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Spatially explicit models in landscape and species management

PhD thesis

Jane Uhd Jepsen

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Abstract: This thesis deals with four main subjects related to the use of spatially explicit models in landscape and species management. These subjects are i) Landscape modelling and the representation of space, ii) Predicting species distribution and abundance, iii) The trade-off of complexity and the choice between simple and complex models, and iv) The importance of individual behaviour and the use of complex behavioural models in evaluating impact of long-tern landscape planning on wildlife. Each subject, and most of the questions raised dealing with it, are of general concern when using simulation models as tools in management and conservation anywhere in the world. The general discussion is illustrated by a set of case studies focused on North-Western European agricultural landscapes.

Keywords: spatial models, model comparison, individual-based ecology, predictive management.

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PREFACE AND ACKNOWLEDGEMENTS

This thesis is presented to fulfil the requirements for a PhD degree at the University of Copenhagen, Department of Population Ecology. My research has been conducted at the National Environmental Research Institute, Department of Wildlife Ecology and Biodiversity (former Department of Landscape Ecology) and supervised jointly by Gösta Nachman, University of Copenhagen and Chris J. Topping, National Environmental Research Institute. I'm grateful to you both for constructive criticism, discussions and enjoyable moments along the way. I'm especially grateful to Chris J. Topping for patiently introducing me into the realm of object-oriented programming and individual-based modelling and for keeping a firm belief in me at all times.

During my PhD, I've enjoyed the hospitality of the Spatial Modelling research group at Alterra Green World Research in Wageningen, The Netherlands. I thank all the staff, in particular Jana Verboom, Claire Vos and Hans Baveco, for making it such an enjoyable time for me. During my last year as a PhD student, I was granted an extended leave to take up a Marie Curie Training Site Fellowship at the UFZ-Centre for Environmental Research Leipzig-Halle, Germany. I'm deeply indebted to Christian Wissel and to Karin Frank for taking me in and offering me a superb working environment. Everyone else in Sektion Ökosystemanalyse contributed to making it an unforgettable and productive stay.

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Numerous other people have contributed with discussions, ideas and comments on manuscripts in course of the last 3½ years. Most noticeably I would like to thank Frank Nikolajsen for assistance in programming and Geoff Groom and Poul N. Andersen for remote sensing classification and support on various GIS issues. Aksel B. Madsen, Chris J. Topping, Gösta Nachman, Peter Odderskær and Mette Hammershøj provided valuable comments on all or parts of the synopsis. A special thanks to all my colleges at the National Environmental Research Institute, in particular my fellow PhD students Mette Hammershøj, Pernille Thorbek, Bettina Nygaard and Erik Aude, for unlimited scientific and moral support.

A Haiku poem separates each section of the thesis. They are all by the Japanese poet Issa (1763 – 1827) in the translation of David G. Lanoue. I put them there, because a skilful Haiku poet can do what no ecological modeller has yet achieved. Namely to capture the essence of life's complexity in less than 17 syllables.

Jane Uhd Jepsen
Kalø, February 2nd, 2004

1. LIST OF PAPERS

I. Topping, C.J., Hansen, T.S., Jensen, T.S., **Jepsen, J.U.**, Nikolajsen, F. & Odderskær, P. 2003. ALMaSS - an agent-based model for animals in temperate European landscapes. Ecological Modelling 167: 65-82.

II. **Jepsen, J.U.,** Madsen, A.B., Karlsson, M. & Groth, D. Predicting distribution and density of European badger (*Meles meles*) setts in Denmark. Submitted to Biodiversity and Conservation.

III. **Jepsen, J.U.**, Baveco, J.M., Topping, C.J., Verboom, J. & Vos, C. Evaluating the effect of corridors and landscape heterogeneity on dispersal probability - a comparison of three spatially explicit modelling approaches. Ecological Modelling in press.

