Opening the black box—Development, testing and documentation of a mechanistically rich agent-based model

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ARTICLE INFO

ABSTRACT

Although increasingly widely used in biology, complex adaptive simulation models such as agent-based models have been criticised for being difficult to communicate and test. This study demonstrates the application of pattern-oriented model testing, and a novel documentation procedure to present a detailed agent-based model of the European brown hare, a species in widespread decline in Europe.

The model was built based on available literature data, using multiple field data patterns from an island hare population study to guide model development. A general and widely applicable approach to the pattern-oriented protocol for testing and developing ecological models of this kind was defined together with the development of the ODdox documentation protocol, a combination of the current ODD protocol for describing agent-based models and source-code documentation. The result is a detailed and yet accessible description of the processes included in the model. Application of the model to a comprehensive historical data set supported the hypothesis that interference competition is the primary population regulating factor in the absence of mammal predators in the brown hare, and that the effect works through reduced fecundity.

With a clearly defined testing protocol and documentation, this in silico modelling approach has clear advantages for applications requiring integration of many factors, especially when spatio-temporal variability is important. Providing multi-facetted output which can be compared to real-world data allows the formulation and testing of varied hypotheses in ways not tractable to experimentation. In the case of the brown hare the results provide a new insight into population regulation and the causes of the declines.

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1. Background

Agent-based models (ABMs) are gaining popularity in most scientific fields due to their ability to describe complex systems from first principles. Yet, they are also criticised for being 'black boxes' and impossible to fully understand. This is mainly due to the difficulty of testing, documenting and communicating the wealth of mechanisms built into such models. However, testing these complex adaptive models has been aided by recent advances in pattern-oriented modelling (POM Grimm et al., 2005b), which is becoming a widely used framework (Grimm et al., 1996; Wiegand et al., 2003, 2004; Grimm and Railsback, 2005a). POM evaluates model behaviour and reduces parameter uncertainty by comparing model responses to real-world data at multiple hierarchical levels.

The greater the number of real world patterns the model can predict simultaneously the greater the confidence in the model.

There have also been advances in the documentation of ABMs. The Overview, Design and Detail protocol (ODD) (Grimm et al., 2006) attempts to divide the model description into overview and detailed sections. The latter section should provide enough information for reconstruction of the model by a third party. However, for large simulation models the ODD approach is impractical for documentation to the level that would allow replication of the model due simply to the volume of information required. On the other hand, simulation models are based on programming code, which provides the complete description of the model, but in a form only accessible to the experienced programmer. Hence, ideally ODD and code should be combined to form a comprehensive but approachable documentation.

Here, we implement a rigorous application of POM and combine the ODD protocol for documentation with a software industry standard tool for documenting object-oriented computer program code (van Heesch, 1997) to provide a highly structured and easily accessible model documentation. We exemplify this procedure

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by presenting the testing, documentation and communication of a mechanistically rich agent-based model (*sensu* DeAngelis and Mooij, 2003) of the European brown hare (*Lepus europaeus*) built upon energetic and behavioural processes. We then apply the model as a theoretical framework to the investigation of population regulating mechanisms in brown hare populations.

The decline in population of the brown hare since the 1960s throughout Europe is well documented (Strandgaard and Asferg, 1980; Tapper and Parsons, 1984; Hutchings and Harris, 1996; Marboutin et al., 2003). Although generally still widespread, local populations are considered endangered (Vaughan et al., 2003) and in Switzerland it is included in the national red list (Pfister et al., 2002). There is also considerable interest in reversing these population trends due to the economics of hunting. Numerous factors have been implicated in the declines including changes in landscape structure, management, climate, predation, and disease, altering food supply, reproduction and/or survival (Smith et al., 2005). Habitat changes caused by agricultural intensification seem to play a major role although it has been difficult to relate this back to demographic changes in hare populations (Smith et al., 2005). This is likely to be due to interactions among multiple causal drivers and because there is considerable spatial and temporal variability in field estimates of demographic variables. For example, the number of leverets per female produced per year varies between 1.4 and 15.0 (Abilgård et al., 1972; Marboutin et al., 2003), and age structure and survival rates appear to show similar variation between populations (Smith et al., 2005).

Integrating the range of factors that are implicated in brown hare declines requires a flexible framework that includes physiological processes at the individual level, hare behaviour and the dynamics of a rapidly changing landscape including agricultural management. This system is therefore an ideal candidate for a complex ABM approach.

This paper presents methods used to generate a well tested and documented brown hare model as a basis for hypothesis generation and testing. The model was tested using a simple POM protocol and sensitivity analysis resulting in the evaluation of a range of potential population control mechanisms. The documentation is presented using a protocol we refer to as ODdox, which together with the POM protocol aims to improve the transparency of detailed agent-based models, previously criticized for being black boxes.

2. Methods

The modelling approach used here implements what is termed 'the modelling cycle' for a complex system of interacting agents (Grimm and Railsback, 2005a). The modelling cycle is an iterative process whereby model formulations are tested against carefully selected performance criteria (see below) in order to develop a model to answer a question, itself potentially changing as part of the cycle. To provide a structure to this process we present the structure of the modelling cycle in stages:

A. Definition of the question.
B. Model construction.
C. Identification of performance criteria.
D. Iterative testing and reformulation of the model, altering 'A, B & C' as necessary (POM approach).
E. Sensitivity analysis of the resulting final model.
F. Model documentation.
G. Application of the model to the question defined in 'A'.

In order to emphasise the importance of documentation we have added step 'F' to the modelling cycle. The brown hare species model presented here was built as part of the ALMaSS model framework (Topping et al., 2003b) and attempts to integrate a wide range of factors related to spatio-temporal patterns of habitat and food availability and interactions between these, agriculture, and the brown hare's biology. ALMaSS is a highly detailed ABM system designed to simulate impacts of human management on key species of Danish wildlife. It utilizes a dynamic landscape providing vegetation growth and management on daily time-steps with a resolution of $1\,m^2$ and a typical extent of $10\,km \times 10\,km$. Management of crops is handled using crop management plans and handled at the farm scale, affecting crop growth and providing spatio-temporally located managements, e.g. harvest. Specific details of ALMaSS affecting the hare model are described under model testing below together with a model overview, however full documentation of the hare model is provided in Appendix I.

2.1. Definition of the model question

The model was designed to evaluate the importance of population control mechanisms on the hare population of island of Illumø, Denmark. Illumø was chosen since it provided a long-term, data rich study of a brown hare population in the absence of confounding factors such as dispersal and mammalian predators. This required the simulation of Illumø under 1960s conditions at a spatial and temporal scale commensurate with the details necessary to include population control mechanisms. It also required an approach that allowed easy experimentation with multiple factors. The ultimate model aim was to create predictions which could be used to test and refine the models applicability to other hare populations.

