max} and HFL_{min}.

The birthdates of succeeding litters, up to a maximum of three, depended on the gestation period of 50 days (Borg et al., 1952, Höglund, 1957) and an inter-litter gap, the interval until the proceeding pregnancy. Although postpartum oestrus allows females to copulate just a few hours after parturition (Höglund, 1957) the distribution of pregnancies across the breeding months (Flux, 1970, Hewson, 1970) and bell-shaped HFL distribution (Iason, 1990; Newey, unpublished data) suggest that there may be considerable variance in inter-litter gaps. To allow variation across females the model included a parameter for the upper limit of a uniform random distribution from which inter-litter gaps could be generated and added to the fixed period of one day. The value of the upper limit was reverse engineered as part of the model selection process.

In the model where the effect of burden on birthdate was removed, the number of days after the earliest birthdate ($B_{earliest}$) when a female gives birth (x) was a modified version of Eqn 5.1:

$$x = \left(\frac{HFL_{\max} - HFL_i}{HFL_{\text{int}}} \right) . \left(B_{1,latest} - B_{earliest} \right)$$

When both the burden-timing and size-timing links were removed then day of birth (x) was a uniform random variate between zero and the latest birthdate for the first litter ($B_{1,latest}$).

Appendix 5.3: Litter size

Although a detailed field study of breeding mountain hares in Scotland categorised litters according to the time of year (Iason, 1990), for the modelling process it was logical to label litters in sequence of birth. Litter size was a rounded integer value of the number of ova shed minus reductions due to previous litters minus prenatal mortality. The number of ova shed depended on litter, parasite loads and the size of previous litters in the current year. In mountain hares the first litter is smaller than proceeding ones (Angerbjörn and Flux, 1995) whilst later litters can potentially reach six. Therefore the number of ova shed was set as either one or two for the first litter and up to six ova in proceeding litters.

Previous litters can impact on the number born in later litters (Iason, 1990). Empirical data suggests litter two is only affected by litter one after early June (Iason's cut-off of 8th June was used in the model). Litters two and three were reduced by 0.7 for each leveret born in litter one, whilst 0.5 young were deducted from litter three for each leveret born to litter two. Prenatal mortality was not applied to the smaller 1st litters but litter-specific prenatal mortalities were assigned to the 2nd litter and 3rd litter using mean values of 8% and 2% respectively (Iason, 1990). Since litter sizes can be as large as six, although usually less (Flux, 1970, Hewson, 1976), the number of ova shed in litter three was set at six ova and deductions made according to previous litter sizes and prenatal mortality.

The effect of parasites on the number of ova shed is weak after April/May (Newey and Thirgood, 2004, Newey et al., 2004) and therefore was only permitted to affect the 1st and 2nd litters in the model. Thresholds were used to allocate hares with ova shed according to their parasite burden. We considered two conceptually different ways to construct these thresholds and used the best available data on the *T. retortaeformis* distribution among mountain hares to generate the six thresholds needed to separate zero and six ova shed (Supplemental Fig 5.1). Modelling the effect of parasites on the size of the first litter was simpler because all females shed only one or two ova in the first litter and therefore only the threshold between one and two ova needed to be parameterized. The value of the threshold in litter one and the method for allocating thresholds in litter two were reverse engineered as part of the model selection process.

Appendix 5.4: Adult hare mortality

Intrinsic mortality (in absence of parasites) was dependent on body size, where each individual was allocated a rate according to a linear relationship between the confidence intervals of the empirically estimated population value of intrinsic hare mortality (Townsend et al., 2009, Chapter 4) and body size. In this way the smallest hares (HFL 115 mm) had the highest mortality (0.61 year^{-1}) and the largest hares (HFL 150 mm) had the lowest mortality (0.08 year^{-1}). Mortality rate for an individual hare was fixed throughout its adult life. Hares surviving to age ten were assumed to die (Macdonald et al., 1998).

Adult mortality occurred once a year with a probability calculated from the sum of intrinsic hare mortality in the absence of parasites and per parasite direct effect on mortality (α) multiplied by parasite burden.

Appendix 5.5: Parasite transmission

The parasite population was monitored by recording burdens within hares. Transmission was calculated from two components, the birth term and the host density-dependent mortality term, taking the general form from the parasite equation in the host-parasite model of Anderson and May (1978):

$$P(t) = \lambda . P(t-1) . \frac{H}{H_0 + H}$$

Two transmission phases were permitted to account for seasonality in parasite burdens (Boag and Iason, 1986). In the spring pulse, parasite burdens of the breeding population were augmented. In the autumn pulse adult worm burdens were augmented and leveret burdens initiated. For simplicity in the model, the year was divided according to the breeding season (treated as ‘summer’ and constituting 56% of the year) and the empirical estimate of *T. retortaeformis* fecundity of 1000 year^{-1} (Townsend et al., 2009, Chapter 4) was split between pulses in proportion to their duration. Since the survival term was a rate, H_o was not split over seasons but sampled within its plausible range as part of the model selection process. Adult parasite mortality was assumed to be zero.

Three transmission mechanisms were devised for the model. In the first mechanism, parasite recruits entered a pool from which they were allocated among the whole hare population. The pool size was calculated using the birth term from the parasite equation in the host-parasite model of Anderson and May (1978):

$$(1-\gamma).\lambda.P(t-1).\frac{H}{H_0+H}$$

where λ = number of eggs per parasite, H_o = transmission inefficiency constant, H = hare density and P = parasite population and 1-γ = proportion of parasite pool distributed globally (see below). The pool was apportioned out using a uniform broken stick distribution, augmenting adult hare burdens and initiating burdens of leverets.

The second mechanism represented local transmission, recognising that hares maintain home ranges (Flux, 1970) and therefore new parasites may be more likely to reinfect the same host. The parasite burden (P_i) of adult hare i was augmented according to:

$$\gamma.\lambda.P_i(t-1).\frac{H}{H_0+H}$$

This was adapted to account for indirect vertical transmission to leverets sharing the same space as their mothers. To augment adult hare burdens:

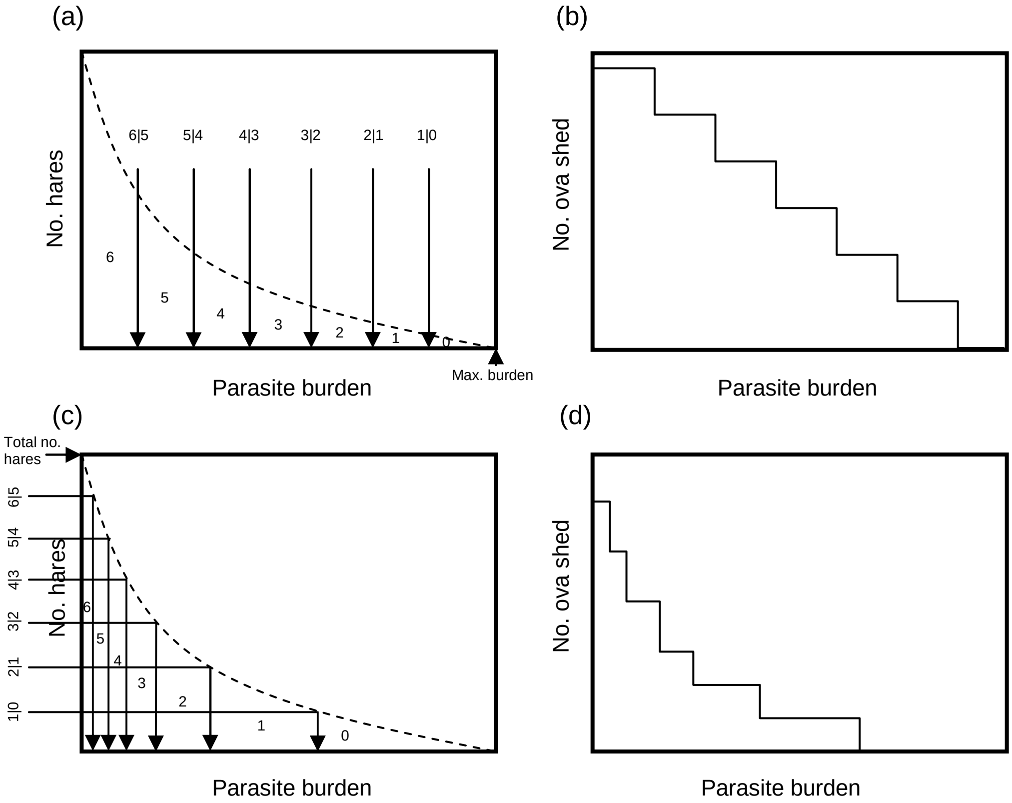
$$\left(\gamma.\lambda.P_i(t-1).\frac{H}{H_0+H}\right).\left(\frac{1}{n}\right)^{\beta}$$

and to initiate leveret burdens:

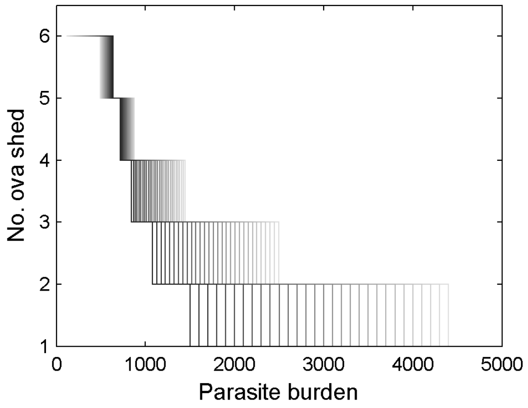
$$\frac{\left(\gamma.\lambda.P_i(t-1).\frac{H}{H_0+H}\right).\left(1-\left(\frac{1}{n}\right)^{\beta}\right)}{n-1}$$

Where n is family size (mother + no. leverets), β is how evenly parasites are distributed within a family (β = 0, mother gets all the parasites, β = 1, parasites allocated evenly among mother and offspring) and γ is the proportion of the parasite pool distributed locally ($\gamma = 0$, parasites distributed population wide only, $\gamma = 1$, parasites distributed locally only).

In the third mechanism, hares were given a lifetime dose of parasites as leverets rather than annual augmentation of infection. Parasite recruits entered a pool from which they were allocated among the leveret population. In this way each cohort had a different mean parasite burden according to parasite availability in that year and variation was generated across years where there were different sized parasite pools. For this mechanism, autumn parasite fecundity was adjusted to the annual empirical estimate of 1000 year^{-1}.



Supplemental Figure 5.1. Schematic diagrams showing the conceptual difference between two approaches to setting burden thresholds in the allocation of fecundity in female hares. (a) In the first approach the maximum number of parasites (14962) in a dataset on *T. retortaeformis* burdens in 654 hares (dataset described in Newey et al. (2005)) was split equally into seven bins. In this way, a female's 2nd litter size was reduced by one ovum for approximately every 2100 parasites in her burden. (b) This assumes a constant per-parasite effect with increasing burden. (c) In the second approach, the same number of hares was assumed to fall into seven bins. Corresponding burdens at the thresholds of these bins were identified using a c.d.f. of a negative binomial distribution with k = 0.55 and p = 0.00026 (these were the available estimates prior to the reanalysis by estate that is described in the main text). This generated thresholds at 100, 350, 770, 1420, 2490 and 4530 parasites. (d) This models per-parasite effect on ova shed as increasing with increasing burden.



Supplemental Figure 5.2. Manipulation of burden thresholds in the allocation of ova shed to female hares in the second litter. The darker the lines, the smaller the increments between thresholds and the stronger the parasite effect on fecundity.

Chapter 6. Periodic travelling waves in a simple host-parasite model parameterised using approximate Bayesian inference

Abstract

Cyclic population dynamics in mountain hares have been documented in nature, but an empirically informed simple host-parasite model has not been able to predict realistic dynamics. Potential inadequacies in the model are investigated in this chapter. First, we lack reliable information about model parameters. Here we use a rejection-sampling approach motivated by Bayesian methods to identify the most likely parameter set to predict observed dynamics. The results imply that the current formulation of the hare-parasite model can only generate realistic dynamics when parasite effects are significantly larger than current empirical estimates. We conclude that the model probably contains an inadequate level of detail. Therefore, second, we structurally modify the model to make it spatially explicit by including diffusion of mountain hares and corresponding advection of parasites. From initial simulations we show that the spatially extended host-parasite equations are able to generate periodic travelling waves (PTWs) of hare and parasite abundance. This is a newly documented behaviour in these widely used host-parasite equations. While PTWs are a new potential scenario under which cyclic hare dynamics could be explained, further mathematical development is required to determine whether adding space can generate realistic dynamics with parameters that lie closer to empirical estimates.

1. Introduction

Population variability may be explained under a multitude of ecological theories. One set of theories arises from the interaction of a host with a macroparasite, and uses simple mathematical models to demonstrate that macroparasites can drive population cycles in host species (Anderson and May, 1978, May and Anderson, 1978). No matter what form the theoretical basis takes, the challenge really lies in the confrontation with data, with essentially two outcomes. In the case of host-parasite modelling, an empirically informed model parameterised with best available data either generates realistic host population dynamics and infection levels, as is the case with the red grouse and a nematode parasite, *Trichostrongylus tenuis* (Dobson and Hudson, 1992), or the predicted dynamics do not lie within the spectrum of dynamics observed, as is the case with the mountain hare - *T. retortaeformis* system (Townsend et al., 2009, Chapter 4). In the latter scenario, it may be concluded that parasites are not driving host cycles. However, failure to predict observed dynamics may also arise from inadequate parameterisation, or missing important biological details causing structural inadequacies in the model formulation. Potential inadequacies in the mountain hare - *T. retortaeformis* model are investigated in this chapter: by using statistical techniques to identify a parameter set that generates observed population dynamics; and by extending the model into the spatial dimension.

Mountain hares (*Lepus timidus*) are the UK's only native lagomorph with 99% of the UK population found in Scotland. Like their American cousin, the snowshoe hare (*Lepus americanus*), mountain hares exhibit cyclic dynamics (Newey et al., 2007b) although unlike the snowshoe hare the cause of mountain hare cycles is not yet well understood. There is little evidence to suggest that heavy predation (Hewson, 1976) or food-limitation (Keith, 1983) are responsible. Mountain hares co-inhabit heather moorland with red grouse, a species which also exhibits cyclic population dynamics. Grouse cycles are thought to be driven by the nematode parasite *T. tenuis* (Hudson et al., 1998, Hudson et al., 1992, Dobson and Hudson, 1992b), territoriality (Moss et al., 1996), or an interaction of both (Mougeot et al., 2003). In comparison, mountain hares are non-territorial (Flux, 1970, Hewson, 1976) but they do suffer from high prevalence and intensity of a parasite of the same genus, *T. retortaeformis*. The discovery that parasites reduce fecundity in Scottish hare populations (Newey and Thirgood, 2004, Newey et al., 2004) has led to the suggestion of *T. retortaeformis* as a driver of mountain hare population dynamics in Scotland. Recently, however, a simple mathematical mountain hare - *T. retortaeformis* model based on the Anderson and May framework (Anderson and May, 1978, May and Anderson, 1978) has suggested the empirically estimated parasite effect on fecundity was not strong enough to predict parasite intensities and account for sustained population cycles (Townsend et al., 2009, Chapter 4).

In the vast majority of biological systems we lack reliable information about parameters of models. The challenge is particularly acute for parameterising dynamical models of wildlife host-parasite systems because independent data are required from studies of host demographics, parasite transmission and manipulative experiments to quantify parasite induced effects. Even if practical difficulties are overcome, small sample sizes may make parameter confidence intervals too wide to easily infer the role of parasites in driving the dynamics. An alternative is to use optimisation techniques to estimate parameters simultaneously, either within the frequentist maximum likelihood or Bayesian framework. Bayesian statistical inference has two key advantages over other optimisation techniques. First it is able to provide the probability distribution of parameters, whereas most conventional optimisation algorithms provide only point estimates (Toni et al., 2009), and second, Bayesian inference integrates existing information on parameters (Clark, 2007) while frequentist approaches typically neglect information gained from independent, empirical (and often hard-earned) data. In this chapter we use a rejection-sampling approach motivated by Bayesian methods to identify the most likely parameter set to predict observed dynamics with the mountain hare - *T. retortaeformis* model.

Spatial structure has commonly been excluded from archetypal models of population dynamical systems despite the fact that ecological processes are unavoidably spatio-temporal. Spatial structure can be explicitly incorporated into mathematical models as either a continuous variable or as a discrete variable. Modelling space as a discrete variable, for example using coupled map lattices (Hassell et al., 1991) or coupled oscillator models (Sherratt et al., 2000), makes simulation relatively straightforward but has a restricted mathematical underpinning that limits the quantitative study of dynamical behaviour (Sherratt, 2001). The simplest way to incorporate continuous space is to add one dimensional dispersal to each component equation of the temporally dynamic model, which assumes individuals diffuse through their environment at a specified rate. This constitutes a simple reaction-diffusion model, where each species equation has a reaction component which models the birth and death processes of that species (also known as the ‘kinetics’) and the dispersal component. These equations can generate a range of spatio-temporal dynamics, such as travelling wave fronts, periodic travelling waves and spatio-temporal chaos (Sherratt and Smith, 2008).