IV. Knauer, F., **Jepsen, J.U.**, Frank, K., Pouwels, R., Wissel, C. & Verboom, J. Approximating reality? Evaluation of a formula for decision support in metapopulation management. Submitted to Oikos.

V. **Jepsen, J.U.** & Topping, C.J. Roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: Behavioural plasticity and choice of cover. Submitted to Canadian Journal of Zoology.

VI. **Jepsen, J.U.**, Topping, C.J., Odderskær, P. & Andersen, P.N. Assessing impacts of land use strategies on wildlife populations using multiple species predictive scenarios. Submitted to Agriculture, Ecosystems and Environment.

Papers are referred to in the synopsis by their Roman numerals. Abstracts of papers I and III are reproduced with permission from the publisher.

2. SYNOPSIS

This thesis deals with four main subjects related to the use of spatially explicit models in landscape and species management. Each subject, and most of the questions raised dealing with it, are of general concern when using simulation models as tools in management and conservation anywhere in the world. But the scene is set in a North-Western European agricultural landscape and this is reflected in my choice of case studies and target species.

The basic consideration before developing or applying any spatial model, be it simple or complex, is the representation of space itself. With the advance of GIS and remote sensing techniques and the increasing availability of digital map data, there is almost no end to the degree of environmental realism that can potentially be incorporated into spatial models. The first section of the synopsis summarises how this has been done under the heading '**Landscape Modelling**'. I place special emphasis on novel approaches that combine landscape features, environmental dynamics and human decision-making to create dynamic landscape simulations and exemplify this by a case study (paper I).

Through the eyes of a wildlife ecologist, the ultimate goal of landscape models is to provide information about how the distribution and availability of wildlife habitat is affected by the interplay between social, economic and natural processes. Consequently, wildlife ecologists tend to place more emphasis on the end products of landscape models (habitat distribution maps, rate of habitat loss etc.), than on the finer mechanisms shaping it. This point is well illustrated by the use of spatial information in predictive habitat models, much of it end products of simple landscape models. Under the heading '**Predicting species distribution**', I address the use of predictive habitat models in management and conservation. Broadly speaking the term 'habitat model' covers approaches that use environmental correlates to predict species presence or abundance based on surveys from a limited region. So while the requirements for landscape data may be large in such models, the need for additional species-specific information is minimal. I firstly discuss some of the current methodological issues related to the development, validation and application of predictive habitat models in conservation and management. The focus is on habitat models developed using regression techniques. I then proceed to summarise the case study of the European badger (*Meles meles*) in Denmark presented in paper II, in the light of the methodological issues raised.

Habitat models can be considered a fairly homogeneous group of simple models, although variation obviously exists in methodology and data requirements. But even within this fairly homogeneous lot, the trade-off between effort and gain is nursing an ongoing discussion. In other words, does an increase in effort and costs (increased spatial resolution, abundance data instead of presence-absence data etc.) improve the quality or predictive ability of the model? This discussion is a fundamental one in ecological modelling. It is even more relevant for spatial population models where the span between the simplest and the most complex approaches is immensely wide. The section under the heading '**The trade-off of complexity**' is rooted in the discussion on complex versus simple models and the consequences of model simplifications. I discuss specifically how the choice of model may affect the conclusions and predictions we make regarding a particular management case (paper III). In addition, I include a case study illustrating the consequences that the structural simplifications necessary in mathematical frameworks may have when applied to real systems (paper IV). The trade-off of complexity is a returning issue in every chapter in this thesis. In fact it constitutes an important part of the rationale behind the thesis in the first place.

Finally, the last subject is concerned with the use of reasonably complex behavioural models in management. Agricultural ecosystems are temporally and spatially dynamic and highly affected by the continuous interference by man. Two important consequences of this are that the degree of fragmentation of natural habitats is high, and that the living conditions for many wild animals change often and rapidly. This places an increased emphasis on the implementation of realistic time, space and behavioural interactions in management models. However, these models are often accused of being overly complex and the results difficult to communicate. Under the heading '**Evaluating impacts of long-term landscape planning on wildlife**' I discuss the motivation for using detailed behavioural models and the issues of generalisation and communication of the results of complex models (papers V and VI).