2.2. Model construction

To answer the model question it was necessary to model all life-stages of the brown hare, which we identified as male, female, juvenile (36–265 days), mobile young (12–35 days), and infant (1–11 days). The definition of the three juvenile stages was related to total dependency on the mother, partial dependency and independency as the hare ages. Knowledge about hares and their decision processes is far from complete; hence a basic mechanistic approach was selected based on fundamental principles of energetics. Energy is therefore the 'currency' of the brown hare model and the primary basis upon which hare decisions are implemented. This approach has been used previously with success in integrative simulation models of this kind (Stillman et al., 2001; Topping and Odderskaer, 2004), and the energetic approach has also been used to model behaviour in individual hares to obtain realistic behaviour (Rizzotto and Focardi, 1997). The details of the hare energetics used to construct the model are presented in Appendix II.

2.3. Identification of performance criteria

2.3.1. Initial debugging and plausibility tests

The structural integrity of the initial model as well and the general responses were evaluated. This involved testing of individual code segments and processes to ensure that responses were as intended. For example in the case where model hares were given excess food to ensure that no starvation occurs, body weights are at maximum. Visual debugging (sensu Grimm, 2002) and standard plausibility tests were also used to evaluate hare spatial behaviour and the set of rules used to construct the model.

2.3.2. Illumø Island population patterns

The hare study carried out on Illumø island off the island of Fynen, Denmark 1957–1970 (Abilgård et al., 1972) provided a unique opportunity to test various aspects of model performance. The island is approximately $1\,km^2$ in area and has a very elongated form (Fig. 1A). The original study documents many aspects of
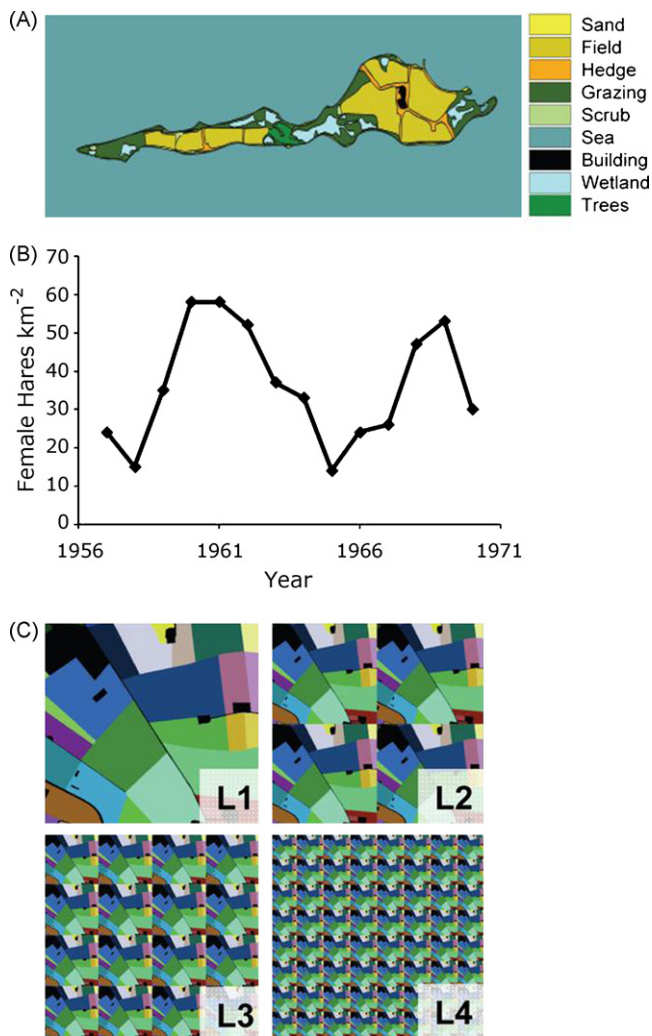
Fig. 1. Map data and field patterns used in simulations. (A) The digital map of Illumø Island used as the basis for the major part of simulations. This island was the location of an extensive field study on brown hares between 1957 and 1970 (Abilgård et al., 1972), resulting in a number of well supported field data patterns such as changes in population number (B). (C) Landscape heterogeneity analyses used four 8 × 8 km landscapes (L1–L4) to test the effect of increasing heterogeneity on the model hare population responses. Colours indicate fields managed identically. The areas of all fields and other habitats, management and vegetation growth were identical in all four landscapes, only the degree of fragmentation of the patches was been altered using a geometrical fragmentation process.

Table 1
Crop area proportions for Illumø island simulations in ALMaSS.

Crop	Proportion
Spring barley	0.34
Grass	0.30
Root crops (fodder beet)	0.14
Oats	0.06
Potatoes	0.06
Winter wheat	0.04
Winter rye	0.04
Pulses	0.01

the hare population over this period with extensive mark-release-recapture experiments. Thus it provides many potential patterns for comparisons with model outputs. Both first order patterns (means) and second order patterns (variances) were considered as potentially useful ways of screening models.

The simulation of the hare population of Illumø was based on a digitised map from 1957 and current aerial photographs. Abilgård et al. (1972) give details of the type and proportion of crops grown during the study period, and these were used together with national agricultural statistics from Denmark for that period to construct a crop rotation for ALMaSS that resulted in a crop by area coverage matching the Illumø situation (Table 1). Daily weather data was not available for Illumø, but a complete time series of air temperature, wind and precipitation was obtained for the years 1957–1970 from the Tranbjerg weather station (55°50′N 10°37′E), 80 km from Illumø (Cappelen et al., 2008). To prevent artificial 14-year cycles, a set of 60 representative weather years was constructed by randomly ordering a set of four copies of the 14-year series such that no

two years occurred consecutively. This 56-year set was appended to a copy of years 1–4 to give a total of 60 weather years used for all simulations. In addition to 1960s crops and weather, pesticides were removed from the management plans and all crops designated as being 'patchy'. This patchy designation simulated the open structure of the crop with wide gaps between rows characteristic of crops of that time and clearly visible in the photographs from the time (see Abilgård et al., 1972).

2.3.2.1. Realised hare weights with age and variance. The Illumø study provided a data set of 1275 age-indexed hare weights over a period of 14-years to compare to model outputs. Since hare weights is an emergent property resulting from the individuals life-time physiological status, and therefore energetic balance, the mean weights with age should provide a sensitive measure of model realism. Variance around model weights of the same scale as that found in the Illumø study was considered to be a secondary target which would indicate that model hares and real world hares varied in weights within the same range in a similar manner (Patterns 1 & 7, Tables 2 and 3).

2.3.2.2. Population size. Mean and variance around population size over the study period was considered to be a very reliable estimate (Patterns 2 & 8, Tables 2 and 3). The Illumø population size fluctuated in what seems like a stable limit cycle (Fig. 1B), hence some form of oscillation was desirable in the model generated population dynamic trends. Combined with pattern 7, these fluctuations were used to screen model configurations, but were not used in subsequent parameter fitting due to the lack of precision.