Periodic travelling waves are a naturally observed phenomenon in some cyclic species including red grouse (Moss et al., 2000) and snowshoe hares (Smith, 1983). Theory on reaction-diffusion equations suggests that they may be caused by dispersal acting on cyclic populations (Smith et al., 2008). However while reaction-diffusion equations are commonly used to model dynamical population growth equations coupled by a trophic interaction, the dispersal of a parasite is clearly not independent of the movement of its host and therefore may be more appropriately modelled by advection (transportation) of the parasite by the host. One aim here is to determine whether periodic travelling waves are predicted by a reaction-diffusion-advection model of the mountain hare - *T. retortaeformis* system.

In this chapter, we give an overview of the rejection-sampling approach we used to infer the most likely parameter combination to generate realistic temporal dynamics with the current formulation of the mountain hare - *T. retortaeformis* model. Then we extend the model to include host dispersal and parasite advection. Hare and parasite population dynamics are presented for both the non-spatial and spatial models parameterised with best empirical estimates and most likely estimates from rejection-sampling.

2. Methods

(2A) THE HOST-PARASITE MODEL

The non-spatial model was a variant of the May & Anderson (1978) deterministic model for macroparasite infections which are detrimental to both host fecundity and survival, that was derived by Diekmann & Kretschmar (1991) to prevent the possibility of a negative birth rate. The model describes continuous growth equations of a host population of density *H* which interacts with a parasite population *P*:

$$\frac{dH}{dt} = -\alpha P - bH + aH\left(\frac{kH}{\delta P + kH}\right)^{k} \qquad \text{Eqn 6.1}$$

$$\frac{dP}{dt} = P\left[\frac{\lambda H}{H_o + H} - (\mu + \alpha + b) - \alpha\frac{P}{H}\left(\frac{k+1}{k}\right)\right] \qquad \text{Eqn 6.2}$$

Parameters are defined in Table 6.1. Standard numerical techniques were used to solve the equations (MATLAB ODE solver ode45 based on an explicit Runge-Kutta (4, 5) formula) and simulate dynamics of the parameterised model. Simulations included a burn-in period of 50 years and post burn-in period of 37 years for reasons explained in §2d. Stability of the interior equilibrium point was determined using linear equilibrium stability analysis by constructing the Jacobian matrix and assessing the associated eigenvalues (see Appendix 4.2 of Chapter 4 for further details). A negative real part of the dominant (most positive) eigenvalue ($\mathrm{Re}\,\lambda_{dom}$) denotes a stable point and its magnitude determines the rate of damping to the equilibrium. Values for parasite dispersion (k) were restricted to 0.5, 1 and 2 in order to obtain analytical solutions for the equilibrium point (see Appendix 4.2 of Chapter 4).

(2B) EMPIRICAL PARAMETER ESTIMATION

Point estimates and plausibility envelopes for parameterising Eqns 6.1-6.2 using empirical evidence are given in Table 6.1. For most parameters the data sources and means of estimation have been described elsewhere (see Appendix 4.1 of Chapter 4 for estimation of α, b, λ, H_0 and μ, and Methods of Chapter 5 for estimation of k), whilst two parameters (a, δ) were estimated by reanalysing available data (see Appendix). As formal confidence limits were not available for all data sources, variation in parameters was defined by a plausible envelope. Both male and female individuals formed the model hare population since both sexes are hosts to *T. retortaeformis*.

(2C) PARAMETER ESTIMATION USING REJECTION-BASED APPROXIMATE BAYESIAN INFERENCE

Bayesian methods require a prior distribution $\pi(\boldsymbol{\theta})$, which reflects prior belief i.e. uncertainties in parameters in the vector $\boldsymbol{\theta}$, and a likelihood function $P(y|\boldsymbol{\theta})$ of the observed data y, the probability that the observed data occurs given the parameter set $\boldsymbol{\theta}$. Bayes' formula yields the posterior distribution $P(\boldsymbol{\theta}|y)$ of the parameters as $P(\boldsymbol{\theta} \mid y) \propto P(y \mid \boldsymbol{\theta})\pi(\boldsymbol{\theta})$. The likelihood function is typically chosen depending on the dynamical model (Patwardhan and Small, 1992, Rosa et al., 2003). Recently however, approximate Bayesian methods have been developed where the evaluation of likelihood is replaced by a simulation-based procedure. Approximate Bayesian computation (ABC) is a family of computational techniques that use rejection-sampling of parameter combinations based on their ability to simulate a data set (Toni et al., 2009) or capture observed summary statistics of a simulated data set (Beaumont et al., 2002). The approach was conceived with the aim of inferring posterior distributions for stochastic, complex models where likelihood functions were computationally intractable or too costly to implement (Beaumont et al., 2002, Marjoram et al., 2003, Plagnol and Tavaré, 2004, Hickerson et al., 2006). However ABC methods are attractive for inferring posterior distributions of deterministic models also, because they combine the computational convenience of summary statistics with the advantages of the Bayesian paradigm, and are closely related to standard Bayesian inference in systems of ordinary differential equations (Toni et al., 2009).

The simplest approach to implementing ABC is to use a rejection sampler (Pritchard et al., 1999). Although there are more sophisticated sampling methods using Markov chain Monte Carlo (MCMC) and sequential Monte Carlo (SMC) algorithms (Marjoram et al., 2003, Sisson et al., 2007), the results are comparable in deterministic models (Toni et al., 2009). The disadvantage of the rejection sampler is that it samples from the prior distribution only, and therefore will have low acceptance rates (and high computational cost) when the posterior is very different from the prior. However, if this is not the case then rejection sampling is very easy to implement and the algorithm can be parallelised (run on multiple computers simultaneously) to speed up acceptances.

Where data are high dimensional, information can be captured using lower dimensional summary statistics and these can be used to compare data sets. As measures of agreement between simulated and real time series, it is common practice to compare dynamical properties (also known as probes) such as the period of cycles (Kendall et al., 1999). We adopt such descriptors as summary statistics (see §2d), denoted here as S_i (for $i=1,\ldots,n$ where n is the number of statistics), with which to conduct rejection sampling. The ABC scheme for data D summarised by vector of summary statistics $\mathbf{S}$ is as follows:

A1. Generate parameter vector $\boldsymbol{\theta}$ from $\pi(\boldsymbol{\theta})$
A2. Simulate D' from the model (Eqn 6.1 and 6.2) with parameter vector $\boldsymbol{\theta}$
A3. Calculate summary statistic vector $\mathbf{S}'$
A4. Calculate distance $\rho(\mathbf{S}, \mathbf{S}')$ between $\mathbf{S}$ and $\mathbf{S}'$
A5. Accept $\boldsymbol{\theta}$ if $\rho \le \varepsilon$, where ε is the tolerance. Return to A1.

ABC rejection sampling was developed to use distance between observed and simulated summary statistics, whereas we found it was more appropriate to provide intervals of acceptable summary statistics (see §2d, Table 6.2). The sampling scheme was modified to reject those simulations which have summary statistics that fall outside the intervals:

B1. Generate parameter vector $\boldsymbol{\theta}$ from $\pi(\boldsymbol{\theta})$
B2. Simulate D' from the model (Eqn 6.1 and 6.2) with parameter vector $\boldsymbol{\theta}$
B3. Calculate summary statistic vector $\mathbf{S}'$
B4. Accept if $S_l < S_i' < S_u$ for all i, where S_l is the observed lower value and S_u is the observed upper value of each summary statistic S_i. Return to B1.

Parameter combinations were generated from prior distributions and those which simulated plausible time series with the observed summary statistics were accepted. Choice of prior distributions was a reflection of two requirements. First, priors needed to capture the probability densities suggested by the empirical data (see §2b), and thus hyper-parameters (mean and variance) for prior distributions were chosen to reflect the empirically determined point estimates and plausible intervals (Table 6.1). Second, previous work has suggested that realistic dynamics require changes to parameters outside the plausible envelope (Townsend et al., 2009, Chapter 4) and therefore, for the majority of parameters, prior distributions were broader than the plausible intervals. Plausibility of simulations was determined by persistence of both species and reasonable hare and parasite abundances. Given that the observed maximum hare density is 200 hares km^{-2} (Watson et al., 1973, Hewson, 1976) and maximum parasite intensity is 16,000 parasites hare^{-1}, simulations which reached four times these figures during the burn-in period, and two times these figures after the burn-in period, were considered implausible.

Posterior distributions were generated from the collection of accepted parameter combinations. Posterior parameter distributions are multidimensional, but for visualisation they were plotted as one-dimensional marginal distributions. The mean of the marginal distributions was used as an estimate of the ‘most likely’ parameter value to generate realistic population dynamics.

(2D) SUMMARY STATISTICS OF HARE AND PARASITE TIME SERIES

Observed dynamical properties were used as summary statistics for conducting parameter estimation using approximate Bayesian inference (see §2c) and to judge model fit to observed (Table 6.2). Mountain hare population dynamics in Scotland are recorded as game bag time series which have a median length of 37 years. Each time series has been statistically classified as cyclic or non-cyclic and summarised by hare cycle period and amplitude (Newey et al., 2007b). The level of *T. retortaeformis* infection in hares has been recorded in several studies (Newey et al., 2005, Boag and Iason, 1986) and recently reanalysed to provide the mean and variation of mean intensities for populations across Scotland (Chapter 5).

We used two different vectors of summary statistics to accept or reject candidate simulations (step B4 in ABC scheme §2c) and therefore obtained two sets of posterior parameter distributions. The first vector contained three summary statistics:

$$\mathbf{S}=\begin{bmatrix}\text{period of hare cycles (years)}\\ \text{hare density (hares km}^{-2}\text{)}\\ \text{mean infection (parasites hare}^{-1}\text{)}\end{bmatrix}\quad S_l=\begin{bmatrix}4\\20\\1375\end{bmatrix}\quad S_u=\begin{bmatrix}15\\200\\2497\end{bmatrix},$$

and the second vector contained five summary statistics:

$$\mathbf{S}=\begin{bmatrix}\text{period of hare cycles (years)}\\ \text{hare density (hares km}^{-2}\text{)}\\ \text{mean infection (parasites hare}^{-1}\text{)}\\ \text{amplitude of hare cycles}\\ \text{stability, }\operatorname{Re}\lambda_{dom}\end{bmatrix}\quad S_l=\begin{bmatrix}4\\20\\1375\\0.39\\>0\end{bmatrix}\quad S_u=\begin{bmatrix}15\\200\\2497\\1.80\\\infty\end{bmatrix}.$$

The first vector of summary statistics accepted transiently cyclic time series as realistic, recognising that random exogenous perturbations could cause dampened oscillations to persist as regular fluctuations (Kaitala et al., 1996). The more stringent second set required the model to generate stable limit hare cycles with a realistic amplitude. Given that the bounded solutions of Eqns 6.1 and 6.2 are expected to possess either a stable equilibrium point or stable limit cycle (Diekmann and Kretzschmar, 1991) and plausible simulations were numerically bounded (see §2c), we assumed that plausible simulations with a locally unstable equilibrium point ($\operatorname{Re}\lambda_{dom}$>0) must exhibit a stable limit cycle.

All model summary statistics were derived from plausible (see §2c) simulated time series of annually recorded hare density and mean infection, with the exception of local stability (see §2a). Mean hare density, mean infection level and the amplitude of hare cycles were estimated over the non-transient 37 year time series. Mean infection was calculated for each year and then averaged over the 37 years. In case of damped oscillations, the first 37 years of the hare time series (at the start of the burn-in period) was used to classify cyclic dynamics and calculate period. Periodicity, period and amplitude of hare time cycles were estimated as for real data (Newey et al., 2007b).

(2E) SPATIAL EXTENSION

Random movement of hares and parasites were modelled by attaching a diffusion term, to denote local dispersal of hares, to the host equation (Eqn 6.1):

$$\frac{\partial H}{\partial t}=-\alpha P-bH+aH\left(\frac{kH}{\delta P+kH}\right)^{k}-\frac{\partial J_H}{\partial x}, \qquad \text{Eqn 6.3}$$

where J_H is the hare flux $J_H = -D_H \partial H / dx$, i.e. we assume that hares move down a population gradient, x is the one-dimensional space coordinate and D_H is the diffusion coefficient for hares. In the absence of any data, we take $D_H = 0.5$ although we expect D_H to influence the dynamics. Assuming parasites move at the same velocity as the hares we attach an advection term to Eqn 6.2 to give:

$$\frac{\partial P}{\partial t} = P\left[\frac{\lambda H}{Ho+H} - (\mu+\alpha+b) - \alpha\frac{P}{H}\left(\frac{k+1}{k}\right)\right] - \frac{\partial}{\partial x}\left(\frac{P}{H}J_H\right) \qquad \text{Eqn 6.4}$$

The movement of parasites in space only occurs via passive convection with the hosts, so that the flux of the parasites at any point is given by P multiplied by the host velocity, J_H/H.

We used the method of lines to reduce the system to that of a coupled system of ordinary differential equations (ODEs) (see Appendix 6.2 for a full description of the numerical scheme). We used a central difference approximation for the diffusion term in the hare equation and second order accurate flux limiters for the convection term in the parasite equation. The boundary conditions for both hares and parasites were no-flux at both left and right boundaries and the resulting ODEs were solved using a fourth order Runge-Kutta method. We assume exponentially decaying (in space) initial conditions:

$$H(x, t=0) = P(x,0) = A\exp(-\xi x),$$

where A and ξ are positive constants, taken to be 1 and 2 respectively. Note that the parameter A affects the time course of the evolution but has no effect on the ultimate solution. Varying ξ will affect the advancing front speed and the selection of the periodic travelling wave when supported. The spatio-temporal dynamics of Eqns 6.3-6.4 were simulated under three parameter sets, the empirical point estimates (§2b) and the two sets of parameter estimates obtained from approximate Bayesian inference (§2c), and inspected for periodic travelling waves.

3. Results

(3A) TEMPORAL DYNAMICS

Table 6.1 presents the empirically-sourced point estimates and plausible intervals for parameters of the non-spatial host-parasite model (Eqns 6.1-6.2). Parameterising the model with the point estimates generated damped oscillations (Fig 6.1a, d). Summary statistics of this time series showed that while period and hare density were within observed ranges, the level of mean infection was much greater than realistic levels (Table 6.2).

We used ABC to identify the most likely parameter set given the observed summary statistics. The acceptance rate under summary statistic vector 1 was 0.1%, and 0.006% under summary statistic vector 2. Running the ABC scheme under summary statistic vector 1 (period, hare density and mean infection) generated the posterior parameter distributions shown in Fig 6.2. From these posteriors the most likely parameter combination was estimated using the mean of the distributions (Table 6.1). With these parameters, the model exhibited cyclic transient dynamics that were strongly damped (Fig 6.1b, e) with a realistic period, mean hare density and annual mean infection (Table 6.2). Running the ABC scheme under summary statistic vector 2 (period, hare density, mean infection, amplitude, stability) generated the posterior distributions for parameters given in Fig 6.3. The time series simulated from the model populated with the most likely parameter set from these posteriors (Table 6.1) exhibited a stable limit cycle (Fig 6.1c, f) with realistic characteristics (Table 6.2), although the mean infection level for this particular combination of parameters was slightly outside the confidence envelope.

The parameter posterior distributions also provided information about parameters and their role in the hare and parasite interaction model. Given that point parameter estimates captured period and mean hare density but not mean infection levels (Table 6.2), the posteriors in Fig 6.2 reflect changes to parameters necessary to drive mean infection down to realistic levels. Since only values of the parasite effect on mortality (α) from the right tail of the prior distribution (10^{-4} to 10^{-3}) were accepted by the ABC algorithm (Fig 6.2b), the results imply that a 100 to 1000 fold increase in the parasite effect on mortality (α) from empirical estimates would be necessary to reduce intensities sufficiently given this model. Lower intrinsic hare fecundity (a, Fig 6.2a) and a stronger parasite effect on fecundity (δ, Fig 6.2d) were also implicated as likely elements of a system with lower parasite intensities.

The posteriors in Fig 6.3 show that for the model to generate sustained cycles also required a 10 to 100 fold increase in parasite effect on fecundity (δ, Fig 6.3d) from empirical estimates, and was more likely when parasites were more dispersed among hares (larger k, Fig 6.3h). The destabilising nature of these two parameters are well known from stability analysis, as the equilibrium point can only be stable if $\alpha<\delta k$ (May and Anderson, 1978). It appears therefore that the large parasite-induced mortality rate (α) required for observed infection levels has a stabilising effect on the dynamics that must be balanced by a strong parasite-reduced fecundity (δ). In conclusion, the hare-parasite model can only generate realistic sustained cycles where parasite effects are significantly larger than current estimates.

(3B) SPATIO-TEMPORAL DYNAMICS

Simulations of the spatio-temporal dynamics of hares and parasites under different parameter sets showed two distinct patterns. Parameterising the model with empirical point estimates (Table 6.1) generated a travelling wave of hares and parasites as the hares diffuse (and parasites advect with the hares) from left to right across the domain from the boundary (Fig 6.4). In the wake of this wave front, both hares and parasites evolve to their non-oscillatory equilibrium states. Parameterising the model with the most likely estimates from posteriors generated using summary statistic vector 1 (Table 6.1) also generated a wave front followed by spatially homogenous dynamics (results not shown). Under parameters estimated using summary statistic vector 2 (Table 6.1), however, a travelling wave front was followed by periodic travelling waves where oscillations in hare and parasite numbers occurred in both space and time (Fig 6.5).

4. Discussion

In this chapter we have identified the most likely parameter set for a simple host-parasite model to reproduce realistic population cycles in mountain hares interacting with a nematode parasite. We used a technique based on approximate Bayesian computation and this work constitutes one of the first applications to dynamical systems in ecology (Toni et al., 2009). This was done under two definitions of ‘realistic’ hare and parasite population dynamics, in which one definition recognised that random exogenous forcing could maintain cycles in damped oscillatory deterministic dynamics (Kaitala et al., 1996). The results imply that the current formulation of the hare-parasite model can only generate realistic dynamics when parasite effects are significantly larger than current empirically determined estimates. We then structurally modified the model to make it spatially explicit by including diffusion of mountain hares and corresponding advection of parasites. From initial simulations we have shown that the spatially extended host-parasite equations are able to generate periodic travelling waves (PTWs, also known as periodic plane wavetrains) of hare and parasite abundance. This is a newly documented behaviour in these widely used host-parasite equations. Our results suggest that the population cycles observed in mountain hares in Scotland are either spatially homogenous oscillations as predicted by the most likely parameter set without diffusion or, with diffusion, the observed temporal cycles are formed by periodic travelling waves.

Travelling waves in natural populations are a long term phenomenon associated with temporally cyclic populations of a prey or host species (Hassell et al., 1991, Hassell et al., 1994, Ranta and Kaitala, 1997, Sherratt and Smith, 2008). Although travelling waves have become renowned in relation to the invasion dynamics of exotics or initial spread of infectious diseases (e.g. Jeltsch et al., 1997), these may be transient phenomena or distinguished as single wave fronts (Lundberg et al., 2000). More permanent travelling waves are hard to demonstrate empirically because detection in field studies requires extensive spatio-temporal data and specialised statistical techniques (Sherratt and Smith, 2008). Nonetheless, where this has been done, they have commonly been found (Sherratt and Smith, 2008), and in a range of taxa (Moss et al., 2000, Lambin et al., 1998, Tenow et al., 2007, Bjornstad et al., 2002). Two of the species for which PTWs have been identified in natural populations, the red grouse (Moss et al., 2000) and the autumnal moth (Tenow et al., 2007), are also hypothesised to have parasite-driven temporal cycles (Tanhuanpää, 2002, Hudson et al., 1998). However, the effects of parasites on their spatial dynamical behaviour has not yet been explored. Here we have demonstrated the possibility of PTWs arising directly from the presence of the parasite in our host system.

The spatially extended host-parasite model presented here adds to a range of theoretical models for cyclic populations which are able to numerically simulate PTWs (e.g. Hassell et al., 1991, Sherratt et al., 2000). The majority of theoretical studies of periodic wave behaviour, including the present study, have been qualitative and not quantitative. The major exception is oscillatory reaction-diffusion equations as a result of mathematical advances over the last few decades (Sherratt, 2001, Dunbar, 1983, Kopell and Howard, 1973, Sherratt, 1994). The special relationship between the space and time dependence of a periodic travelling wave means the solution is a function of a single ‘travelling wave’ variable. Reaction-diffusion systems modelled using PDEs can be rewritten in terms of the travelling wave variable, giving rise to a system of first order ODEs. PTWs correspond to a limit cycle solution of these ODEs. The simplicity and widespread application of the host-parasite model used here makes conducting the equivalent analysis a natural mathematical goal, and this is ongoing work. There are several reasons why this may be of interest.

First, to determine whether the inclusion of dispersal is a sufficient structural change to the hare-parasite model to predict realistic dynamics within the empirical ranges of parameter plausibility. Initial investigation suggests parameters within the empirical envelope can generate a PTW (Supplemental Fig 6.1), but whether the properties of these dynamics match observed values requires the necessary mathematical development described above. The system of ODEs are required to quantify wave characteristics such as wave speed, stability (unstable waves typically develop into spatio-temporal chaos, whereas stable waves persist over large domains and long times (Smith et al., 2006)), amplitude and the temporal and spatial periods of the cycles (Sherratt, 2001).

Second, to determine whether dispersal acting on non-cyclic populations is able to generate PTWs. The assumption in population cycle studies is generally that populations exhibit cycles even in the absence of dispersal. However the abundance of a species in space influences the density an individual experiences, thus affecting density dependent processes and, potentially, population stability. PTWs can be occur in models which are non-oscillatory without diffusion such as excitable systems (Sherratt and Smith, 2008). Further, in reaction-diffusion equations, diffusive instabilities can destabilise a uniform spatial state into wave-like patterns (also known as the Turing effect) (Czárán, 1998, Levin, 1976, Turing, 1952). In our simulations, the parameter combination that exhibited PTWs also exhibited a stable limit cycle in the reaction kinetics, but it is unclear whether the spatial extension could destabilize non-oscillatory temporal dynamics. Further analysis of the model would allow us to determine whether space increases the region of parameter space where unstable dynamics occur.

Third, this modelling work coincides with ongoing field research into the dispersal of mountain hares, and it would be useful to have a model within which the quantitative effect of diffusion rates on the dynamics could be explored. A brief consideration of the effect of hare diffusion rates (D_H) on the PTWs shown in Fig 6.5, suggests that slower diffusion increases spatial amplitude and period (Supplemental Fig 6.2), whilst faster diffusion of hares has the opposite effect (Supplemental Fig 6.3). However the dispersal rates we have considered do not yet have any empirical basis. Relating diffusion in the model to real hare movement forces consideration of the spatial scale of interest, something which we have left unspecified in this study to simplify mathematical tractability and analysis. In Scotland, mountain hare habitat is fragmented into upland islands, so it will be important to determine the influence of the size of the spatial domain on the predicted spatio-temporal dynamics of a single population. To consider a spatial scale larger than an upland island would necessitate population structuring and a move away from the PDE model to a model formulation with discrete space. Preliminary data on hare movements suggest mountain hare habitat islands are linked by rare dispersal events which may enhance the likelihood of PTWs on a geographical scale. Sherratt et al. (2000) used coupled oscillator models to show that weak dispersal between local populations could generate PTWs across individually oscillating populations of Kielder forest field voles, while the spatial heterogeneity was lost with strong dispersal. Empirical data on spatially referenced mountain hare abundance in Scotland has previously been used to quantify broad geographical variation in temporal hare population dynamics (Newey et al., 2007b), and warrants revisiting to study spatio-temporal patterns.

Fourth, having the mathematics in place is necessary to make a detailed assessment of wave generation mechanisms (Sherratt, 2001). PTWs must be generated in an ecological population, just as impurities are required for PTWs in oscillatory chemical reactions (Sherratt and Smith, 2008). Reaction-diffusion systems require spatial noise in parameters, invasion of enemy species or certain ‘hostile’ boundary conditions in order to generate PTWs (Sherratt, 2001, Sherratt and Smith, 2008). However these were not aspects of our simulations, suggesting a new mechanism of wave generation.

In contrast, the minimal mathematics required for the implementation of ABC is an attractive feature of this technique to ecologists in general. ABC offers the benefits of standard Bayesian inference without the need to express or calculate parameter likelihoods, although there is a cost in the degree of transparency in the modelling process. Also, these methods are in development and accordingly should be applied with care. For example, as yet there is no systematic method for identifying and assessing the adequacy of summary statistics as replacements for full data sets. Simply using more statistics brings posteriors closer to the full data posterior (Plagnol and Tavaré, 2004), although it may be better to have fewer statistics with clear independence (Kendall et al., 1999). Hickerson et al. (2006) state that summary statistics should clearly show a ‘strong correspondence with parameter values’. Although their meaning is unclear, the summary statistics used here were shown to capture substantial information about parameters in sensitivity analyses (Townsend et al., 2009, Chapter 4). However, despite ongoing issues with ABC and the particularly simple version adopted here, results from our implementation appear robust. A previous parameter sensitivity analysis has been used to guide the direction of changes to parameters with similar conclusions as found here concerning the inadequacy of empirical parameters (Townsend et al., 2009, Chapter 4). Both approaches indicated that parasite effects were critical for stability and mean infection intensities, and showed that the current (non-spatial) hare-parasite model required much stronger parasite effects to be able to generate realistic dynamics.

This chapter began by presenting a situation where a species with cyclic population dynamics has been documented in nature but for which an empirically informed model could not predict realistic dynamics. The aim was to progress by engaging with two constructive criticisms of the model. The first was that model structure was adequate but parameterisation was inadequate. In the case of the mountain hare-parasite system, whilst the parameters can only be loosely quantified using current empirical data, we have a much clearer picture of the time series. By using a method that rejects time series without realistic dynamics we have shown that the necessary parameter values, in particular for parasite effect sizes, are very different from empirical estimates. It is therefore likely that the model is lacking important detail, the second of the constructive criticisms. A recent attempt at modelling an infected population of hares individually included seasonality and leveret biology and found that delayed life history effects could theoretically strengthen the parasite effect on hare recruitment (Chapter 5). In this chapter, the structure of the model was changed by allowing hares and parasites to diffuse across space and we identified a new potential scenario under which cyclic hare dynamics could be explained - periodic travelling waves. However, to determine whether adding space can generate realistic dynamics with parameters that lie closer to empirical estimates, further mathematical development is required. Once this is achieved, we could even compare the ability of different models, such as the spatial host-parasite model and individual-based model, to simulate realistic dynamics by using the approximate Bayes factor within the ABC framework (Toni et al., 2009). In fact the simulation-based method of ABC means the approach can be applied to models of arbitrary biological complexity (Hickerson et al., 2006, Beaumont et al., 2002), which in the future should also include human exploitation of mountain hares.

Table 6.1. Model parameter estimates from empirical data sources and approximate Bayesian inference.

Parameter	*Description*	*Units*	*Lower plausible limit*	*Empirical point estimates*	*Upper plausible limit*	*Most likely estimates using summary statistic vector 1*	*Most likely estimates using summary statistic vector 2*
a	Intrinsic fecundity of hares (in absence of parasites)	year^{-1}	1.1	2.3	3.4	1.7	1.8
α	Parasite-induced hare mortality	year^{-1}	0	0.000008	0.000104	0.000541	0.000310
b	Intrinsic mortality of adult hares (in absence of parasites)	year^{-1}	0.08	0.35	0.61	0.40	0.41
δ	Parasite-induced reduction in hare fecundity	hare parasite^{-1}	0	0.000017	0.000166	0.000175	0.000716
λ	Parasite fecundity	year^{-1}	80	1000	2800	1160	1170
H_0	Transmission inefficiency constant	hare	13500	38200	66800	35900	38200
μ	Adult parasite mortality	year^{-1}	0	0	1.2	0.6	0.6
k	Negative binomial parameter/ parasite dispersion		0.85	1.16 (1 for analyses)	1.47	1	2

Table 6.2. Summary statistics of real and modelled mountain hare and *T. retortaeformis* population dynamics. Model parameterisation from Table 6.1.

Characteristic of dynamics	*Variation in observed values*	*Model parameterisation*		
		Empirical point estimates	*Most likely estimates using summary statistic vector 1*	*Most likely estimates using summary statistic vector 2*
Period (years)	4-15 (range)	6	4	7
Mean hare density (hares km^{-2})	20-200 (range)	65	91	62
Annual mean infection averaged over time series (parasites hare^{-1})	1375-2497 (95% CI)	79129	1793	2618
Amplitude of hare cycles	0.39-1.80 (range)	-	-	1.62
Stability (real part of dominant eigenvalue)	$[0, \infty]$	-0.05	-0.32	0.16

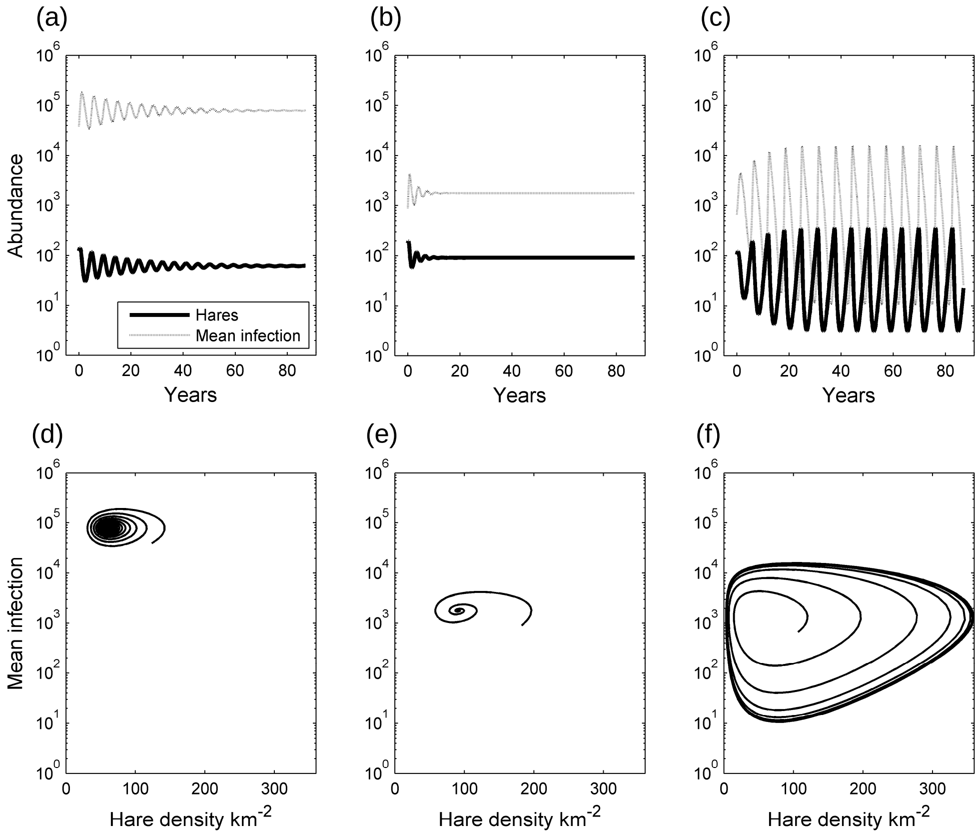


Figure 6.1. Population dynamics of the non-spatial mountain hare - *T. retortaeformis* model parameterised with estimates using empirical data sources and approximate Bayesian inference. Simulated time series (top row) and dynamics in state space (bottom row) of the model parameterised with (a, d) empirical point estimates, (b, e) most likely estimates using summary statistic vector 1 and (c, f) most likely estimates using summary statistic vector 2. For the time series, the solid line represents the hare population size (hares per km^2) whilst the dashed line is mean parasite intensity per hare.

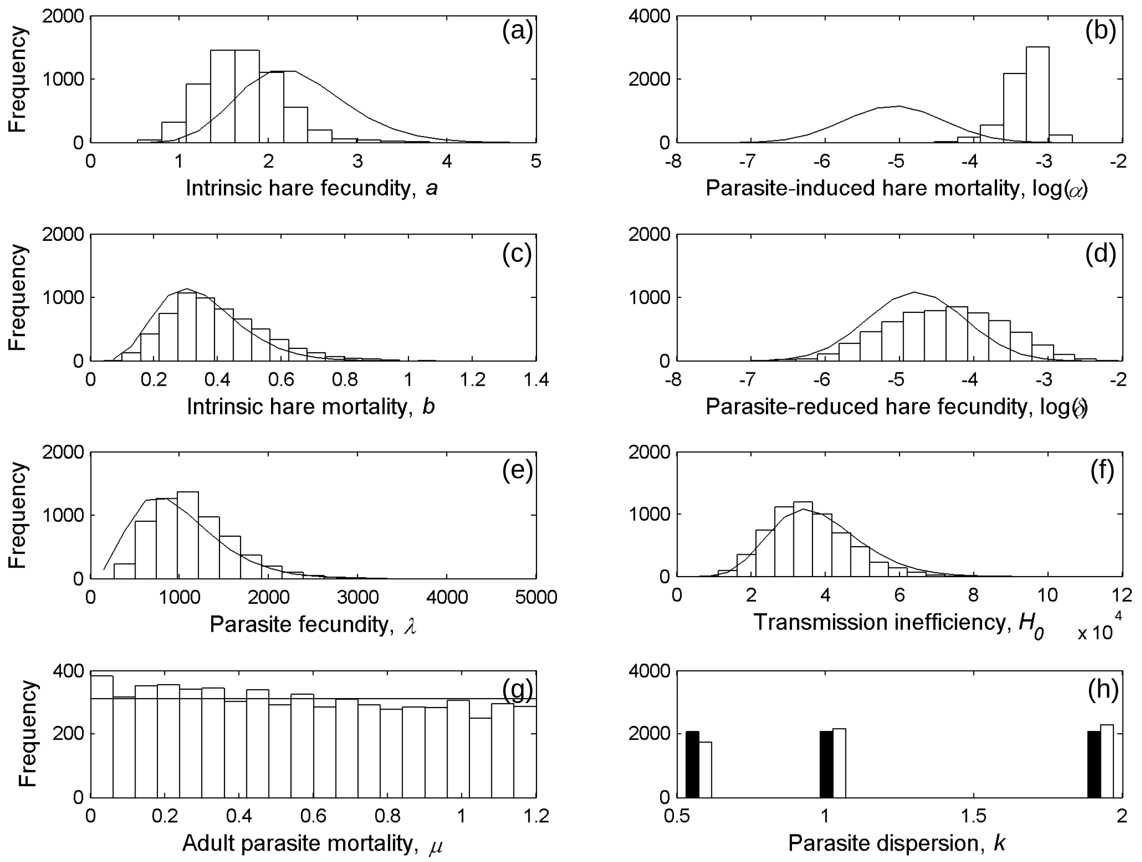


Figure 6.2. Parameter prior distributions based on empirical data and posterior distributions based on ABC using summary statistic vector 1. Parameter combinations sampled from the priors (solid lines) were accepted into posteriors (histograms) if they generated feasible and plausible runs that had a period of hare cycles, hare density and mean parasite intensity that fell within the observed interval (summary statistic vector 1). Amplitude of hare cycles and local stability of the equilibrium point were not included as criteria. (a) Intrinsic hare fecundity, (b) parasite-induced hare mortality (c) intrinsic hare mortality, (d) parasite effect on hare fecundity, (e) parasite fecundity, (f) transmission inefficiency, (g) adult parasite mortality and (h) parasite dispersion among hares. The black bars in (h) represent the prior. Posteriors were based on 6192 simulations. Prior distributions were empirically informed: a~gam(15,0.1533), α~logn(-11.7,1.5), b~gam(7,0.05), δ~logn(-11.0,1.5), λ~gam(4,250), H_0~gam(10,3820), μ~unif(0,1.2) and k could take the value 0.5, 1 or 2 with equal probability.