2.3.2.3. Adult and juvenile survival rates. Abilgård et al. (1972) measured annual survival rates of 0.438 and 0.552 for juveniles and adult females, respectively. These data were based on 1275 hares using capture, mark and recapture methods with up to 10 recaptures per individual. Mean survival rates were used with their variances (Patterns 3, 4, 9, 10, Tables 2 and 3).

2.3.2.4. Population age structure. The relative proportion of juvenile and adults was well documented in the original study. The measure used here was the proportion of young females (i.e. females < 1 year old/total females) (Patterns 5 & 11, Tables 2 and 3).

2.3.2.5. Sex ratio. The sex ratio on Illumø was rather consistently biased towards males, even though the influx of new animals recorded at the time was slightly biased in the opposite direction. In only 3 years out of 14 were the as many males as females, and in one of these years this was achieved by experimental manipulation. The mean annual proportion of females in adults over 1 year old prior to experimental manipulation was 0.429 ($n = 8$, variance = 0.004). This figure and its variance were adopted as a target pattern (Pattern 6 & 12, Tables 2 and 3).

Table 2
Slopes of fitted regressions using first order response patterns as the dependent variable. Slopes of less than 0.1 or with $p > 0.05$ are not shown. Bold indicates $p < 0.001$. Parameters are described in Table 4.

Parameter	Female hare weights (P1)	Female density (P2)	Female adult surviv (P3)	Juv surviv (P4)	Juv::ads (P5)	Sex ratio (P6)	Litter no. (P13)	Litter size (P14)
1 ExtEff	–	**3.11**	–	−0.16	0.10	–	**0.38**	**0.35**
2 YLoss	–	**−0.49**	–	0.12	–	–	–	**0.12**
3 JLoss	**0.14**	**−1.19**	–	**−0.40**	0.13	0.23	**0.28**	**0.33**
4 ALoss	**0.38**	**−2.84**	**−6.68**	**−3.86**	**4.91**	**0.59**	**−2.16**	**0.98**
5 DDconst	–	**−1.15**	–	–	–	–	–	–
6 BreedWt	–	**−0.23**	–	**0.24**	−0.12	0.12	–	**0.25**
7 RepEnd	–	–	–	–	–	–	–	–
8 Rep Start	–	**0.87**	–	**0.98**	**−0.50**	**0.51**	**−0.85**	–
9 SwitchJA	–	**−0.33**	–	**−0.62**	0.29	**−0.36**	**−0.22**	–
10 ADispThr	–	**−0.14**	–	–	–	–	**−0.10**	**−0.75**
11 FoetalGrProp	**−0.56**	**4.83**	–	**−2.57**	**2.29**	**−0.78**	**3.06**	**28.78**
12 GrAttain	**0.11**	**−0.53**	–	–	–	0.11	**0.64**	**0.32**
13 RainF	–	**−0.17**	–	–	–	–	–	–
14 JStarve	–	–	–	–	–	–	–	–

2.3.3. General hare patterns

2.3.3.1. Breeding patterns. The number of litters is an emergent property because it is based upon the physiological condition of the model hares limiting breeding to periods when fat reserves are sufficient. The number of litters (Pattern 14, Table 2) can be compared to the range of 2.3–5.2 found by Pielowski (1975, 1976), Raczynski (1964), Hansen (1992) and Marboutin et al. (2003). The mean number of leverets per litter is also variable (range 2.2–2.8) from the same studies (Pattern 13, Table 2). In both these cases, precise values are not possible to obtain, however likely values are at the lower end of these ranges since on Illumø the mean number of juveniles per adult was 3 (range 1.4–5.0) (Abilgård et al., 1972). Targets selected were therefore a mean litter size of 2.2–2.5 and an annual number of litters 2.3–3.0.

2.3.3.2. Positive effect of increasing habitat heterogeneity. A review of hare research found that increased habitat heterogeneity had a positive impact on overall hare numbers (Smith et al., 2005). This pattern was tested by isolating heterogeneity as a factor. This was achieved by creating a set of four artificial landscapes based on an actual 1×1 km area and running the simulations using the Illumø simulation settings. All four landscapes were 8×8 km, the first being a scaled up version of 1 km² area, the second formed of four 4×4 km areas scaled in the same way, the third made from 16 2×2 km scaled areas, and the last of 64 copies of the original 1 km² (Fig. 1C). This method of manipulating the landscapes ensured that the only factor that varied was the location of individual units of particular habitat patches, which become more and more fragmented as the grain of the landscape was increased. In this experimental manipulation, management carried out in one field in the homogenous landscape is carried out simultaneously in four fields of one quarter the size in the next landscape, and likewise 16 and 64 fields in the following landscapes. Means of 10 replicates of 60 year runs were used to assess model population responses to increasing habitat heterogeneity (Pattern 15).

2.4. Iterative testing and reformulation of the model

Iterative testing was carried out in two stages: (i) Initially the aim was to simulate the Illumø population by matching patterns 1–8 as closely as possible; (ii) thereafter checking if the other patterns were adequately matched and if not continuing the iterative cycle by modifying the model and testing the patterns again.

The range of parameter space was enormous and hence a Monte Carlo approach was not possible, rather the parameters were adjusted manually to obtain responses; using the responses as a guide, further manipulations were made to find the optimal fit. To speed up initial identification of the area of optimal fit an *ad hoc* iterative sub-procedure was adopted for 'i' which was to minimise a weighted least squares estimate of the difference between a mean of replicated scenario runs with a specific model configuration and parameter-set values. Weights used were 4 to pattern 3 (density) which was considered to be the most secure real-world data, 0.1 to patterns 2 and 4, which were considered to be of lower strength patterns since they are second order descriptors and highly variable, and 1.0 to all other patterns. The purpose of the weighting was to quickly direct the parameter selection to the optimal area, in particular to avoid too great a reliance on variable and numer-

Table 3
Slopes of fitted regressions using second order response patterns (variances) as the dependent variable. Slopes of less than 0.1 or with $p > 0.05$ are not shown. Bold indicates $p < 0.001$.

Parameter	Var female hare weights (P7)	Var female density (P8)	Var female adult surviv (P9)	Var juv surviv (P10)	Var juv::ads (P11)	Var sex ratio (P12)
1 ExtEff	**−0.77**	**−0.83**	**−2.77**	**−1.24**	–	**−1.13**
2 YLoss	–	–	–	0.63	–	–
3 JLoss	**−0.83**	**2.12**	**2.76**	0.77	–	1.06
4 ALoss	**−1.92**	**10.63**	**7.15**	**−2.18**	–	**6.85**
5 DDconst	0.16	**−2.64**	1.14	0.33	–	0.43
6 BreedWt	−0.19	**0.57**	**0.96**	0.57	–	0.26
7 RepEnd	–	–	**−0.14**	–	–	–
8 Rep Start	–	**−1.32**	**−4.01**	–	–	−1.11
9 SwitchJA	–	–	**0.99**	0.38	–	0.48
10 ADispThr	–	0.16	–	–	–	–
11 FoetalGrProp	**2.89**	**−10.66**	**−14.10**	**−6.07**	–	**−3.14**
12 GrAttain	−0.14	**−0.89**	**0.88**	0.32	–	0.41
13 RainF	–	–	**0.31**	0.17	–	0.14
14 JStarve	**−0.77**	**−0.83**	**−2.77**	**−1.24**	–	**−1.13**

Table 4
Parameters used in the sensitivity analysis. See OODox documentation in Appendix III for detailed information.