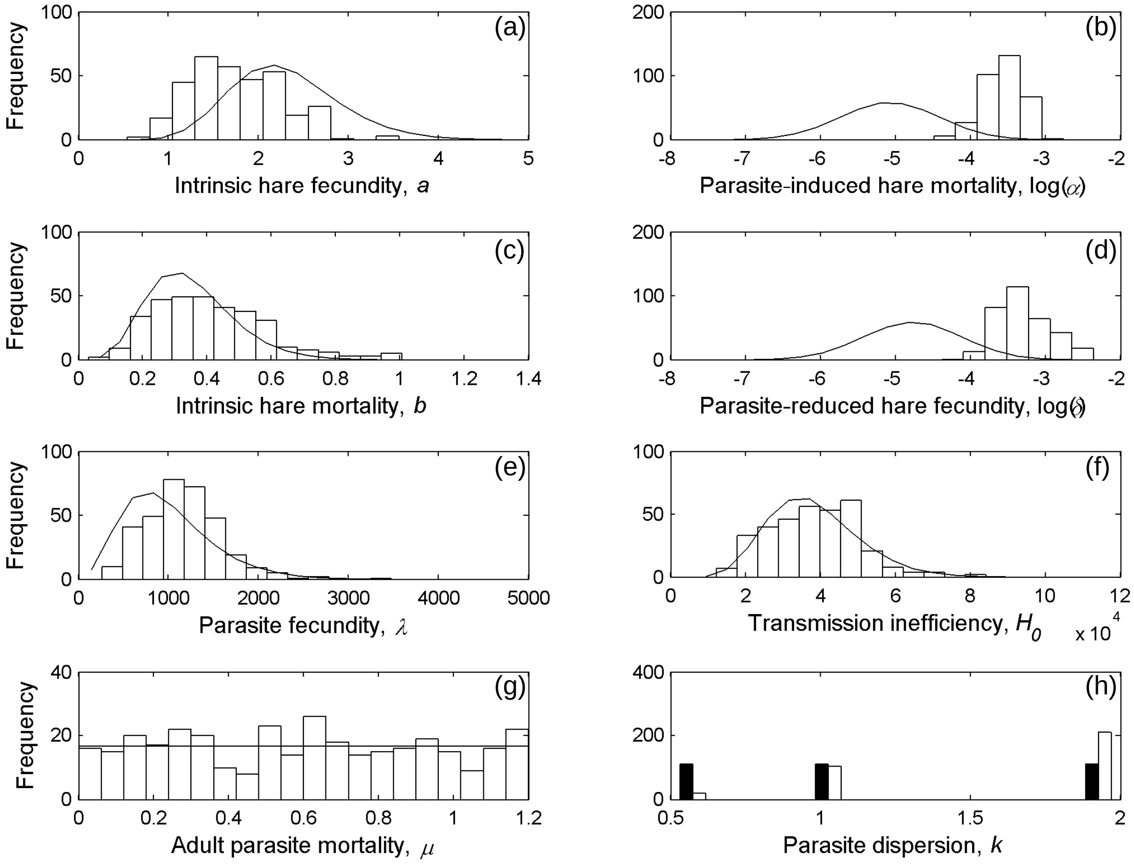


Figure 6.3. Parameter prior distributions based on empirical data and posterior distributions based on ABC using summary statistic vector 2. Parameter combinations sampled from the priors (solid lines) were accepted into posteriors (histograms) if they generated feasible and plausible runs that had an unstable equilibrium point and realistic amplitude, period of hare cycles, mean hare density and annual mean infection (summary statistic vector 2). Posteriors were therefore a subset of those in Fig 6.2 and based on 335 simulations. (a) Intrinsic hare fecundity, (b) parasite-induced hare mortality (c) intrinsic hare mortality, (d) parasite effect on hare fecundity, (e) parasite fecundity, (f) transmission inefficiency, (g) adult parasite mortality and (h) parasite dispersion among hares. The black bars in (h) represent the prior. Priors as in Fig 6.2.

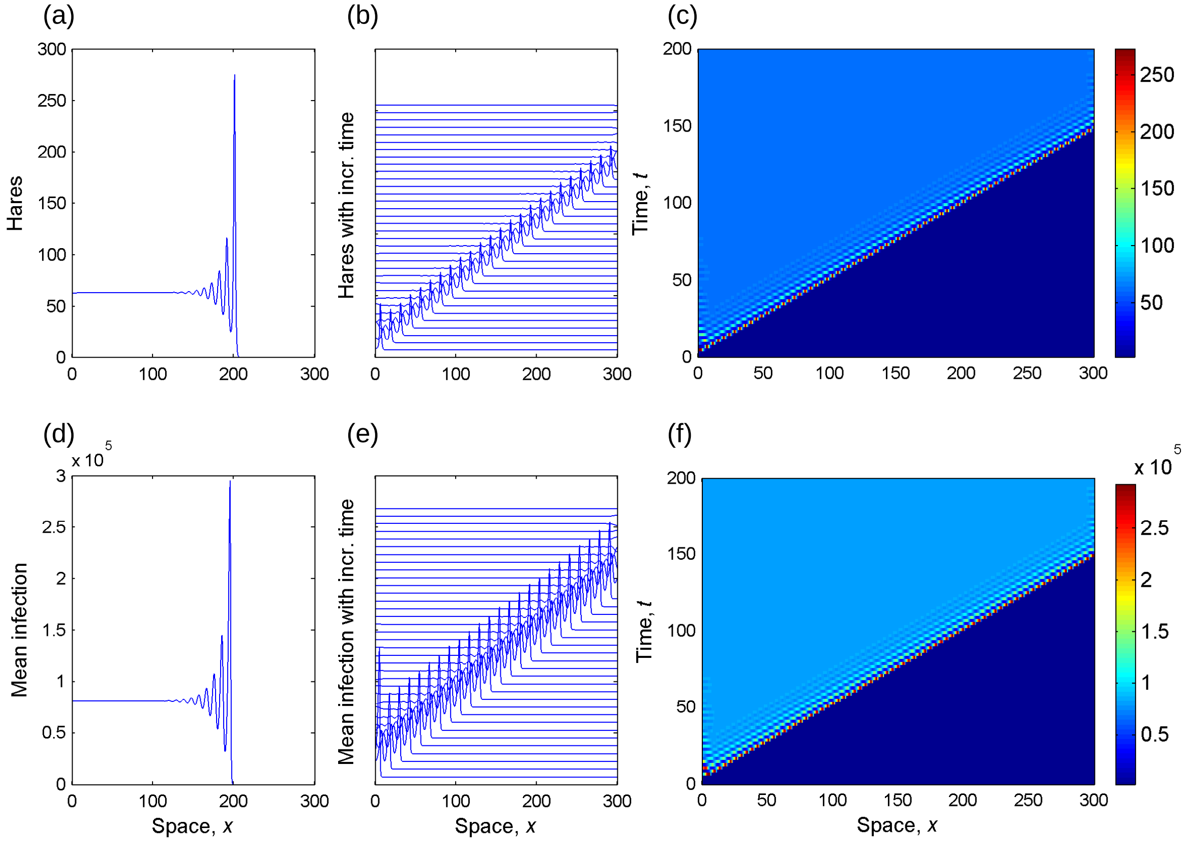


Figure 6.4. The spatial mountain hare - *T. retortaeformis* model parameterised with empirical point estimates generates a wave front of hares and parasites. (a, d) A snapshot (*t*=100) of the wave front as it moves along the one-dimensional spatial domain from left to right. The wave front leaves in its wake equilibrium population levels. In (b, e, c and f) the wave front and succeeding equilibrium dynamics are shown in both time and space, with hare abundances indicated in (c) and mean parasite loads in (f). The dynamics were initialised with exponentially decaying initial conditions (see §2e of main text).

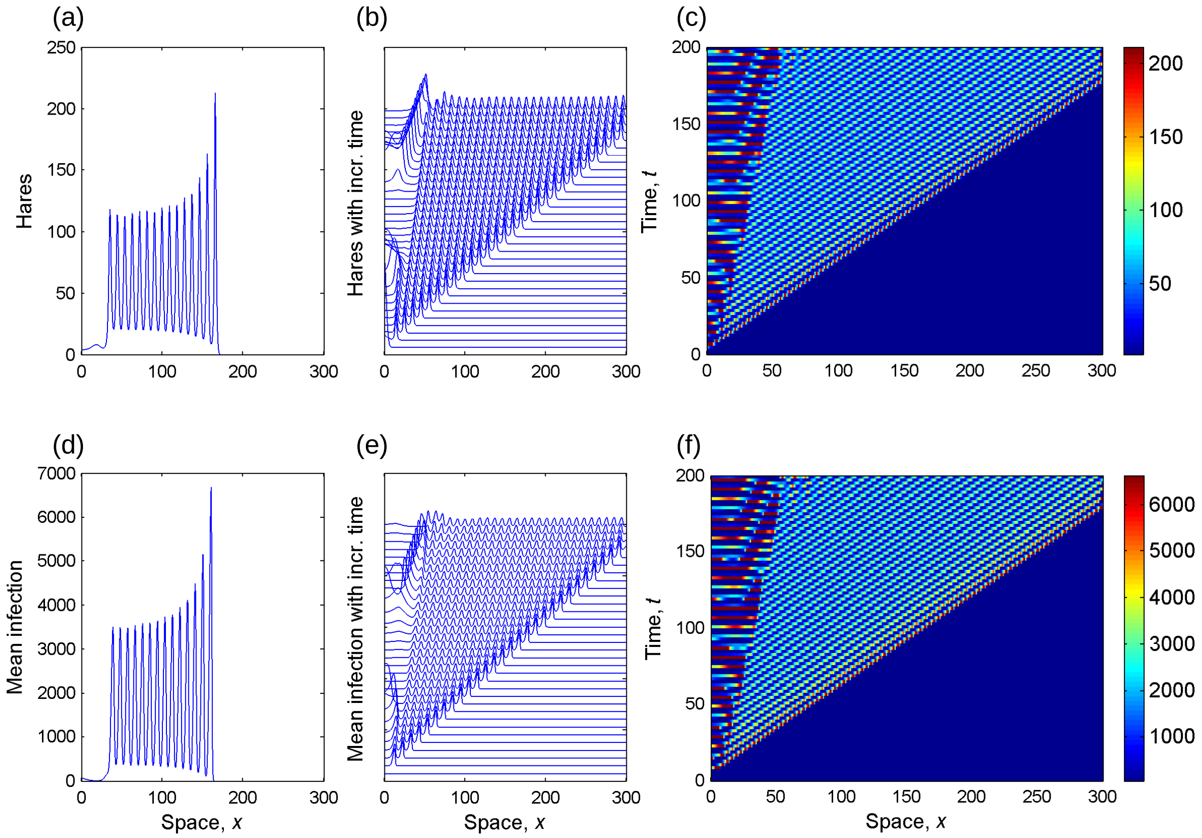


Figure 6.5. Spatio-temporal dynamics of the spatial mountain hare - *T. retortaeformis* model parameterised with the most likely estimates using summary statistic vector 2. A wave front moves across the spatio-temporal domain with succeeding periodic travelling waves (PTWs). These dynamics correspond to cyclic temporal dynamics in the non-spatial model (Fig 6.1c, f). (a, d) A snapshot (*t*=100) of the PTWs as they moves along the one-dimensional spatial domain from initial conditions at the left boundary. In (b, c, e, f) the PTWs are shown in time and space, with hare abundances indicated in (c) and mean infection levels in (f).

Appendix 6.1: Re-analysis of empirical parameter estimates

a, Intrinsic fecundity of hares (in absence of parasite) (year^{-1})

To estimate intrinsic fecundity we used data on individual intensities of *T. retortaeformis* and female annual fecundity measured by counts of the number of ova shed at the end of the breeding season (Newey, Thirgood & Hudson, 2004). Previously intrinsic fecundity was estimated from the intercept of a linear regression of ova shed on parasite intensity (Chapter 4, Appendix 4.1). This failed to account for non-normal errors in the residuals as a result of the count data and therefore we re-estimated intrinsic fecundity using a Poisson regression. To account for males in the population at an assumed ratio of 1:1, the estimate was halved. The point estimate matched the previous estimate of 2.3 young per year, but had a wider 95% CI of 1.1 to 3.4 young per year.

δ, Parasite-induced reduction in hare fecundity (hare parasite^{-1})

Hares which were treated for parasites prior to the breeding season had significantly lower parasite intensities and higher fecundity, measured as counts of ova shed by females (Newey & Thirgood, 2004). In a previous analysis of this data, parasite reduced fecundity was estimated from the slope of a linear regression of parasite intensity vs. ova shed (Chapter 4, Appendix 4.1). We regressed this data using a Poisson regression with an identity link function, which permitted us to obtain the slope of a linear regression but accounting for Poisson distributed errors. The absolute value of the (negative) slope gave an estimate of parasite reduced fecundity, once halved to include males, of 0.000017 hares per parasite. The lower plausible limit was taken as zero and the upper 95% confidence limit was 0.000166 hares per parasite per year.

Appendix 6.2: Numerical scheme for the spatial host-parasite model

(1) Spatial Discretisation

The real interval *[0,L]* is divided into N intervals of length dx and we use the standard notation $P_j(t)$ as an approximation of $P(jdx,t)$ for $j=0,1,..,N$. Similarly defined is $H_j(t)$.

(2) Treatment of the hare equation

The PDE is of a standard reaction-diffusion type and is discretised using a second order accurate central difference scheme,

$$\frac{\partial H}{\partial t} = D_H \frac{H_{j+1} - 2H_j + H_{j-1}}{dx^2} - aP - bH + aH\left(\frac{kH}{\delta P + kH}\right)^k, \quad j = 0,1,...,N.$$

In order to satisfy the prescribed no-flux boundary conditions and to maintain second order accuracy, we set the fictitious values $H_{-1}=H_1$ and $H_{N+1}=H_{N-1}$.

(3) Treatment of the parasite equation

The parasite equation has a reaction term and a convection term. A first order upwind semidiscretisation could be used and that would maintain positivity but could also introduce a large amount of numerical diffusion, unless the spatial discretisation is sufficiently fine. On the other hand, high order spatial discretisations often lead to oscillations in solutions which may break the positivity requirement when the solutions values are small. Instead we use *flux limiters*, which we now describe.