Parameter	Short description
1 ExtEff	The rate of energy intake, assuming no reduction due to impedance or palatability.
2 YLoss	The daily rate of loss of young and infant stages not accounted for by other factors (primarily predation).
3 JLoss	The daily rate of loss of juveniles not accounted for by other factors (primarily predation).
4 ALoss	The daily rate of loss of adults not accounted for by other factors (predation, disease).
5 DDconst	A negative exponent used to decrease the proportion of time available for feeding with increase local density.
6 BreedWt	A minimum weight below which a female hare cannot breed.
7 RepEnd	The last day of the reproductive season after which oestrous is not possible.
8 Rep Start	The date of onset of oestrous at the start of a new season.
9 SwitchJA	The length of the period between becoming adult and switching to zero probability of starvation with negative energy deficit.
10 ADispThr	The threshold energy depot level at which the adult will attempt to disperse.
11 FoetalGrProp	The proportion of energy surplus used for production of foetal mass.
12 GrAttain	The proportion of age-indexed maximum possible growth which must be achieved to avoid death due to under-development.
13 RainF	The scaling factor applied to the increase in RMR with rainfall.
14 JStarve	A probability of starving to death if in negative energy deficit.

ically large second order patterns. The weights have little bearing on the final parameter values selected assuming that the final fit is good but do affect the speed of identification of these values. Once a close enough fit was achieved, loosely defined as all responding patterns being within 10% of their targets, a structured set of scenarios was created by varying all parameters under testing by fixed proportions either side of the current chosen value. If parameters were not already in the optimum range this was identified by a lower least squares value for a non-centre parameter value. In this case the parameter value was altered and the structured set of scenarios re-run. The scenarios were replicated a minimum of 10 times. Initial criteria for a fit were that all first order patterns should be within ±5% of the Illumø population targets, and that within this the least squares statistic should be minimised. Model configurations that did not achieve this were abandoned; those that did were tested against patterns 9–12. The best model configuration and parameter-set values found were fixed and the sensitivity analysis was started.

Since we used sex ratio and female density as target patterns, male patterns were superfluous and were not used in the analysis, although males were modelled in as great detail as females.

Model versions used for testing were based on combinations of configuration options (see Appendix III), and were designed to evaluate the potential for different population controlling factors to produce the patterns observed on Illumø. Four primary mechanisms were tested:

C1—Disease: implemented as a delayed density-dependent probability of a female being unable to produce young. The density effect was related to the mean density experienced during the previous year.

C2—Density-dependent mortality: implemented as an exponentially increasing likelihood of predation of an individual with increasing experienced density. This effect was applied to leveret, young and juvenile stages only since predators capable of killing adults were not present on Illumø.

C3—Stochastic variation on mortality and food quality: implemented as an annual modifier applied independently to food quality (±max 10%) and all mortality probabilities (±10%). Density-dependent mortality was also utilised above a threshold value of 80 hares km^{-2} to prevent population explosions, as C2.

C4 – Interference competition – implemented as an exponentially increasing proportion of time spent 'communicating' with nearby hares as local hare density increased. Local density was defined as being within a fixed radius. Time spent in this way was unavailable for foraging and therefore resulted in a lowered energy intake and ultimately affected the physiological condition of the hares.

Within each of these basic model configurations a range of options were also tested, e.g. with and without threshold density dependence.

2.5. Sensitivity analysis of the resulting final model

The parameter values achieving the best fit from 3D above were used as a pivot point, and the parameters identified as important in the iterative development process (Table 4) were adjusted independently to ±5, 10, 20 and 40% of their pivot point values. A minimum of 40 replicates were obtained for each scenario. The deviation from target patterns 1–14 was used as the dependent variable and linear regressions were fitted to each target/parameter combination.

All statistical analyses were performed using SAS ver 9.13 (SAS, 2002), simulation lengths were 60 years with the first 20 years ignored to allow model stabilization. Due to the high annual variability approximately 4.5% of simulation runs resulted in population extinction. Although these runs contained useful information, the disproportionate impact on the fit to patterns made us exclude them from the analyses.