We denote the velocity of the convective flux at grid point j by

$$w_j = \frac{D_H}{H}\frac{\partial H}{dx}, \quad j = 0,1,...,N.$$

We define the derivative of H at grid point j using central differences as standard. Let f_j denote the semidiscretised convective flux at grid point j, i.e.

$$f_j = w_j P_j, \quad j = 0,1,...,N.$$

and we introduce the semidiscretised general flux function $F_{j+1/2}$ which is a function of the fluxes *f* surrounding gird point *j*. Using a central difference approximation for the spatial derivative, the convection term can be approximated by the expression

$$\frac{1}{dx}\left(F_{j+1/2} - F_{j-1/2}\right), \quad j = 0,1,\ldots,N.$$

The semidiscretisation of the parasite equation then yields

$$\frac{\partial P}{\partial t} = \frac{1}{dx}\left(F_{j+1/2} - F_{j-1/2}\right) + P\left[\frac{\lambda H}{H_0 + H} - \mu - \alpha - b - \frac{\alpha P}{H}\left(\frac{k+1}{k}\right)\right], \quad j = 0,1,\ldots,N.$$

We set $F_{-1/2} = F_{N+1/2} = 0$ to ensure that the no-flux boundary conditions are satisfied. It no only remains to choose the flux functions $F_{j+1/2}$. To this end, we define the function

$$r_j = \frac{f_{j+1} - f_j + \varepsilon}{f_j - f_{j-1} + \varepsilon}, \quad j = 0,1,\ldots,N,$$

which encapsulates the ratio of the gradients of fluxes about grid point *j*. Note that the quantity ε is a small number that ensures that r_j is well defined even when the fluxes surrounding gird point *j* are identical. For simplicity, we set $\varepsilon=10^{-30}$. Consistent with the boundary conditions we set $f_{-1} = f_{N+1} = 0$. Finally we introduce a *limiter function* $\phi(r)$ and define the general flux function for a non-negative velocity as

$$F_{j+1/2} = f_j + \frac{1}{2}\phi(r_j)(f_j - f_{j-1}), \quad j = 0,1,\ldots,N-1.$$

However, for a negative velocity $w_j<0$ we reflect all the indices about $j+1/2$ to obtain

$$F_{j+1/2} = f_{j+1} + \frac{1}{2}\phi\left(\frac{1}{r_{j+1}}\right)(f_{j+1} - f_{j+1}), \quad j = 0,1,\ldots,N-1.$$

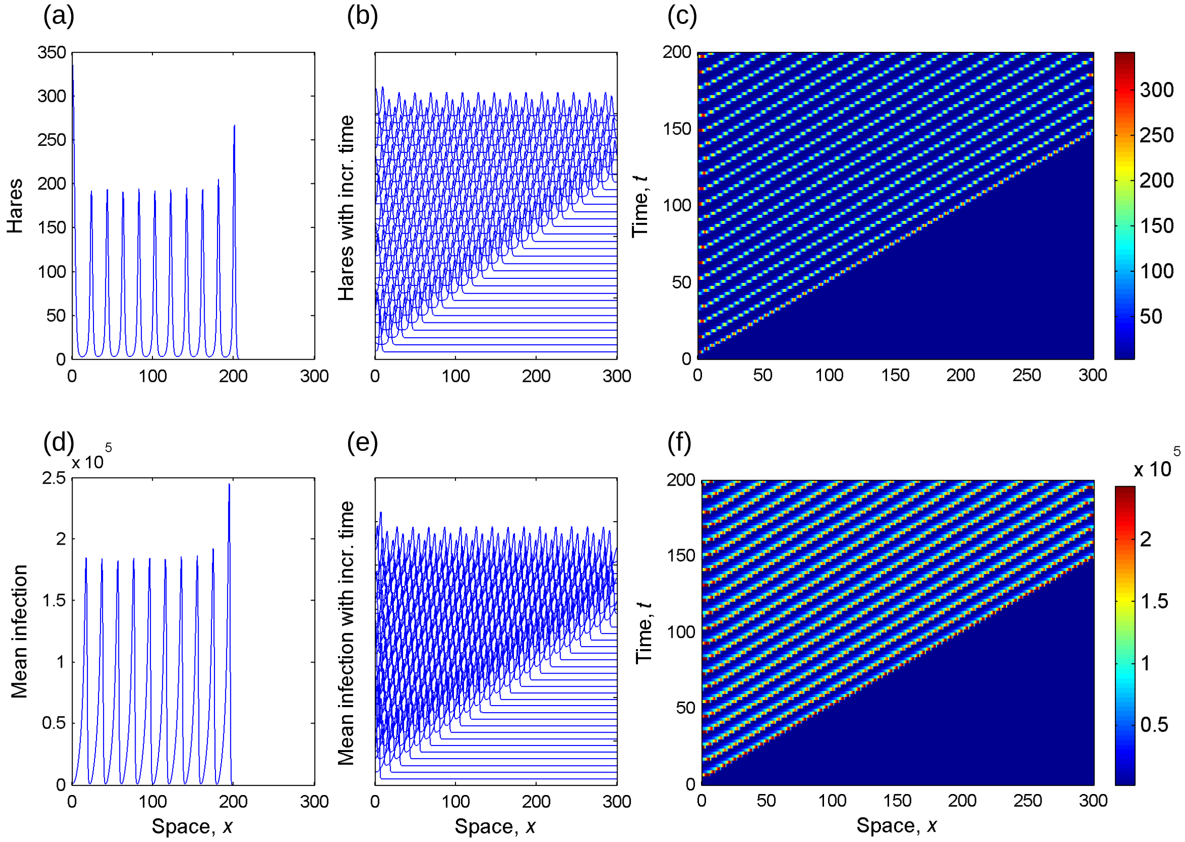
We choose a van Leer’s flux limiter function, namely

$$\phi(r) = \frac{r + |r|}{1 + |r|}.$$

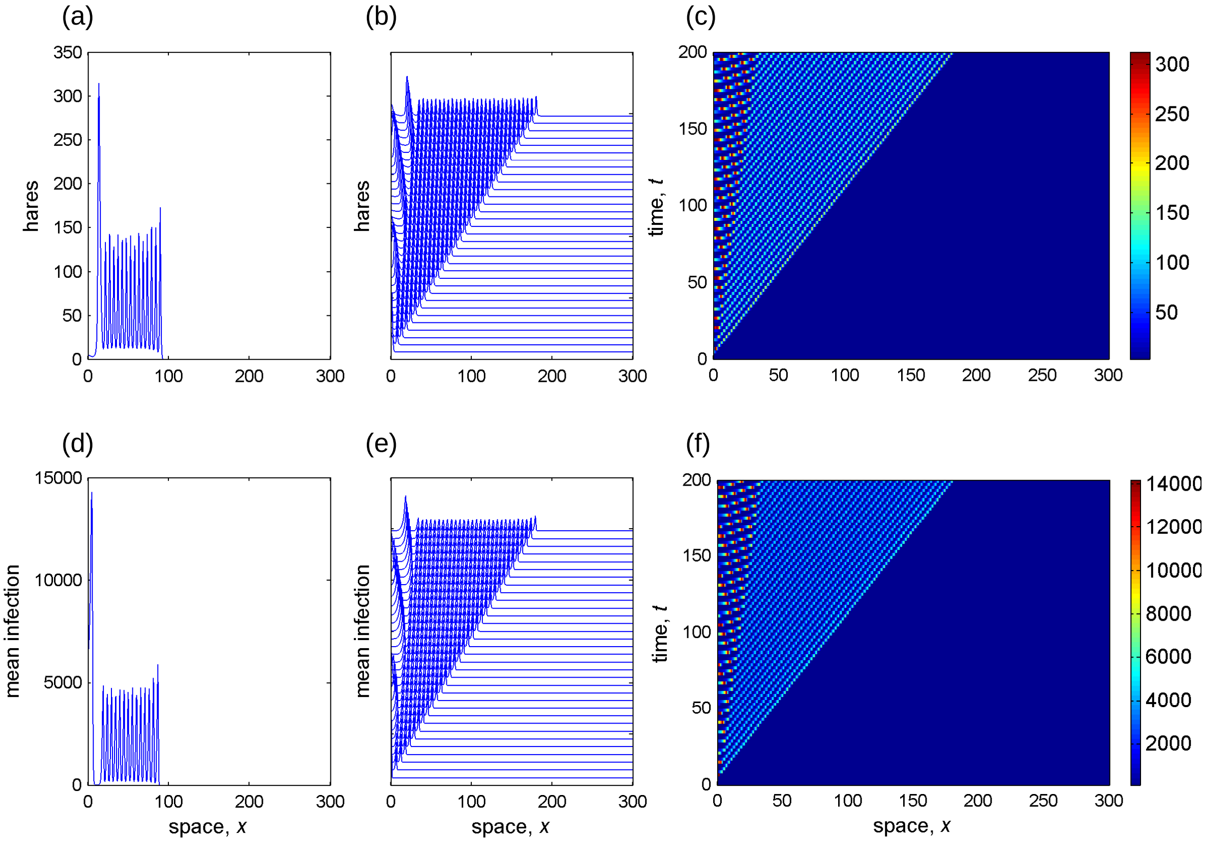
Note that $\phi(r) = 0$ would be equivalent to a first-order upwind discretisation.

(4) Numerical integration of the ODE system

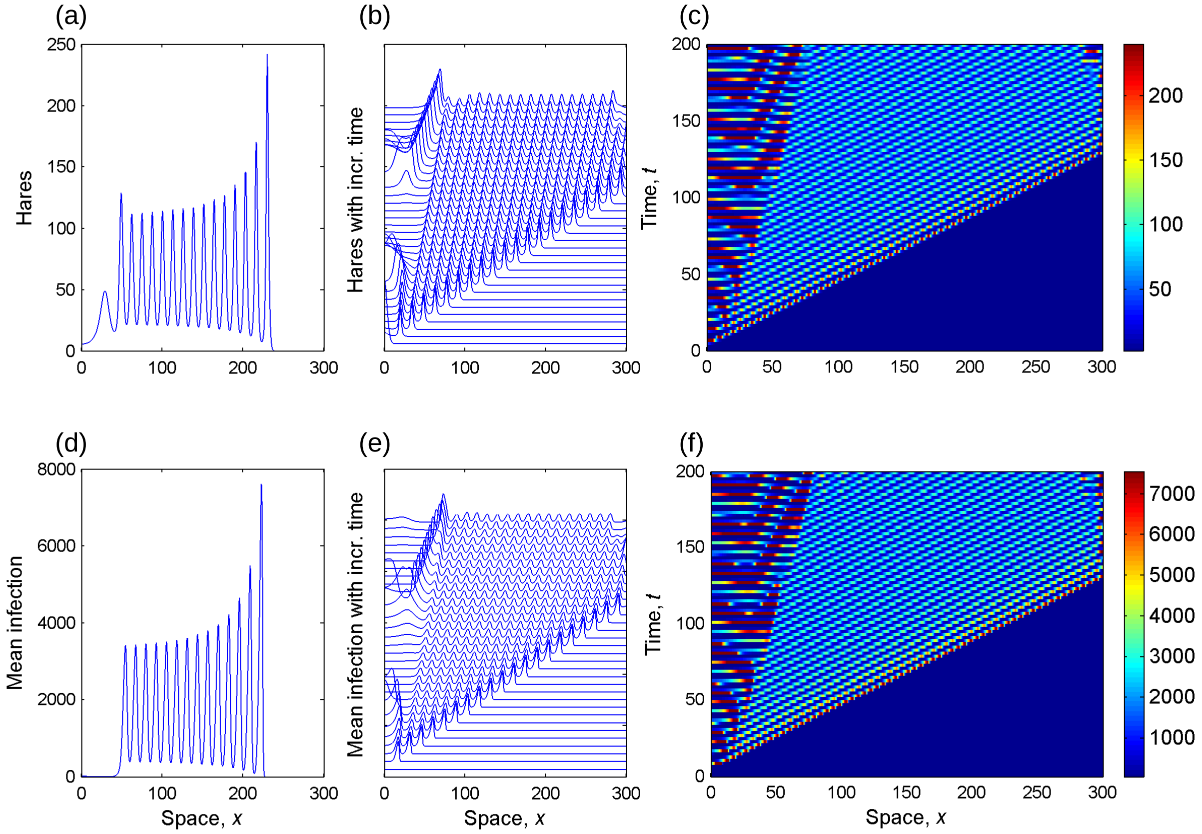
The spatial discretisation described above reduces the PDE system to a system of ODES which we solve using a fourth order Runge-Kutta method.



Supplemental Figure 6.1. Periodic travelling waves (PTWs) generated within the empirical parameter plausible envelope. Parameters were empirical point estimates, as for Fig 6.4, except the parasite-reduced hare fecundity δ was increased to the empirically determined upper plausible limit (Table 6.2). (a, d) A snapshot (t=100) of the PTWs. (b, c, e, f) The PTWs in time and space.



Supplemental Figure 6.2. Slowing hare diffusion rate appears increases the spatial period and amplitude of periodic travelling waves (PTWs). Parameters as in Fig 6.5 except diffusion rate D_H was reduced to 0.1. (a, d) A snapshot (*t*=100) of the PTWs. (b, c, e, f) The PTWs in time and space.



Supplemental Figure 6.3. Speeding up hare diffusion rate decreases the spatial period and amplitude of periodic travelling waves (PTWs). Parameters as in Fig 6.5 except diffusion rate D_H was increased to 1. (a, d) A snapshot (t=100) of the PTWs. (b, c, e, f) The PTWs in time and space.

Chapter 7. General discussion

Ecologists would like to understand how complexity persists in nature. In this thesis I have taken two fundamentally different routes to study ecosystem stability of model ecosystems: classical community ecology and classical population ecology. One of the major unresolved issues in community ecology is the relationship between ecosystem stability and complexity. Lacking a resolution to this fundamental question leaves community ecology in a poor position to argue for the conservation of natural diversity for the benefit of all species, including humans. Below I discuss how my results in Chapters 2 and 3 contribute to this debate over stability - complexity relationships and its resolution. In classical population ecology, a major unresolved issue is the cause of non-equilibrium population dynamics. In Chapters 4 to 6 I use models to study the drivers of cyclic dynamics in Scottish populations of mountain hares, for the first time in this system. After summarising the findings I discuss whether a model has been identified which can be considered the right balance between abstraction and relevant detail for this system. During the discussion I deliberate on the utility of the work presented in this thesis, as this aspect has been of increasing importance to me during the course of my Ph.D candidacy.

The stability - complexity debate

In 1958 Charles Elton made the conjecture that the stability of an ecological system was coupled to its complexity (Elton, 1958). The expression in mathematical terms forced clarity and precision upon the conjecture, and led to definitions of stability and complexity. The earliest and simplest model systems were randomly constructed and exhibited a negative association between stability and complexity (May, 1971, Gardner and Ashby, 1970). This finding sparked the stability - complexity debate and initiated the search for organising principles that enhanced stability in real ecosystems (Lawlor, 1978).

Since the debate began, the negative relationship has been inverted in theoretical studies under numerous conditions. In this thesis, I identify further novel conditions for positive stability - complexity relationships: resilience increases with interactivity if there is high variance in the abundance distribution or if the abundance distribution is even but there is skew symmetry in the community (Jacobian) matrix (Chapter 2); the probability of permanence and local stability increases either with variance in the interspecific interaction strengths, or with the mean if the variance is held constant (Chapter 3). In fact it seems that one does not have to venture too far from the original randomly constructed model ecosystems to find conditions under which stability can increase with complexity. This leads to the question of at what point do such ‘inversion conditions’ constitute a resolution of the stability - complexity debate?

First, ‘inversion conditions’ must be supported by real food web patterns. Research presented here (Chapter 2 and 3) and in other studies (Jansen and Kokkoris, 2003, Kokkoris et al., 2002, Haydon, 1994, Haydon, 2000) has shown that the statistical properties (i.e. mean and variance) of the distribution of interactions within and between species have strong effects on the stability of model ecosystems. These can be related to real food web patterns: variance in the interspecific interaction strengths to the common community property of skew towards weak links (Berlow, 1999, Paine, 1992, Bascompte et al., 2006, De Ruiter et al., 1995), and variance in the intraspecific interactions to the ubiquitous unevenness of the relative abundance distribution (McGill et al., 2007). Skew symmetry and increasing mean with constant variance are inversion conditions which are more difficult to link to documented real patterns.

Second, patterns must be reflected in real food web structure. Numerous studies have revealed that community and interaction matrices reflecting the structure of real communities have a special internal configuration which, when randomised, has detrimental effects on stability (Emmerson and Raffaelli, 2004, Yodzis, 1981, De Ruiter et al., 1995). Some promising structures which confer stability have been identified as common features of real food webs, such as slow and fast energy channels (McCann et al., 1998, Rooney et al., 2006) and low biomass ratios in long trophic loops (Neutel et al., 2002, Neutel et al., 2007). In the webs studied by Neutel et al. (2002), interaction strengths were organised in trophic loops such that weak links tended to aggregate in longer loops. This patterning made their food webs much more stable than randomised counterparts and explains three common observations in real food webs: predators tend to feed on several types of prey; there are many weak and few strong interactions between species (Berlow, 1999, Paine, 1992, Bascompte et al., 2006, De Ruiter et al., 1995); and biomass generally decreases with trophic level (Elton, 1927).

The work of Neutel et al. (2002) is significant because it demonstrates a link between structure, the uneven distribution of abundance, the uneven distribution of interactions and stability in real food webs: a rare achievement. An interesting aspect of their study was the way in which they determined the relative stability of real and randomised Jacobian matrices. Rather than assign all the elements of the Jacobian matrix and analyse local stability of the full system, they filled the off-diagonal elements and then determined how much intraspecific interaction (determined by the size of diagonal elements) was required for the matrix to become locally stable. The patterning Neutel et al. (2002) describe required only a relatively small degree of intraspecific stabilisation. While their study focused on patterns in off-diagonal elements which (pretty much) guarantee the local stability of real matrices, I have studied theory of how patterns in the diagonal elements affect the relative stability of stable matrices (Chapter 2), and show that high variance in the diagonal elements can allow stability to increase with food web interactivity. Since intraspecific interaction strengths are (in part) determined by species abundances, the off-diagonal configuration of Neutel et al's. (2002) Jacobians combined with the abundance pyramid reflected in the diagonal elements is a plausible architecture that allows complex food webs to persist and confers stability as their interactivity increases.

Nevertheless, revealing the pattern is not the same as understanding the mechanism. A third requirement for the resolution of the stability - complexity debate is mechanistic explanation of the underlying processes which generate observed patterns (and their statistical properties) in real webs. These are much more complicated to show than community patterns and structure, which is why they are rarely uncovered in empirical studies (Ives and Carpenter, 2007). The majority of theoretical studies on stability - complexity relationships use the community (Jacobian) matrix to make *associations* between introduced changes or patterning in the matrix to changes in the eigenvalues of the matrix. The Geršgorin disc theory I adopt in Chapter 2 has assisted me a great deal in visualising how the properties of the matrix determine the distribution of eigenvalues. However, I am yet to grasp how the translation of ecological order into eigenvalues occurs. A mechanism has been proposed for models of special and small trophic structures where the community matrix was not used. McCann et al. (1998) used nonlinear models to study non-equilibrium dynamics and proposed that weak interactions stabilise community dynamics by generating negative covariances that dampen strong destabilising consumer-resource interactions (McCann, 2000). Polis (1998) argues that research like that of McCann et al. (1998) is evidence that ecologists are progressing well in providing the "theoretical basis for the paradigm shift that is now taking over ecology". The paradigm shift he refers to is the one from 'complexity is destabilising' to a 'cohesive role of complexity'. I consider the work of McCann et al. (1998), along with that of Neutel and colleagues (Neutel et al., 2002, Neutel et al., 2007) to be about the closest theoretical community ecologists have come to resolving the stability - complexity debate.

While there is growing evidence that the stability - complexity debate is progressing towards a resolution, community ecology has become increasingly subject to major criticism. Recently there has been considerable debate over whether community ecology is a weak science that should be abandoned because it is so complex and contingent that it can only very occasionally lead to generalisation (Lawton, 1999, Simberloff, 2004). A more long-standing criticism is the heavy reliance on the assumption that communities are at equilibrium and assessment of stability is often made only close to the equilibrium point. Judson (1994) sums up the argument that, with an equilibrium approach, generality is a holy grail:

> “If even the simplest nonlinear equations can often give rise to chaotic and therefore intrinsically unpredictable behaviours (May, 1974), then the hope of deriving simple, general laws for systems in which nonlinearity is the norm must be illusory”

However we can circumvent the understanding of complicated quantitative dynamics with a global property called permanence, at least in the restricted, though widely used Volterra formulation of the Lotka-Volterra (LV) equations. In Chapter 3 I find that the probabilities of local stability and permanence correlate closely with changing ecosystem complexity suggesting that local stability is a better measure of persistence than previously thought. We should therefore have greater confidence in qualitative results from local stability analysis, such as stabilising food web structure of Neutel et al. (2002, 2007) and inversion of the stability - complexity relationship by skewed species abundance distributions (Chapter 2). However, the question which will always follow from results on such grossly simple equations is whether the ball game is completely different when realistic non-linearities (e.g. functional responses other than type I) are incorporated. I was relieved to find the close correlation between local stability and permanence (otherwise I would have had cause to question much of theoretical ecology) and may find myself relieved again.

Although much progress has been made towards a resolution of the stability - complexity debate, the complexity of the problem continues to divide ecologists. A recent review of stability-diversity (species richness) relationships by Ives and carpenter (2007) sums up some of the arguments. First, in simple theoretical models, different measures of stability can show opposite stability-diversity relationships in response to the same perturbation. Moreover, not all empirical studies have found positive stability-diversity relationships – of 59 reported diversity-stability relationships from 52 studies, 14% found negative associations and 17% found no or ambiguous relationships. Ives and Carpenter (2007) conclude bleakly that they do not find, and we cannot expect, a resolution:

> “…the absence of a resolution reflects the complexity of the problem. Much of the complexity derives from the multiplicity of diversity-stability relationships, depending on the definitions of diversity and stability and on the context in which an ecosystem is perturbed. We cannot expect a general conclusion about the diversity-stability relationship”.

The problem is complicated further by the fact that ecological complexity forms just a fraction of many forces that govern stability in ecosystems, others include species composition, productivity, disturbance regimes, climate and edaphic factors (Tilman, 1999). The future looks even more nebulous when we start to worry how to couple dynamics of natural systems with human socio-economic systems (Liu et al., 2007).

What is also concerning is how rifts in opinion impact the perception of community ecologists to policy makers and the public. In 1999, the Ecological Society of America released a pamphlet on the importance of biodiversity to ecosystem functioning (Naeem et al., 1999). This was called a “propaganda document” by Hutson and other sceptics of ecosystem experiments of some of the authors of the pamphlet (Tilman, Lawton, Naeem and others), with one sceptic (Wardle) claiming “the results of these studies provide just the answers that many environmentalists want to hear” (Kaiser, 2000). Of course criticism is justified if the science is not balanced, but the rift was not about whether a large pool of species is required for ecosystem functioning, but rather how this works – by lots of species increasing the recruitment of a few key component species, or by the facilitation of community properties (Loreau et al., 2001). On a positive note, it is sometimes said that debates and rifts can be seen as a sign of health in a young field in which ideas are growing and paradigms challenged. On a less positive note, I am concerned that ecologists are not making a strong case for Elton’s concept of a “wise principle of co-existence between man and nature” in the protection of diversity for the promotion of ecological stability. Polis (1998) reminds us of what would be possible:

> “The understanding that complexity is vital to the integrity and stability of natural systems allows ecologists to argue, more coherently, why we must preserve the diverse elements and species that coexist in a healthy, sustainable and well-functioning ecological community. Indeed, as we enter what E.O. Wilson calls the ‘century of the environment’, one crucial function of ecology is to provide an unbiased, scientific basis on which political and social decisions can be made about how best to treat our natural environment”.

From my generation’s perspective, Elton’s warnings of the danger in the simplification by humans and human domination of ecosystems are playing out. Given that the stability - complexity debate is neither sufficiently precisely posed or clearly resolved enough to form the basis for policy development, the argument for the conservation of natural diversity for the benefit of all species must be coming from elsewhere. The alternative argument is fundamentally the same as Elton’s but couched in a different language: human well-being depends on ecosystem services which in turn depend on biodiversity (Millennium Ecosystem Assessment, 2005, Knee, 2008, Daily, 1997). The value of ecosystem services has been illustrated primarily through their loss or disturbance and through efforts to substitute them with technology (Daily, 1997).

The challenge ahead is to generate results that are useful to society. Vitousek et al. (1997) give a dramatic statistical summary of the extent of current human domination of the Earth, and Lubchenco (1998) expresses how these changes "are so different in magnitude, scale and kind from past changes that even our best records and models offer little guidance concerning the scale or even the character of likely responses to these challenges". Lubchenco (1998) calls for a 'new social contract for science' that will require much of science to refocus its energies and talents to produce results that are useful to society. In the UK, ecologists must form a stronger link to policy in order to face the major national issues of environmental concern, which include agriculture, marine fisheries, climate change, ecosystem function and land management (Sutherland et al., 2006).

What approach to studying ecology is best for facing these challenges? Policy makers want answers to general questions (Sutherland et al., 2006), but generalisation is not a strength of community ecology (Lawton, 1999, Simberloff, 2004). The next section discusses Chapters 4-6 in which a population ecology approach was taken to study the stability of interacting species. The transition from simple, strategic models of community ecology was necessary to be able to include the necessary level of detail in the interactions between two populations. However, while a population ecology approach offers empirical tractability, it has a poor track record in natural resource management: the global fisheries crisis is testament enough that future species management outside of the ecosystem context is out of the question. We must study real communities but we appear largely unable to do so. Perhaps one direction forward may be to find a middle ground between the two disciplines of population and community ecology.

Periodic fluctuations in the numbers of mountain hares

The cyclic population dynamics of mountain hares in Scotland have recently gained attention because field experiments had identified a possible causal factor for the cycles: a highly prevalent nematode parasite that reduced the fecundity of female hares (Newey and Thirgood, 2004, Newey et al., 2004). The work presented in Chapters 4-6 constitute a first attempt at using modelling techniques to explore the question: 'Can parasites drive population cycles in mountain hares?' This question forms the title of Chapter 4, in which I tested whether realistic hare stable limit cycles could be generated with a simple strategic ODE model parameterised with the best available empirical data. I found that parasitism could not account for hare cycles. This verdict left three options: either the parameterisation was inadequate, there were missing important biological details or simply that parasites did not drive host cycles. The remaining chapters focused on incorporating previously ignored ecological complexity that may strongly influence the dynamics. An individual based model was developed to envelop a lot of this complexity, and found that maternal effects could be weakly destabilising (increasing the propensity to cycle, but not by very much) and that stability was very sensitive to the parasite transmission mechanism (Chapter 5). Another important ‘detail’ missing from the strategic models of classical population dynamics was space. In collaboration with Steve Webb, a mathematics lecturer at the University of Strathclyde, we extended the non-spatial model and found some intriguing spatiotemporal patterns, although it is not clear as yet whether it increases the likelihood of periodic behaviours in this system (Chapter 6) and further analysis of the spatial model that is not presented here suggests it does not. It must be concluded, therefore, that the question ‘can parasites drive mountain hare population cycles?’ has not yet been answered. The following discussion touches upon some of the possible reasons for this and evaluates whether the process has been useful nonetheless.

In order to understand, predict and manage nature, Levins (1966) asserts that ideally we would like our models to maximise generality, realism and precision, although this is impossible and sacrifices have to be made. In the study of stability - complexity relationships in communities of interacting species, I sacrificed precision for the sake of generality. This was appropriate because my interests lay purely in qualitative results and I could only obtain model parameters from fabricated probability distributions. Whether the models could be considered realistic depends on which of Lotka’s or Volterra’s perspective on the LV equations was adopted. In order to model the quantitative population dynamics of mountain hares, generality had to be sacrificed for precision. This was appropriate because my questions were quantitative and I had access to real data from which to estimate model parameters. While realism was arguably achieved in the IBM model, I think that in order to answer the question at hand maximising realism in this system is not the appropriate approach. Rather, a different strategy is required - to find the right balance between abstraction and relevant detail (Berlow et al., 2004).

The usual technique for analysing the behaviour of generic models is to increase the complexity of the simplest plausible model in small increments and to examine the significance of that change in stepwise fashion. In contrast I have swung between the two extremes, from the generic ODE model to the detail-rich IBM. Another way of expressing my approach was that it started with Einstein’s dictum “models should be as simple as possible, but not more so” and in one step reached almost all the way to "the best material model of a cat is another, or preferably the same, cat" (Rosenblueth and Wiener, 1945). As an attempt at justification therefore, the IBM route was in part taken because my supervisors encouraged me to gain experience of developing a highly complex model, and the process did make me appreciate the relative ease of managing and interpreting a simple analytical model. Having gained this experience my future approach to modelling will be more incremental.

To consider the utility of the modelling work in aiding understanding of mountain hare ecology I recently asked the empirical biologist who instigated our collaboration, Scott Newey, to describe his perception of the impact of the modelling component:

> “The initial impetus for the Anderson & May hare-parasite modelling work was a question from a colleague about whether the increased fecundity observed in parasite reduced females was sufficient to drive cycles, especially given the small effect on survival. This question was subsequently asked a number of times when ever I gave a talk on that work. This pre-dated the time-series work, so we did not know any of the detail about hare cycles. The impact of your modelling work has to been to show that given our current understanding parasites alone are not sufficient to drive cycles that are consistent with the nature of cycles observed in time-series of mountain hare harvest data, has highlighted that other mechanisms are likely involved, and our paucity of knowledge on the parasite side of the story.
>
> The initial stimulus for the IBM work came more from a hypothesis testing point of view. In that a number of colleagues argued that the most, or the only, important parasite mediated affects may be indirect and act through influencing the timing of breeding and quality of young. A secondary question was whether we could assess how important the timing and productivity of the first litter was to overall population dynamics. Here I think the important finding was that delayed effects have a destabilising effect, reducing the "needed" parasite impact, but in themselves only weakly destabilising. Again the IBM highlights areas of ignorance and areas of future work, and the finding that the transmission mechanism is potentially so critical to the model behaviour is also really interesting (though how on earth you can ever research this in the field is some what perplexing). Again the IBM suggests that parasites are not the whole story.
>
> Overall the models suggest that parasites likely play a role in destabilising hare populations but are not the whole story, and that there is a need to better understand the parasitology and prenatal effects of parasites.”

In conclusion, I think that the primary aim of future modelling work on mountain hares should be to find a model that is considered by theoreticians and empiricists alike to be ‘the right balance between abstraction and relevant detail’. During the review of the PRSB paper one of the reviewers Kyrre Kausrud, a PhD student working on lemming cycles at the Centre for Ecological and Evolutionary Synthesis (CEES) at the University of Oslo, suggested some intermediate dynamical models midway in complexity between the ODEs and IBM. Preliminary investigation of these models indicated that adding complexity to the ODE model meant parameters did not need to be stretched as far from their current empirical estimates to obtain the observed hare dynamics. If an appropriately balanced abstraction-detail model was identified it could be a tool for investigating the major pressures on the persistence of individual mountain hare populations in Scotland, including large-scale culls for tick control (Kinrade et al., 2008), changes in upland ecosystem management practices (Kerlin, 2008) and climate change (Anderson et al., 2009). We may well need to increase the dimensionality of the model to capture the fluctuations of mountain hares or to study the impact of the pressures hares are facing. This would require transition from a single species population focus towards a more community-based perspective, and once again into the briar patch between population and community ecology.

Cited literature

Albon, S. D., Stien, A., Irvine, R. J., Langvatn, R., Ropstad, E. & Halvorsen, O. (2002) The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269**, (1500) 1625-1632.

Allander, K. & Bennett, G. F. (1995) Retardation of breeding onset in great tits (*Parus major*) by blood parasites. *Functional Ecology,* **9**, (4) 677-682.

Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M. & Rohani, P. (2006) Seasonality and the dynamics of infectious diseases. *Ecology Letters,* **9**, (4) 467-484.

Anderson, B. J., Akcakaya, H. R., Araujo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W. & Brook, B. W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society of London. Series B, Biological Sciences,* **276**, (1661) 1415-1420.

Anderson, H. M., Hutson, V. & Law, R. (1992) On the conditions for permanence of species in ecological communities. *American Naturalist,* **139**, (3) 663-668.

Anderson, R. M. & May, R. M. (1978) Regulation and stability of host-parasite population interactions. 1. Regulatory processes. *Journal of Animal Ecology,* **47**, (1) 219-247.

Angerbjörn, A. & Flux, J. E. C. (1995) *Lepus timidus*. *Mammalian Species,* **495**, 1-11.

Arneberg, P., Skorping, A., Grenfell, B. & Read, A. F. (1998) Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **265**, (1403) 1283-1289.

Bascompte, J., Jordano, P. & Olesen, J. M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science,* **312**, (5772) 431-433.

Bascompte, J. & Sole, R. V. (1995) Rethinking complexity - modeling spatiotemporal dynamics in ecology. *Trends in Ecology & Evolution,* **10**, (9) 361-366.

Battersby, J. (2005) UK Mammals: Species Status and Population Trends. First Report by the Tracking Mammals Partnership. JNCC/Tracking Mammals Partnership, Peterborough.

Beaumont, M. A., Zhang, W. Y. & Balding, D. J. (2002) Approximate Bayesian computation in population genetics. *Genetics,* **162**, (4) 2025-2035.

Beckerman, A., Benton, T. G., Ranta, E., Kaitala, V. & Lundberg, P. (2002) Population dynamic consequences of delayed life-history effects. *Trends in Ecology & Evolution,* **17**, (6) 263-269.

Benton, T. G., Ranta, E., Kaitala, V. & Beckerman, A. P. (2001) Maternal effects and the stability of population dynamics in noisy environments. *Journal of Animal Ecology,* **70**, (4) 590-599.

Berlow, E. L. (1999) Strong effects of weak interactions in ecological communities. *Nature,* **398**, (6725) 330-334.

Berlow, E. L., Neutel, A. M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Jones, J. I., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M. & Petchey, O. (2004) Interaction strengths in food webs: issues and opportunities. *Journal Of Animal Ecology,* **73**, (3) 585-598.

Berryman, A. A. (2002) *Population Cycles; The Case for Trophic Interactions,* Oxford University Press, New York.

Bjornstad, O. N. & Grenfell, B. T. (2001) Noisy clockwork: Time series analysis of population fluctuations in animals. *Science,* **293**, (5530) 638-643.

Bjornstad, O. N., Peltonen, M., Liebhold, A. M. & Baltensweiler, W. (2002) Waves of larch budmoth outbreaks in the European Alps. *Science,* **298**, (5595) 1020-1023.

Blasius, B., Huppert, A. & Stone, L. (1999) Complex dynamics and phase synchronization in spatially extended ecological systems. *Nature,* **399**, (6734) 354-359.

Boag, B. & Iason, G. (1986) The occurrence and abundance of helminth-parasites of the mountain hare *Lepus timidus* (L) and the wild rabbit *Oryctolagus cuniculus* (L) in Aberdeenshire, Scotland. *Journal of Helminthology,* **60**, (2) 92-98.