2.6. Model documentation (ODdox)

Model documentation was created by combining a modified version of the ODD protocol with documented code using doxygen (van Heesch, 1997) to create what we term ODdox documentation. The ODD (Overview, Design, Detail) protocol divides the model documentation into defined sections covering aspects of model structure and functioning, and finally model details. The new ODdox protocol (Overview, Design, doxygen) broadly follows ODD protocol, but is completed and augmented by extracting comments from the source code. The details of the model are therefore described via descriptions of classes, methods, and variables using hyperlinks to the relevant sections in the source code. In contrast to the ODD, this means that by far the major part of the documentation is placed outside the traditional ODD sections, but linked to them via hyperlinks. The ODdox was specifically designed to facilitate documentation of large object-oriented models with many interacting components, and to provide a flexible way of building documentation as the software is developed. It is therefore structured following logical divisions of the model entities, primarily base class types. At each subdivision there is a class or set of linked classes in focus, and six of the seven ODD sections are written for these classes. The "Submodels" section of ODD becomes superfluous since any links to sub-models are covered by class descriptions for the classes in focus, and submodels per se should not exist. However, there may be important connections between the focus classes and other ODdox sections (e.g. other species, environment).
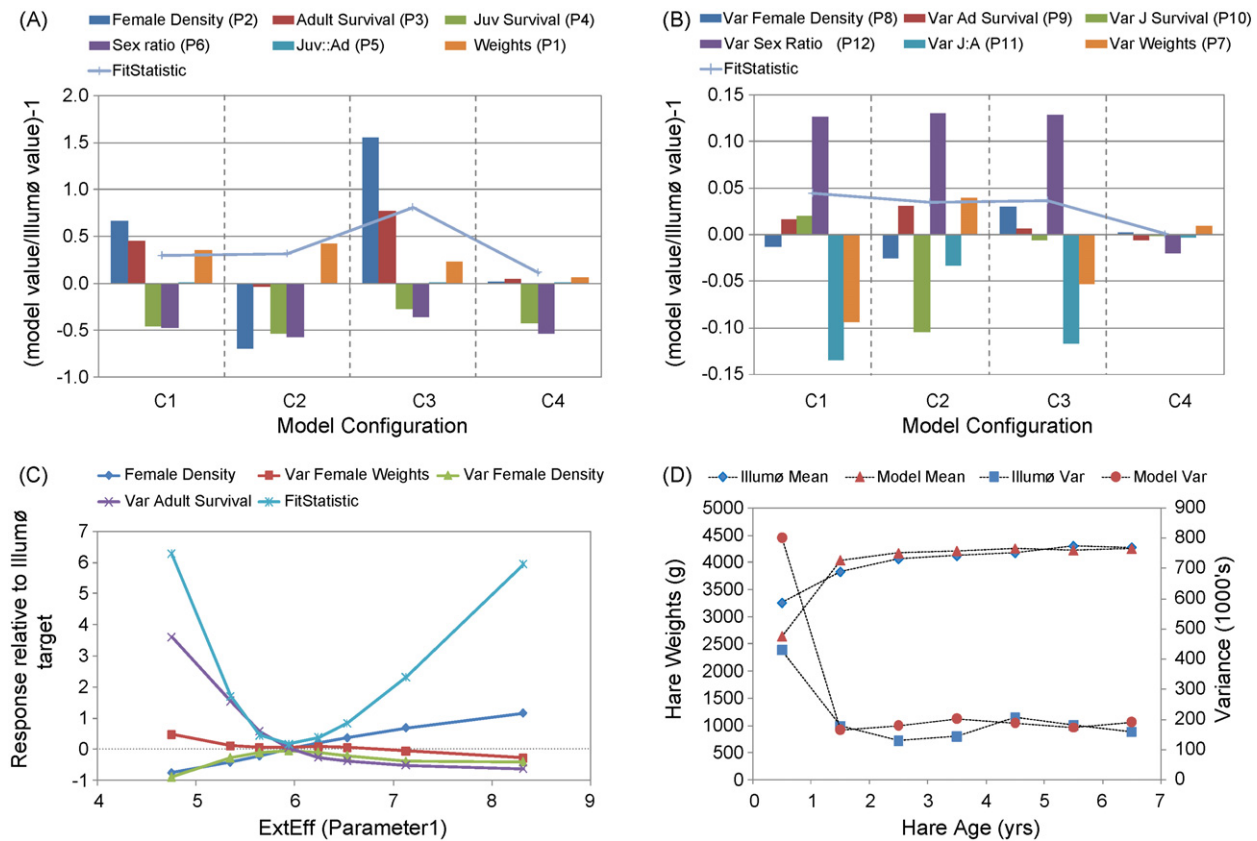
Fig. 2. Pattern-oriented testing using comparisons of field data and model output. Configuration C1—delayed density dependence such as disease; C2—direct density-dependent mortality; C3—stochastic processes with a high density-dependent mortality threshold; C4—interference competition leading to reduced time available for foraging. The fit of all four configurations was compared to field data from Illumø with the aim of reducing all deviances using a single set of parameters for each configuration. (A) Best fit to first order target patterns (means) for C1–C4, (B), the same parameter sets' fit to second order target patterns (variances). Fit statistic is a weighted mean deviance of all patterns. (C) Shows the use of the fit statistic to fine tune the parameter values to minimise all deviances between model output and field patterns for a single parameter (food extraction efficiency, ExtEff). Response variables with very weak or no response have been removed for clarity. (D) After parameter fitting was completed the optimal set of parameter values obtained was used to predict female hare weights providing a close fit to the Illumø data.

A new section, "Interconnections", is used to describe these and provide html links to them. This approach permits the documentation of large models to be built as an expandable library, and rather than rewriting documentation for additions only requires judicious updating of the interconnection section, doxygen performs the rest of the tasks based on software comments in the new code. Our aim in developing ODdox was therefore to provide an easier, more complete, and more flexible method of documenting large models together with a more user friendly interface, benefitting developers and readers alike.

The resulting html documentation presented here provides an overview of the brown hare model as well as a fully hyperlinked class hierarchy showing the relationships between classes, their methods and variables in the program together with descriptions of their function. At the lowest level, source code is provided for the methods. This allows the reader to obtain an overview as well as to verify the implementation of model details.

3. Results

An important result from initial testing was the identification of incoherencies in the published field data. Model fitting suggested that no model could simultaneously satisfy the requirement for matching survival rates and population sizes of females and juveniles to the Illumø data set. It was therefore necessary to test the validity of the field-data patterns. A two-stage matrix model

using transition rates based on adult and juvenile survival was constructed to obtain a stable solution matching either the observed age structure or the observed survival rates. The solution demonstrated that it was not possible to obtain the observed age structure using the mean survival rates given by Abilgård et al. (1972), and that to match this age structure would require a population with an annual growth rate of 15%. The population on Illumø showed no indications of such an increase. Since the mark-capture-recapture methodology used in the original study was a potential source of error, an assessment of the likelihood of generating bias of this kind was made by simulating hare capture data in ALMaSS and deliberately introducing bias in re-capture. In all cases these simulations indicated that any feasible introduced bias would exacerbate the observed incoherencies. This left only the possibility that the observed discrepancy between age structure and survival rates was the result of stochasticity and that the 14-year time series was not long enough to elucidate stable mean patterns. Since it was impossible to determine which of the three measures (age structure, female survival or juvenile survival) were at fault the approach taken was to project the juvenile/female ratio from the survival rates and iteratively modify survival rates inside their 95% confidence limits to minimise the least squares deviation from all three target patterns. The original and resulting target patterns were: 0.438, 0.552, 0.575 cf. 0.425, 0.519, 0.531 for juvenile survival, adult female survival and age structure (juveniles/(juveniles + females)), respectively. These new values were then used in subsequent iterative testing.
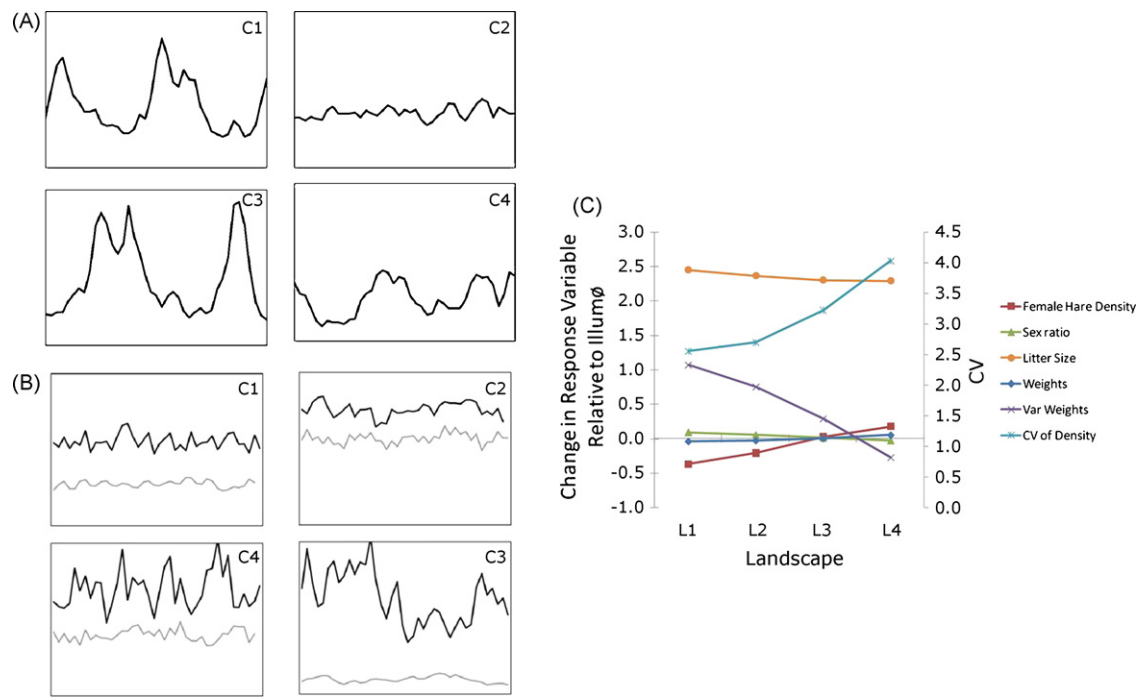
Fig. 3. Model time series outputs and changes in response variables with changing landscape heterogeneity. (A) Typical population size time-series from main configurations tested (C1–C4) from simulation year 21 to 60. *Y*-axis range is 0–150 female hares km^{-2}. Three out of the four configurations produced ostensibly similar dynamics to those found on Illumø (Fig. 1B). (B) Changes in number of female hares with time from the best parameter fit for model configurations C1–C4 from simulation year 21 to 60 on the most homogenous and most heterogeneous landscapes (L1 grey & L4 black). *Y*-axis range is 0–150 females km^{-2}. (C) Using the best fit parameter set with configuration C4 it is clear that density changes with landscape heterogeneity, but that variance in density decreases and variance in female weights increases. These patterns form secondary predictions that could be tested against further field data if available.

3.1. Iterative testing and reformulation of the model

The scope of the problem when testing a model of this type is large since there are an unknown number of potential model configurations to test and an unknown level of difficulty in optimally fitting the parameters. Running a fully replicated set of all parameter values by all configurations would take many years, so a guided parameter value selection process was used, even so in excess of 250,000 scenario runs were executed using 47 model configurations before a satisfactory fit was achieved. A single run of 60 years in daily time-steps took a mean of 25 minutes, resulting in a total CPU time of approximately 12 years on standard 2.3 GHz PCs, or nine months in real time with our PC cluster. The primary constraint to testing was therefore available CPU time.

Fitting C1, C3 and C4 configurations resulted in less than 5% deviation from the first order target patterns of mean density, adult and juvenile survival and variance in juvenile:adult ratio (Fig. 2A). Density-dependent mortality (C2) failed to simultaneously fit sex-ratio, survival and age-structure patterns. Fits to juvenile survivorship could only be obtained by targeting density-dependent mortality on the leveret and young hare life-stages (not shown). Only C4 permitted simultaneous fits of all six first order target patterns. None of the configurations fitted variance in juvenile survivorship nor variance in sex ratio, with model results consistently having too low variance, but C4 clearly provided the overall best fit to the second order target patterns (Fig. 2B). Some form of oscillatory dynamics was evident in all four configurations (Fig. 3A), but variance around density suggests that C1 & C3 were too extreme and C2 too stable relative to the Illumø situation.

3.2. Breeding patterns

Litter sizes of all configurations tested fell in realistic ranges, although the actual values varied (1.9, 2.3, 2.1, and 2.3 C1–C4,

respectively). Similar variation around acceptable values of litter numbers also emerged (2.9, 2.7, 2.5 and 2.6, C1–C4, respectively).

3.3. Positive effect of increasing habitat heterogeneity/negative effect of homogenous crop areas (Pattern 15)

All four configurations produced the expected increased density with increasing heterogeneity but with differing slopes (Fig. 3B and C, Table 5), and all configurations produced litter sizes and mean numbers of litters within acceptable ranges. Interestingly, the models make a strong secondary prediction that variance in hare weights should increase with homogeneity of the landscape together with a slight increase in mean weight. In all cases where significant effects were found the model configurations agreed in terms of the direction if not the magnitude of the effects.

Table 5
Slopes of fitted regressions using first order response patterns as the dependent variable against four structurally different landscapes only differing in their heterogeneity for four model configurations. Bold indicates $p < 0.05$.

	C1	C2	C3	C4
Weights (P1)	**0.08**	**0.07**	**0.05**	**0.03**
Female density (P2)	**0.17**	**0.10**	**0.30**	**0.19**
Adult survival (P3)	0.00	0.00	0.00	0.00
Juv survival (P4)	0.02	−0.08	0.00	**0.00**
Juv::Ad (P5)	−0.01	0.04	−0.01	0.00
Sex ratio (P6)	0.02	**0.00**	0.00	**−0.04**
Var weights (P7)	**−1.71**	**−1.98**	**−1.43**	**−0.45**
Var F. density (P8)	**34.49**	16.48	**554.59**	**615.07**
Var Ad survival (P9)	−0.03	**0.00**	−0.02	**0.00**
Var J survival (P10)	−0.01	0.00	0.00	0.06
Var J:A (P11)	0.00	0.00	0.00	**0.00**
Var sex ratio (P12)	−0.01	0.00	−0.01	0.04
Litter size (P13)	**0.17**	−0.01	**0.13**	0.00
No litters (P14)	**−0.07**	**0.16**	−0.02	**−0.05**

Although not one of the target patterns, cyclic dynamics were not easy to obtain on the larger landscapes. It was also evident that the same controlling mechanism was capable of generating very different time series patterns even though the only factor varied was the spatial arrangement of landscape features, with homogenous landscapes producing much less variable dynamics (Fig. 3B).

3.4. Sensitivity analysis of the resulting final model

Model configuration C4 performed better in the iterative tests than any other configuration and was used for detailed sensitivity testing. The most impressive fit of C4 to the Illumø patterns is perhaps to hare weights. The weight of each hare is emergent, determined by the energetic relationships described above and the local conditions affecting resource availability. Model hares experimentally fed *ad libitum* in the model all reached maximum weight of 5.2 kg. The fact that the model not only generates the mean Illumø weights accurately at 4.2 kg, but also fits the sensitive pattern of variance of weight, promotes confidence in model behaviour (Fig. 2D). Fig. 2C shows an example response of the model to varying single parameter values in the range ±40%. This example also shows one of the most pronounced curvilinear responses observed, that of Pattern 9, variance of adult survival. Significant linear responses were found in 76% of all parameter/target pattern combinations tested together with a range of strengths of responses as indicated by the slopes (Tables 2 and 3). The potential of a strong curvilinear fit to cause a false negative was not considered a serious problem since a strong curvilinear response will also produce a linear fit as evidenced by Pattern 9. The model outputs for this pattern were strongly curved; nevertheless it was not excluded as an important response variable because of the steep slope.