Borg, K., Höglund, N. & Notini, G. (1952) Nytt om haren. *Svenska Jägar Meddelanden,* **17**, 1-90.

Borrvall, C., Ebenman, B. & Jonsson, T. (2000) Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters,* **3**, (2) 131-136.

Brauer, A. (1947) Limits for the characteristic roots of a matrix 2. *Duke Mathematical Journal*, **14**, (1) 21-26.

Brualdi, R. A. & Mellendorf, S. (1994) Regions in the complex plane containing the eigenvalues of a matrix. *American Mathematical Monthly,* **101**, (10) 975-985.

Cattadori, I. M., Boag, B., Bjornstad, O. N., Cornell, S. J. & Hudson, P. J. (2005) Peak shift and epidemiology in a seasonal host-nematode system. *Proceedings of the Royal Society B-Biological Sciences,* **272**, (1568) 1163-1169.

Cattadori, I. M., Haydon, D. T., Thirgood, S. J. & Hudson, P. J. (2003) Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. *Oikos,* **100**, (3) 439-446.

Chen, X. & Cohen, J. E. (2001) Global stability, local stability and permanence in model food webs. *Journal Of Theoretical Biology,* **212**, (2) 223-235.

Christianou, M. & Kokkoris, G. D. (2008) Complexity does not affect stability in feasible model communities. *Journal of Theoretical Biology,* **253**, (1) 162-169.

Clark, J. S. (2007) *Models for Ecological Data: An Introduction,* Princeton University Press.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982) *Red Deer: Behavior and Ecology of Two Sexes,* Edinburgh University Press, Edinburgh.

Cohen, J. E. & Newman, C. M. (1985) A stochastic-theory of community food webs .1. Models and aggregated data. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **224**, (1237) 421-448.

Cohen, J. E., Pimm, S. L., Yodzis, P. & Saldana, J. (1993) Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology,* **62**, (1) 67-78.

Crofton, H. D. (1948) The ecology of immature phases of Trichostrongyle nematodes .2. The effect of climatic factors on the availability of the infective larvae of *Trichostrongylus retortaeformis* to the host. *Parasitology,* **39**, (1-2) 26-38.

Czárán, T. (1998) *Spatiotemporal models of population and community dynamics*, Chapman & Hall, London.

Daily, G. C. (1997) Nature's services: societal dependence on natural ecosystems pp. 392. Island Press, Washington, D.C.

De Angelis, D. L. & Waterhouse, J. C. (1987) Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs,* **57**, (1) 1-21.

De Ruiter, P. C., Neutel, A. M. & Moore, J. C. (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science,* **269**, (5228) 1257-1260.

Diekmann, O. & Kretzschmar, M. (1991) Patterns in the effects of infectious diseases on population growth. *Journal of Mathematical Biology,* **29**, (6) 539-570.

Dobson, A. & Hudson, P. J. (1992a) The Population Dynamics and Control of the Parasitic Nematode *Trichostrongylus tenuis* in Red Grouse in the North of England. *Applied Population Biology* (eds S. K. Jain & L. W. Botsford), pp. 149-171. Kluwer Academic Publishers.

Dobson, A. P. & Hudson, P. J. (1992b) Regulation and stability of a free-living host-parasite system - *Trichostrongylus tenuis* in red grouse. 2. Population-models. *Journal of Animal Ecology,* **61**, (2) 487-498.

Dunbar, S. R. (1983) Travelling wave solutions of diffusive Lotka-Volterra equations. *Journal of Mathematical Biology,* **17**, (1) 11-32.

Dunne, J. A., Williams, R. J. & Martinez, N. D. (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters,* **5**, (4) 558-567.

Elton, C. S. (1924) Periodic fluctuations in the numbers of animals - Their causes and effects. *British Journal of Experimental Biology,* **2**, (1) 119-163.

Elton, C. S. (1927) *Animal Ecology*, Sidgwick and Jackson, London.

Elton, C. S. (1958) *The Ecology of Invasion by Animals and Plants*, London.

Emmerson, M. & Yearsley, J. M. (2004) Weak interactions, omnivory and emergent food-web properties. *Proceedings Of The Royal Society Of London Series B-Biological Sciences,* **271**, (1537) 397-405.

Emmerson, M. C. & Raffaelli, D. (2004) Predator-prey body size, interaction strength and the stability of a real food web. *Journal Of Animal Ecology,* **73**, (3) 399-409.

Fagan, W. F. (1997) Omnivory as a stabilizing feature of natural communities. *American Naturalist,* **150**, (5) 554-567.

Feore, S. M., Bennett, M., Chantrey, J., Jones, T., Baxby, D. & Begon, M. (1997) The effect of cowpox virus infection on fecundity in bank voles and wood mice. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **264**, (1387) 1457-1461.

Flux, J. E. C. (1962) The ecology of the Scottish mountain hare (*Lepus timidus scoticus* Hilzheimer). *University of Aberdeen*.

Flux, J. E. C. (1970) Life history of mountain hare (*Lepus timidus scoticus*) in northeast Scotland. *Journal of Zoology,* **161**, 75-123.

Fowler, M. S. & Lindstrom, J. (2002) Extinctions in simple and complex communities. *Oikos,* **99**, (3) 511-517.

Gardner, M. R. & Ashby, W. R. (1970) Connectance of large dynamic (cybernetic) systems - critical values for stability. *Nature,* **228**, (5273) 784.

Geršgorin, S. (1931) Über die abgrenzung der eigenwerte einer matrix. *Izv. Akad. Nauk. USSR Otd. Fiz.-Mat. Nauk,* **7**, 749-754.

Gibson, K. (2009) *The ovals of Cassini*. WWW document, http://online.redwoods.cc.ca.us/instruct/darnold/CalcProj/sp07/ken/CalcPpr.pdf

Ginzburg, L. R. & Taneyhill, D. E. (1994) Population cycles of forest lepidoptera - a maternal effect hypothesis. *Journal of Animal Ecology,* **63**, (1) 79-92.

Goldwasser, L. & Roughgarden, J. (1993) Construction and analysis of a large Caribbean food web. *Ecology,* **74**, (4) 1216-1233.

Greenman, J., Kamo, M. & Boots, M. (2004) External forcing of ecological and epidemiological systems: a resonance approach. *Physica D-Nonlinear Phenomena,* **190**, (1-2) 136-151.

Gulland, F. M. D. (1992) The role of nematode parasites in Soay sheep (*Ovis aries* L). Mortality during a population crash. *Parasitology,* **105**, 493-503.

Gulland, F. M. D., Albon, S. D., Pemberton, J. M., Moorcroft, P. R. & Cluttonbrock, T. H. (1993) Parasite-associated polymorphism in a cyclic ungulate population. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **254**, (1339) 7-13.

Gulland, F. M. D. & Fox, M. (1992) Epidemiology of nematode infections of Soay sheep (*Ovis aries* L) on St. Kilda. *Parasitology,* **105**, 481-492.

Hassell, M. P., Comins, H. N. & May, R. M. (1991) Spatial structure and chaos in insect population dynamics. *Nature,* **353**, (6341) 255-258.

Hassell, M. P., Comins, H. N. & May, R. M. (1994) Species coexistence and self-organising spatial dynamics. *Nature,* **370**, (6487) 290-292.

Haydon, D. (1994) Pivotal assumptions determining the relationship between stability and complexity - an analytical synthesis of the stability-complexity debate. *American Naturalist,* **144**, (1) 14-29.

Haydon, D. T. (2000) Maximally stable model ecosystems can be highly connected. *Ecology,* **81**, (9) 2631-2636.

Haydon, D. T. & Lloyd, A. (1999) On the origins of the Lotka-Volterra equations. *Bulletin of the Ecological Society of America,* **80**, 205-206.

Hewson, R. (1962) Food and feeding habits of the mountain hare *Lepus timidus scoticus*, Hilzheimer. *Proceedings of the Zoological Society of London,* (139) 515-526.

Hewson, R. (1968) Weights and growth rates in mountain hare - *Lepus timidus scoticus*. *Journal of Zoology,* **154**, 249-262.

Hewson, R. (1970) Variation in reproduction and shooting bags of mountain hares on 2 moors in north-east Scotland. *Journal of Applied Ecology,* **7**, (2) 243-252.

Hewson, R. (1976) Population study of mountain hares (*Lepus timidus*) in northeast Scotland from 1956-1969. *Journal of Animal Ecology,* **45**, (2) 395-414.

Hickerson, M. J., Stahl, E. A. & Lessios, H. A. (2006) Test for simultaneous divergence using approximate Bayesian computation. *Evolution,* **60**, (12) 2435-2453.

Hilborn, R. C. (2000) *Chaos and Nonlinear Dynamics: an Introduction for Scientists and Engineers,* Oxford University Press, Oxford.

Hofbauer, J. & Sigmund, K. (1988) *The Theory of Evolution and Dynamical Systems,* Cambridge University Press.

Höglund, N. H. (1957) Fortplantningen hos skogsharen (*Lepus t. timidus* Lin.). *Viltrevy,* (1) 267-282.

Hubbell, S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography,* Princeton University Press.

Hudson, P. J., Dobson, A. P. & Newborn, D. (1998) Prevention of population cycles by parasite removal. *Science,* **282**, (5397) 2256-2258.

Hudson, P. J., Newborn, D. & Dobson, A. P. (1992) Regulation and stability of a free-living host-parasite system - *Trichostrongylus tenuis* in red grouse. 1. Monitoring and parasite reduction experiments. *Journal of Animal Ecology,* **61**, (2) 477-486.

Hutchinson, G. E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals. *American Naturalist,* **93**, (870) 145-159.

Hutson, V. & Schmitt, K. (1992) Permanence and the dynamics of biological systems. *Mathematical Biosciences,* **111**, (1) 1-71.

Iason, G. R. (1989a) Growth and mortality in mountain hares - the effect of sex and date of birth. *Oecologia,* **81**, (4) 540-546.

Iason, G. R. (1989b) Mortality of mountain hares in relation to body size and age. *Journal of Zoology,* **219**, 676-680.

Iason, G. R. (1990) The effects of size, age and a cost of early breeding on reproduction in female mountain hares. *Holarctic Ecology,* **13**, (2) 81-89.

Inchausti, P. & Ginzburg, L. R. (1998) Small mammals cycles in northern Europe: patterns and evidence for a maternal effect hypothesis. *Journal of Animal Ecology,* **67**, (2) 180-194.

Inchausti, P. & Ginzburg, L. R. (2009) Maternal effects mechanism of population cycling: a formidable competitor to the traditional predator-prey view. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **364**, (1520) 1117-1124.

Ives, A. R. & Carpenter, S. R. (2007) Stability and diversity of ecosystems. *Science,* **317**, (5834) 58-62.

Ives, A. R. & Murray, D. L. (1997) Can sublethal parasitism destabilize predator-prey population dynamics? A model of snowshoe hares, predators and parasites. *Journal of Animal Ecology,* **66**, (2) 265-278.

James, G. (2001) *Modern Engineering Mathematics,* Prentice Hall, Harlow.

Jansen, V. A. A. & Kokkoris, G. D. (2003) Complexity and stability revisited. *Ecology Letters,* **6**, (6) 498-502.

Jansen, V. A. A. & Sigmund, K. (1998) Shaken not stirred: On permanence in ecological communities. *Theoretical Population Biology,* **54**, (3) 195-201.

Jansen, W. (1987) A permanence theorem for replicator and Lotka-Volterra systems. *Journal of Mathematical Biology,* **25**, (4) 411-422.

Jeltsch, F., Muller, M. S., Grimm, V., Wissel, C. & Brandl, R. (1997) Pattern formation triggered by rare events: Lessons from the spread of rabies. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **264**, (1381) 495-503.

Jorgensen, J., Rossignol, A. M., Puccia, C. J., Levins, R. & Rossignol, P. A. (2000) On the variance of eigenvalues of the community matrix: Derivation and appraisal. *Ecology,* **81**, (10) 2928-2931.

Judson, O. P. (1994) The rise of the individual-based model in ecology. *Trends in Ecology & Evolution,* **9**, (1) 9-14.

Kaiser, J. (2000) Rift over biodiversity divides ecologists. *Science,* **289**, (5483) 1282-1283.

Kaitala, V., Ranta, E. & Lindstrom, J. (1996) Cyclic population dynamics and random perturbations. *Journal of Animal Ecology,* **65**, (2) 249-251.

Keeling, M. J. & Rohani, P. (2007) Chapter Seven: Spatial Models. *Modelling Infectious Diseases in Humans and Animals*, pp. 232 - 290. Princeton University Press.

Keith, L. B. (1983) Role of food in hare population-cycles. *Oikos,* **40**, (3) 385-395.

Kendall, B. E., Briggs, C. J., Murdoch, W. W., Turchin, P., Ellner, S. P., McCauley, E., Nisbet, R. M. & Wood, S. N. (1999) Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology,* **80**, (6) 1789-1805.

Kerlin, D. H. (2008) Modelling the spatial and temporal dynamics of upland birds in Scotland. *Faculty of Biomedical and Life Sciences*, pp. 135. University of Glasgow, Glasgow.

Kinrade, V., Ewald, J., Smith, A., Newey, S., Iason, G., Thirgood, S. & Raynor, R. (2008) The distribution of mountain hare (*Lepus timidus*) in Scotland (2006/07). *Scottish Natural Heritage Commissioned Report No.278 (ROAME No. R07AC308).*

Knee, A. (2008) A world without biodiversity? *World Conservation: the Magazine of the World Conservation Union*.

Kokkoris, G. D., Jansen, V. A. A., Loreau, M. & Troumbis, A. Y. (2002) Variability in interaction strength and implications for biodiversity. *Journal Of Animal Ecology,* **71**, (2) 362-371.

Kopell, N. & Howard, L. N. (1973) Plane wave solutions to reaction-diffusion equations. *Studies in Applied Mathematics,* **52**, (4) 291-328.

Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E. & Taylor, W. W. (2003) Compartments revealed in food-web structure. *Nature,* **426**, (6964) 282-285.

Krebs, C. J., Boonstra, R., Boutin, S. & Sinclair, A. R. E. (2001a) What drives the 10-year cycle of snowshoe hares? *Bioscience,* **51**, (1) 25-35.

Krebs, C. J., Boutin, S. & Boonstra, R. (2001b) Ecosystem Dynamics of the Boreal Forest: the Kluane Project. pp. 511. Oxford University press, New York.

Kristensen, N. P. (2008) Permanence does not predict the commonly measured food web structural attributes. *American Naturalist,* **171**, 202-213.

Lambin, X., Elston, D. A., Petty, S. J. & MacKinnon, J. L. (1998) Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **265**, (1405) 1491-1496.

Lambin, X., Krebs, C. J., Moss, R., Stenseth, N. C. & Yoccoz, N. G. (1999) Population cycles and parasitism. *Science,* **286**, (5449) 2425.

Law, R. & Blackford, J. C. (1992) Self-assembling food webs - a global viewpoint of coexistence of species in Lotka-Volterra communities. *Ecology,* **73**, (2) 567-578.

Law, R. & Morton, R. D. (1993) Alternative permanent states of ecological communities. *Ecology,* **74**, (5) 1347-1361.

Law, R. & Morton, R. D. (1996) Permanence and the assembly of ecological communities. *Ecology,* **77**, (3) 762-775.

Lawlor, L. R. (1978) Comment on randomly constructed model ecosystems. *American Naturalist,* **112**, (984) 445-447.

Lawton, J. H. (1999) Are there general laws in ecology? *Oikos,* **84**, (2) 177-192.

Levin, S. A. (1976) Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics,* **7**, 287-310.

Levins, R. (1966) The strategy of model building in population biology. *American Scientist,* **54**, (4) 421-431.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America,* **15**, (3) 237-240.

Levins, R. (1975) Evolution in Communities Near Equilibrium. *Ecology and Evolution of Communities* (ed J. M. Cody M.L. and Diamond), pp. 16–50. The Belknap Press of Harvard University, Cambridge, Massachusetts.

Lindstrom, J. & Kokko, H. (2002) Cohort effects and population dynamics. *Ecology Letters,* **5**, (3) 338-344.

Lindstrom, J., Ranta, E., Kokko, H., Lundberg, P. & Kaitala, V. (2001) From arctic lemmings to adaptive dynamics: Charles Elton's legacy in population ecology. *Biological Reviews,* **76**, (1) 129-158.

Liu, J. G., Dietz, T., Carpenter, S. R., Alberti, M., Folke, C., Moran, E., Pell, A. N., Deadman, P., Kratz, T., Lubchenco, J., Ostrom, E., Ouyang, Z., Provencher, W., Redman, C. L., Schneider, S. H. & Taylor, W. W. (2007) Complexity of coupled human and natural systems. *Science,* **317**, (5844) 1513-1516.

Loehle, C. (2006) Species abundance distributions result from body size-energetics relationships. *Ecology,* **87**, (9) 2221-2226.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D. A. (2001) Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science,* **294**, (5543) 804-808.

Lotka, A. J. (1925) *Elements of physical biology,* Williams and Wilkins, Baltimore.

Lubchenco, J. (1998) Entering the century of the environment: A new social contract for science. *Science,* **279**, (5350) 491-497.