Slopes can be compared directly between patterns but not between parameters since units and potential ranges of values differ greatly. We scaled the slopes by the corresponding fitted parameter value, which permits direct comparison of slopes by assuming equivalency of coefficients of variation.

All parameters that had large impacts affected mean female density, with ExtEff, ALoss and FoetalGrProp (see explanations of abbreviations in Table 4) producing the strongest responses. This indicates the sensitivity of the model to food supply, adult survivorship and reproductive capacity.

Sensitivity of the oscillatory pattern was investigated by altering details of the C4 model configuration in order to determine the driving factor behind this pattern, since this was not immediately obvious. These manipulations indicated that oscillations would disappear, even though population control would still be achieved above the target level, if there was no energy deficit for adult hares moving from negative to positive energy balance. The model is therefore sensitive to the assumption that the hares cannot replenish a long negative energy deficit immediately but are limited by their daily intake capacity.

3.5. Model documentation

The ODdox for the brown hare model is provided in the supplementary materials (Appendix 1) and should be referred to for full documentation. A summary of the final model is presented here:

The hare model runs inside a dynamic landscape simulation incorporating detailed topography, weather, and human activities in the form of agricultural management and infrastructure. The hares are simulated in five life-stages: infants up to 11 days during which they are totally dependent on the lactating doe; young 12–35 days old after which they are fully weaned, juveniles 35–365 days old, adult males and females. The model hare is quite mobile and able to find suitable forage over a wide area when not encumbered with young. Breeding starts in Spring if body condition allows for the production of foetal mass. After birth the female must increase her energy intake in order to provide enough energy for lactation. Energy comes from foraging from green shoot material and the amount of energy obtained depends on the age of the shoot and the overall structure of the vegetation. Dense vegetation may therefore have a high food value in terms of biomass but a poor digestibility and high impedance. A female that cannot support lactation because her combined energy intake and reserves fall too low will abandon her young. Reproduction will not be attempted again until energy reserves are replenished. Growth of model hares is also dependent on energy balance and hares which do not achieve 45% of their potential weight at any age will die. Adults rarely die of energy shortage and are assumed to be able to "carry" a negative energy balance. Since they will remain in the population contributing to social stress, which is the primary density-dependent regulation factor in the hare model. Hunting occurs in Autumn but other non-energetic related losses are based on life-stage specific constant daily probabilities or on events driven by human management activities.

3.6. Application to model question

Naturally, none of the model configurations tested gave perfect fits, but the final model chosen could match 13 out of 15 real world patterns, leaving only variation in juvenile survivorship and sex ratio unaccounted for. The result erects the testable hypothesis that controlling factors on Illumø were primarily related to density-dependence working via body condition, and not generated by the mechanisms simulated in C1–C3.

In addition, the slopes of the parameter responses and interactions from the fitted model provide a direct means to evaluate the impact of changing a factor on the population dynamics. Several of the parameters investigated had no direct analogues to real-world drivers. Two examples are changing food extraction efficiency (ExtEff) and the proportion of energy that the female is assumed to give to producing young, both of which are important parameters resulting in strong responses. In some cases where parameters have real world analogues, the slopes can be used directly (loss rates and rainfall), whereas the response to landscape structural changes required the application of scenarios and further analysis. Overall it is clear that factors affecting the survival of the adult female hares have a marked impact on total population numbers, juvenile and young loss also having a major impact. Rainfall is likely to be important too, but does not seem to have as strong an impact. The strong response to increasing habitat heterogeneity also indicates the importance of habitat quality and provides a direct indication of one practical approach to improving conditions for hares also suggested in UK hare conservation (Vaughan et al., 2003; Smith et al., 2004).

4. Discussion

The pattern-oriented approach to testing models is becoming widely used both in ecology and other branches of biology, as well as other sciences. Examples vary from testing shorebird models (Goss-Custard et al., 2006) to consumer behaviour (Zhang and Zhang, 2007) and wound healing (Mi et al., 2007). The range of applications makes generalisations difficult, but the refinement of existing protocols for testing and communicating model structure may facilitate progress. We propose the adoption of 'the modelling cycle' for a complex system of interacting agents (Grimm and Railsback, 2005a), together with a documentation process based on using OOD for smaller models, and ODdox for larger simulations systems. However, during development of the hare model it was clear that a primary cause for concern was the incomplete
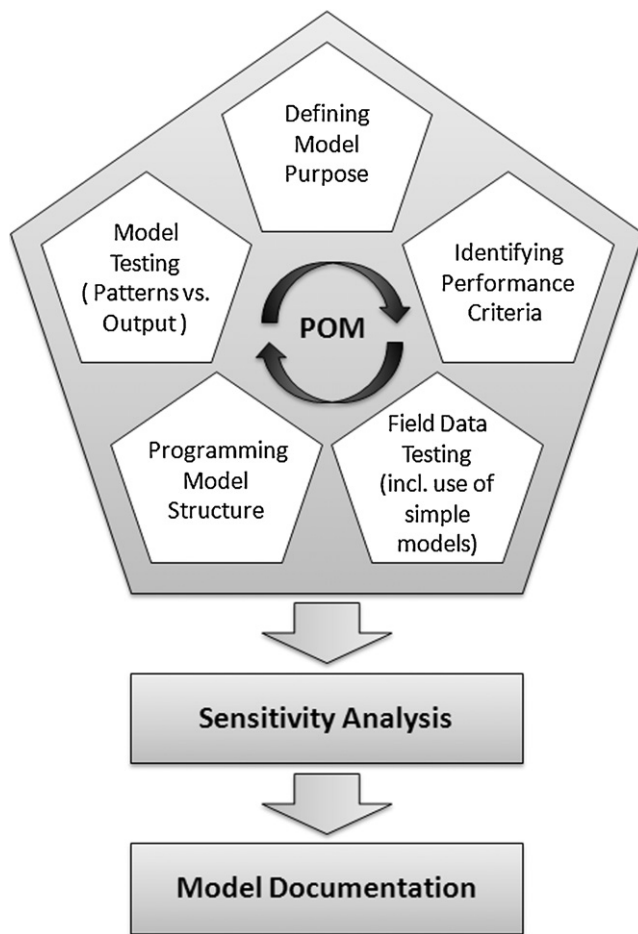
Fig. 4. Diagramatic representation of the modelling cycle protocol. After initialising the cycle by defining a model question it is necessary to traverse the complete POM (Pattern Oriented Modelling) process at least once, thereafter should the model performance meet the performance criteria the cycle will be interrupted and sensitivity analysis and documentation performed.

understanding of the field data patterns used for testing. Limitations of these data sets only became apparent after considerable model testing, requiring re-formulation and the use of simple models for screening, suggesting that inconsistencies in published data are not always easy to identify. It would therefore be useful to add a further stage to the modelling protocol designed to explore field data patterns and check for inconsistencies as part of the iterative model cycle (Fig. 4).

The subsequent parameter fitting of the chosen model configuration should lead into a sensitivity analysis. In the case of the brown hare model long run times required efficient sensitivity analysis procedures. There are a number of methods of sensitivity analysis suitable for ABMs such as the hare simulation, but complex approaches like Extended Fourier Amplitude Sensitivity Test (Saltelli et al., 1999) or Bayesian MCMC approaches do not provide information with a clear physical meaning (Ravalico et al., 2005). Ravalico et al. (2005) compared sensitivity analysis methods for complex models in environmental management, concluding that none of the current methods met all criteria of efficiency and applicability. With multiple response variables, the number of runs required to carry out in this study would have been too great so we adopted a simple scaled regression approach, providing a physical reference for the results. This easily accessible approach provided the basic information that was required for understanding the system responses.

In contrast to other hare species, cycling has not been described for the brown hare, it being considered a non-cyclic species (Keith,

1983). Although there are no reports of clear cyclicity, support for the fact that this might occur does exist. There is evidence to suggests there may be phases of 8 years in some British game-bag data (Tapper, 1992), and there has been some indication of phases of population change related to fecundity (Marboutin et al., 2003). The lack of observed cycling may be due to the spatial and temporal heterogeneity in brown hare habitats, and also to the fact that cycles might disappear or be hard to find in declining populations, or in larger landscapes as we showed in this study (Fig. 2, C4). In contrast to factors causing decline, the lack of clear cyclicity means that population regulation in the brown hare has not been well studied. However, there is strong evidence that adult survival is generally constant and high (Smith et al., 2005), whereas fecundity is highly variable both in terms of reproductive output and survival of young hares (Marboutin and Peroux, 1995; Marboutin and Hansen, 1998), both factors matching with the conditions required to produce oscillations in C4.

The POM testing produced a new hypothesis for brown hare population regulation that does not appear to have been discussed previously. Testing of model configurations clearly suggested that the configuration based upon interference competition (C4) produced the best fit to observed patterns. This is in contrast to mountain hare *Lepus timidus* populations which are thought to cycle due to host–parasite interactions (Newey et al., 2007). Abilgård et al. (1972) indicated that there was no epidemic disease on Illumø, but that hares were found dead from both disease and parasitic causes, so the role played by parasites and disease cannot be entirely ignored. However, the role of interference as a regulating factor is indicated in other studies. High natal dispersal and inverse density dependent dispersal rates have been shown in the brown hare (Bray et al., 2007). These were considered to arise from two possible hypotheses: the social fence hypothesis (Hestbeck, 1988) whereby movement is limited by avoidance of social stress in high density areas; and an alternative whereby social stress causes only small-scale movements high density areas to accommodate re-distribution of resources. In both cases they make the explicit assumption of social stress or interference competition. The C4 configuration invokes dispersal by the hare in response to food stress, primarily in females (evidenced by the skewed sex ratio in C4 model hares). This dispersal to obtain resources for females conforms to expectations based upon Greenwood's resource competition hypothesis (Greenwood, 1980) and general expectations for polygynous-promiscuous mammals (Perrin and Mazalov, 2000). Further support for this hypothesis comes from Monaghan and Metcalfe (1985) who describe increasing aggressive behaviour and time spent running as hare density around a food source increased.

If we accept that interference competition was the main population regulating factor on Illumø, this does not necessarily mean that it is a powerful effect. Indeed, we found that cyclic population dynamics was very much reduced in a larger landscape and low heterogeneity, which suggests that the phenomenon would be easily disrupted should further environmental variability be introduced. Experimentation with the model demonstrated that the effect was primarily linked to reproductive output via temporary deterioration of female physiological status due to lowered energy intake. Cyclicity was a result of carrying an energy deficit and acted as a synchronising factor causing low fecundity in the period following low food and high density. The longevity of the hares exacerbates this effect whereby a high density of adults will have a long-term effect on the growth rates and fecundity of subsequent young. This situation is analogous to snowshoe hare population dynamics where cyclicity has been attributed to a tri-trophic effect whereby food stress is caused by avoidance of predation (Krebs et al., 1995), and may be a more widespread phenomenon (Creel and Christianson, 2008). There is also evidence from the snowshoe hare that different morphs alternate through different phases of the

cycle and that this could work synergistically with extrinsic causes (Sinclair et al., 2003). This situation is very close to the interference competition with a minimum breeding weight configuration (C4) which was selected as the best fit to the Illumø conditions.

In terms of identifying the primary regulating factor on Illumø we would clearly choose interference competition. However, success should not only be judged by the models explanatory or forecasting ability (Conroy et al., 1995), but also on its contribution to understanding the system. In the real world we would expect multiple mechanisms to contribute to the dynamics, but in varying degrees. This argues for the inclusion of mechanisms that we know exist but cannot justify in terms of the information used to fit the model. One approach to this problem would be to build in all mechanisms subsequent to fitting the primary mechanism and to adjust the fit from this point; providing the most optimal framework for testing population control hypotheses. This argues for a systems approach to modelling for ecologically complex questions. Thus complex ABM systems models such as ALMaSS could be used as a framework for understanding the biological system when linked to field studies to create a cycle of improvement of understanding. This would eventually lead to realistic models that would be mechanistically rich enabling better predictive potential, since they are mechanistic and more complete, than using reductionist modelling approaches. Completeness also infers the added advantage of flexibility, for example if dispersal and mating behaviour are realistic in a population model, then it could easily be augmented for tackling population genetic questions (e.g. Topping et al., 2003a). Similar approaches have been advocated in landscape ecology, as generative landscape science (Brown et al., 2006), and in immunology and cell biology as a complementary approach to wet-laboratory study (Kleppe et al., 2006) where they have clear advantages in terms of pedagogy, testing and study of emergent phenomena and quantitative predictions (Bersini, 2006). When using models of this type experimentation and hypothesis testing is easier, it is easier to isolate and test single mechanisms, and data can be integrated from several different experiments into a single in silico experimental system (Forrest and Beauchemin, 2007).

Better communication of the models, perhaps using the ODdox method, may open up the 'black-box' sufficiently to provide access to the scientific community. It may then be possible to develop these larger and complex models as longer term collaborations, such as seen in development of open source programming projects. In this case, discussion and data to challenge the mechanisms implemented ought to be forthcoming as a community function.

5. Conclusions

An agent-based model of the European brown hare was evaluated by pattern-oriented modelling resulting in new insights into the species' ecology and population regulation. Most of the known behavioural biology and mechanistic details of the species was incorporated into the model. This holistic modelling approach provided the flexibility to evaluate contrasting population regulation hypotheses by integrating multiple factors in space and time to produce systems level responses. The approach therefore lends itself to studying multifactor whole organism systems. The common criticism of lack of model transparency was addressed by defining simple but effective protocols for the application of model development and documentation; potentially paving the way for a community-based collaborative study of complex systems.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.09.014.

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