Lundberg, P., Ranta, E., Ripa, J. & Kaitala, V. (2000) Population variability in space and time. *Trends in Ecology & Evolution,* **15**, (11) 460-464.

MacArthur, R. (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology,* **36**, (3) 533-536.

Macdonald, D. W., Mace, G. M. & Rushton, S. (1998) Proposals for future monitoring of British mammals. *Department of the Environment, Transport and the Regions, London.*

Magurran, A. E. (2004) *Measuring Biological Diversity,* Blackwell Publishing, Malden, Mass; Oxford.

Marjoram, P., Molitor, J., Plagnol, V. & Tavare, S. (2003) Markov chain Monte Carlo without likelihoods. *Proceedings of the National Academy of Sciences of the United States of America,* **100**, (26) 15324-15328.

May, R. M. (1971) Stability in multispecies community models. *Mathematical Biosciences,* **12**, (1-2) 59-79.

May, R. M. (1972a) Limit cycles in predator-prey communities. *Science,* **177**, (4052) 900-902.

May, R. M. (1972b) Will a large complex system be stable? *Nature,* **238**, (5364) 413-414.

May, R. M. (1973) Stability and complexity in model ecosystems. *Monographs in population biology,* **6**, 1-235.

May, R. M. (1974) Biological populations with nonoverlapping generations - stable points, stable cycles, and chaos. *Science,* **186**, (4164) 645-647.

May, R. M. & Anderson, R. M. (1978) Regulation and stability of host-parasite population interactions. 2. Destabilizing processes. *Journal of Animal Ecology,* **47**, (1) 249-267.

McCann, K., Hastings, A. & Huxel, G. R. (1998) Weak trophic interactions and the balance of nature. *Nature,* **395**, (6704) 794-798.

McCann, K. S. (2000) The diversity-stability debate. *Nature,* **405**, (6783) 228-233.

McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., He, F. L., Hurlbert, A. H., Magurran, A. E., Marquet, P. A., Maurer, B. A., Ostling, A., Soykan, C. U., Ugland, K. I. & White, E. P. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters,* **10**, (10) 995-1015.

McGradySteed, J., Harris, P. M. & Morin, P. J. (1997) Biodiversity regulates ecosystem predictability. *Nature,* **390**, (6656) 162-165.

McNaughton, S. J. (1978) Stability and diversity of ecological communities. *Nature,* **274**, (5668) 251-253.

Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-being: General Synthesis. World Resources Institute, Washington, DC.

Moss, R., Elston, D. A. & Watson, A. (2000) Spatial asynchrony and demographic traveling waves during Red Grouse population cycles. *Ecology,* **81**, (4) 981-989.

Moss, R., Watson, A. & Parr, R. (1996) Experimental prevention of a population cycle in red grouse. *Ecology,* **77**, (5) 1512-1530.

Mougeot, F., Piertney, S. B., Leckie, F., Evans, S., Moss, R., Redpath, S. M. & Hudson, P. J. (2005) Experimentally increased aggressiveness reduces population kin structure and subsequent recruitment in red grouse *Lagopus lagopus scoticus*. *Journal of Animal Ecology,* **74**, (3) 488-497.

Mougeot, F., Redpath, S. M., Leckie, F. & Hudson, P. J. (2003) The effect of aggressiveness on the population dynamics of a territorial bird. *Nature,* **421**, (6924) 737-739.

Mulvey, M., Aho, J. M. & Rhodes, O. E. (1994) Parasitism and white-tailed deer - timing and components of female reproduction. *Oikos,* **70**, (2) 177-182.

Murray, J. D. (1993) *Mathematical Biology,* Springer-Verlag, Berlin; London.

Naeem, S., Chapin III, F. S., Costanza, R., Ehrlich, P. R., Golley, F. B., Hooper, D. U., Lawton, J. H., O Neill, R. V., Mooney, H. A., Osvaldo, E. S., Symstad, A. J. & Tilman, D. (1999) Biodiversity and Ecosystem Functioning: Maintaining Natural Life Support Processes. *Issues in Ecology*. Ecological Society of America.

Neutel, A. M., Heesterbeek, J. A. P. & de Ruiter, P. C. (2002) Stability in real food webs: Weak links in long loops. *Science,* **296**, (5570) 1120-1123.

Neutel, A. M., Heesterbeek, J. A. P., van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C., Berendse, F. & de Ruiter, P. C. (2007) Reconciling complexity with stability in naturally assembling food webs. *Nature,* **449**, (7162) 599-U11.

Newey, S., Dahl., F., Willebrand, T. & Thirgood, S. (2007a) Unstable dynamics and population limitation in mountain hares. *Biological Reviews,* **82**, 527-549.

Newey, S., Shaw, D. J., Kirby, A., Montieth, P., Hudson, P. J. & Thirgood, S. J. (2005) Prevalence, intensity and aggregation of intestinal parasites in mountain hares and their potential impact on population dynamics. *International Journal for Parasitology,* **35**, (4) 367-373.

Newey, S. & Thirgood, S. (2004) Parasite-mediated reduction in fecundity of mountain hares. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **271**, S413-S415.

Newey, S., Thirgood, S. J. & Hudson, P. J. (2004) Do parasite burdens in spring influence condition and fecundity of female mountain hares *Lepus timidus*? *Wildlife Biology,* **10**, (3) 171-176.

Newey, S., Willebrand, T., T., H. D., Dahl, F., Aebischer, N. J., Smith, A. A. & Thirgood, S. J. (2007b) Do mountain hare populations cycle? *Oikos,* **116**, (9) 1547-1557.

Nicholson, A. J. & Bailey, V. A. (1935) The balance of animal populations. *Proceedings of the Zoological Society of London,* **3**, 551-598.

Odum, E. P. (1953) *Fundamentals of Ecology,* Saunders, Philadelphia.

Olsen, O. W. (1986) Family Trichostongylidae. *Animal Parasites: their Life Cycles and Ecology,* pp. 564. University Park Press, Baltimore, London.

Paine, R. T. (1992) Food web analysis through field measurement of per capita interaction strength. *Nature,* **355**, (6355) 73-75.

Patwardhan, A. & Small, M. J. (1992) Bayesian methods for model uncertainty analysis with application to future sea level rise. *Risk Analysis,* **12**, (4) 513-523.

Pimm, S. L. (1982) *Food Webs,* Chapman and Hall, London; New York

Pimm, S. L. (1991) *The Balance of Nature. Ecological Issues in the Conservation of Species and Communities,* University of Chicago Press, Chicago & London.

Pimm, S. L. & Lawton, J. H. (1978) Feeding on more than one trophic level. *Nature,* **275**, (5680) 542-544.

Plagnol, V. & Tavaré, S. (2004) Approximate Bayesian computation and MCMC. *Monte Carlo and Quasi-Monte Carlo Methods 2002,* 99-113.

Polis, G. A. (1998) Ecology - Stability is woven by complex webs. *Nature,* **395**, (6704) 744-745.

Press, W., Teukolsky, S., Vetterling, W. & Flannery, B. (1992) Quasi- (that is, Sub-) Random Sequences. *Numerical Recipes in C: The Art of Scientific Computing,* pp. 309-315. Cambridge University Press, Cambridge.

Pritchard, J. K., Seielstad, M. T., Perez-Lezaun, A. & Feldman, M. W. (1999) Population growth of human Y chromosomes: A study of Y chromosome microsatellites. . *Molecular Biology and Evolution,* **16**, (12) 1791-1798.

Pugliese, A., Rosa, R. & Damaggio, M. L. (1998) Analysis of a model for macroparasitic infection with variable aggregation and clumped infections. *Journal of Mathematical Biology,* **36**, (5) 419-447.

Ranta, E. & Kaitala, V. (1997) Travelling waves in vole population dynamics. *Nature,* **390**, (6659) 456-456.

Real, L. A. & Levin, S. A. (1991) Theoretical advances; the role of theory in the rise of modern ecology. *Foundations of ecology: classic papers with commentaries* (eds L. A. Real & J. H. Brown), pp. 177-191. University of Chicago, Chicago, Illinois, USA.

Redpath, S. M., Mougeot, F., Leckie, F. M., Elston, D. A. & Hudson, P. J. (2006) Testing the role of parasites in driving the cyclic population dynamics of a gamebird. *Ecology Letters,* **9**, (4) 410-418.

Rejmanek, M. & Stary, P. (1979) Connectance in Real Biotic Communities and Critical-Values for Stability of Model Ecosystems. *Nature,* **280**, (5720) 311-313.

Roberts, A. (1974) Stability of a feasible random ecosystem. *Nature,* **251**, (5476) 607-608.

Rooney, N., McCann, K., Gellner, G. & Moore, J. C. (2006) Structural asymmetry and the stability of diverse food webs. *Nature,* **442**, (7100) 265-269.

Rosa, R. & Pugliese, A. (2002) Aggregation, stability, and oscillations in different models for host-macroparasite interactions. *Theoretical Population Biology,* **61**, (3) 319-334.

Rosa, R., Rizzola, A., Pugliese, A. & Genchi, C. (2003) Mathematical models and wildlife diseases: techniques of parameter estimation for nematode infections. *Ibex Journal of Mountain Studies,* **7**, 99-106.

Rosenblueth, A. & Wiener, N. (1945) The role of models in science. *Philosophy of Science,* **12**, (4) 316-321.

Roughgarden, J. (1975) A simple model for population dynamics in stochastic environments. *American Naturalist,* **109**, (970) 713-736.

Rozdilsky, I. D. & Stone, L. (2001) Complexity can enhance stability in competitive systems. *Ecology Letters,* **4**, (5) 397-400.

Saunders, P. T. (1978) Population dynamics and length of food chains. *Nature,* **272**, (5649) 189-190.

Saunders, P. T. & Bazin, M. J. (1975) Stability of complex ecosystems. *Nature,* **256**, (5513) 120-121.

Shaw, D. J. & Dobson, A. P. (1995) Patterns of macroparasite abundance and aggregation in wildlife populations: A quantitative review. *Parasitology,* **111**, S111-S133.

Shaw, D. J., Grenfell, B. T. & Dobson, A. P. (1998) Patterns of macroparasite aggregation in wildlife host populations. *Parasitology,* **117**, 597-610.

Shaw, J. L., Moss, R. & Pike, A. W. (1989) Development and survival of the free-living stages of *Trichostrongylus tenuis,* a cecal parasite of red grouse *Lagopus lagopus scoticus*. *Parasitology,* **99**, 105-113.

Sherratt, J. A. (1994) On the evolution of periodic plane waves in reaction-diffusion systems of lambda-omega type. *Siam Journal on Applied Mathematics,* **54**, (5) 1374-1385.

Sherratt, J. A. (2001) Periodic travelling waves in cyclic predator-prey systems. *Ecology Letters,* **4**, (1) 30-37.

Sherratt, J. A. & Smith, M. J. (2008) Periodic travelling waves in cyclic populations: field studies and reaction-diffusion models. *Journal of the Royal Society Interface,* **5**, (22) 483-505.

Sherratt, T. N., Lambin, X., Petty, S. J., Mackinnon, J. L., Coles, C. F. & Thomas, C. J. (2000) Use of coupled oscillator models to understand synchrony and travelling waves in populations of the field vole Microtus agrestis in northern England. *Journal of Applied Ecology*, **37**, 148-158.

Simberloff, D. (2004) Community ecology: Is it time to move on? *American Naturalist,* **163**, (6) 787-799.

Sinclair, A. R. E., Chitty, D., Stefan, C. I. & Krebs, C. J. (2003) Mammal population cycles: evidence for intrinsic differences during snowshoe hare cycles. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **81**, (2) 216-220.

Sisson, S. A., Fan, Y. & Tanaka, M. M. (2007) Sequential Monte Carlo without likelihoods. *Proceedings of the National Academy of Sciences of the United States of America,* **104**, (6) 1760-1765.

Skorping, A., Read, A. F. & Keymer, A. E. (1991) Life-history covariation in intestinal nematodes of mammals. *Oikos,* **60**, (3) 365-372.

Smith, C. H. (1983) Spatial trends in canadian snowshoe hare, *Lepus americanus*, population-cycles. *Canadian Field-Naturalist,* **97**, (2) 151-160.

Smith, M. J., Sherratt, J. A. & Lambin, X. (2008) The effects of density-dependent dispersal on the spatiotemporal dynamics of cyclic populations. *Journal of Theoretical Biology,* **254**, (2) 264-274.

Smith, M. J., White, A., Lambin, X., Sherratt, J. A. & Begon, M. (2006) Delayed density-dependent season length alone can lead to rodent population cycles. *American Naturalist,* **167**, (5) 695-704.

Sobol', I. (1967) On the distribution of points in a cube and the approximate evaluation of integrals. *Computational Mathematics and Mathematical Physics,* **7**, 86-112.

Sugihara, G. (1983) Niche hierarchy: structure, organisation and assembly in natural communities. *Department of Biology*. Princeton University.

Sutherland, W. J. (1996) *From Individual Behaviour to Population Ecology,* Oxford University Press.

Sutherland, W. J., Armstrong-Brown, S., Armsworth, P. R., Brereton, T., Brickland, J., Campbell, C. D., Chamberlain, D. E., Cooke, A. I., Dulvy, N. K., Dusic, N. R., Fitton, M., Freckleton, R. P., Godfray, H. C. J., Grout, N., Harvey, H. J., Hedley, C., Hopkins, J. J., Kift, N. B., Kirby, J., Kunin, W. E., Macdonald, D. W., Marker, B., Naura, M., Neale, A. R., Oliver, T., Osborn, D., Pullin, A. S., Shardlow, M. E. A., Showler, D. A., Smith, P. L., Smithers, R. J., Solandt, J. L., Spencer, J., Spray, C. J., Thomas, C. D., Thompson, J., Webb, S. E., Yalden, D. W. & Watkinson, A. R. (2006) The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology,* **43**, (4) 617-627.

Tanhuanpää, M., Ruohomäki, K., Turchin, P., Ayres, M. P., Bylund, H., Kaitaniemi, P., Tammaru T., & Haukioja, E. (2002) Population cycles of the autumnal moth in Fennoscandia. *Population Cycles: The Case For Trophic Interactions* (ed A. A. Berryman). Oxford University Press.

Tenow, O., Nilssen, A. C., Bylund, H. & Hogstad, O. (2007) Waves and synchrony in *Epirrita autumnata*/*Operophtera brumata* outbreaks. I. Lagged synchrony: regionally, locally and among species. *Journal of Animal Ecology,* **76**, (2) 258-268.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: A search for general principles. *Ecology,* **80**, (5) 1455-1474.

Tompkins, D. M. & Begon, M. (1999) Parasites can regulate wildlife populations. *Parasitology Today,* **15**, (8) 311-313.

Toni, T., Welch, D., Strelkowa, N., Ipsen, A. & Stumpf, M. P. H. (2009) Approximate Bayesian computation scheme for parameter inference and model selection in dynamical systems. *Journal of the Royal Society Interface,* **6**, (31) 187-202.

Townsend, S. E., Newey, S., Thirgood, S. J., Matthews, L. & Haydon, D. T. (2009) Can parasites drive population cycles in mountain hares? *Proceedings of the Royal Society B: Biological Sciences,* **276**, (1662) 1611-1617.

Turchin, P. (2003) *Complex Population Dynamics: A Theoretical/Empirical Synthesis,* Princeton University Press, Princeton.

Turing, A. M. (1952) The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **237**, (641) 37-72.

Vandermeer, J. (2006) Omnivory and the stability of food webs. *Journal of Theoretical Biology,* **238**, (3) 497-504.

Varga, R. S. (2004) *Geršgorin and His Circles,* Springer, Berlin.

Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997) Human domination of Earth's ecosystems. *Science,* **277**, (5325) 494-499.

Volterra, V. (1926) Fluctuations in the abundance of a species considered mathematically. *Nature,* **118**, 558-560.

Warren, P. H. & Lawton, J. H. (1987) Invertebrate predator-prey body size relationships - an explanation for upper-triangular food webs and patterns in food web structure. *Oecologia,* **74**, (2) 231-235.

Watson, A., Hewson, R., Jenkins, D. & Parr, R. (1973) Population-densities of mountain hares compared with red grouse on Scottish moors. *Oikos,* **24**, (2) 225-230.

Whittaker, R. H. (1970) *Communities and Ecosystems* Macmillan; Collier Macmillan, New York; London.

Wilson, W. G. & Lundberg, P. (2006) Non-neutral community dynamics: empirical predictions for ecosystem function and diversity from linearized consumer-resource interactions. *Oikos,* **114**, (1) 71-83.

Wilson, W. G., Lundberg, P., Vazquez, D. P., Shurin, J. B., Smith, M. D., Langford, W., Gross, K. L. & Mittelbach, G. G. (2003) Biodiversity and species interactions: extending Lotka-Volterra community theory. *Ecology Letters,* **6**, (10) 944-952.

Wootton, J. T. (1997) Estimates and tests of per capita interaction strength: Diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs,* **67**, (1) 45-64.

Yodzis, P. (1980) The connectance of real ecosystems. *Nature,* **284**, (5756) 544-545.

Yodzis, P. (1981) The stability of real ecosystems. *Nature,* **289**, (5799) 674-676.