2.1. Landscape Modelling – Supplying spatial data for simulation models of animal populations

2.1.1. Representing space

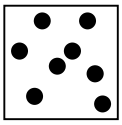
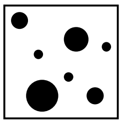
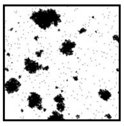
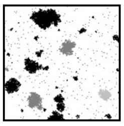
Richard Levins first conceptualised the importance of spatial structuring in population dynamics when he coined the term *metapopulation* (though formulated in a non-spatial framework; Levins 1969, Levins and Culver 1971). Since then metapopulation theory has become an established concept in ecology and the metapopulation structure the most common approach adopted in models of spatially structured populations (Gilpin and Hanski 1991, Hanski 1997 and references therein). A metapopulation space is a patch-based view of the world, where a landscape consists of a number of suitable habitat patches in a uniform unsuitable matrix. Patches may be of varying size and placed in a non-uniform spatial arrangement (table 1, I and II). A metapopulation space is thus the simplest possible representation of an explicit, spatially structured environment.

One of the fundamental assumptions when adopting a metapopulation structure in a spatial model, is that patch attributes (size, inter-patch distance) is of overriding importance, compared to matrix attributes, for the dispersal of organisms in a landscape. This conflicts somewhat with the strong focus on landscape structure and heterogeneity prevailing in landscape ecology. An early attempt to bridge this gap and incorporate additional environmental information, while maintaining a traditional metapopulation model structure, was made by Moilanen and Hanski (1998). In one experiment they used landscape structural data obtained from satellite images to modify patch isolation estimates according to matrix attributes along straight-line transects between patches. Hence, the presence of a suitable habitat would decrease patch isolation, while the presence of an unsuitable habitat would increase patch isolation. This translates into a decrease or an increase in patch connectivity. Their results were discouraging, since the approach failed to significantly improve the fit of the metapopulation model (Moilanen and Hanski 1998).

More recent approaches have used 'least-cost' modelling techniques to integrate matrix attributes in connectivity measures and metapopulation structures (Roland et al. 2000, Michels et al. 2001, Schadt et al. 2002, Sutcliffe et al. 2003, Adriaensen et al. 2003). Least-cost modelling is similar to the approach used by Moilanen and Hanski (1998) in that the Euclidean inter-patch distances are modified according to a set of habitat specific rules (generating 'ecological' distances) with a basis in species ecology. The major difference is that least-cost approaches use spatial algorithms (now available in most GIS systems) to determine the 'cost' of moving in all possible directions from a source cell. Hence it is able to identify the 'least-cost' path which may not be a straight line between patches. The traditional mathematical framework of a metapopulation model can in principle be retained, by substituting the resulting 'least-cost' distances for the Euclidean distances. Least-cost modelling has proved to be a significantly better predictor of species movement patterns in real landscapes than Euclidean distances (e.g. Roland et al. 2000, Sutcliffe et al. 2003). It must be considered a promising tool to evaluate and modify distance variables according to landscape heterogeneity and general species behaviour.

Mathematical formulations of spatially structured populations (incl. classical metapopulations) typically treat space as a continuous variable. Local dispersal is incorporated by assuming a distance-dependent or nearest-neighbour relationship for the dispersal probability between two locations. A space-continuous approach is not compatible with modern rasterized or vectorized digital data sources, nor is it suitable for portraying detailed local dispersal or explicit movement patterns. Most spatially explicit approaches therefore represent space as discrete units, typically square- or hexagonal grids (table 1, III-VI). Simplified grid-based representations of space such as cellular automata or neutral landscape models (Gardner et al. 1987, Gardner and O'Neill 1991, With 1997) have been invaluable in exploring local dispersal (e.g. Hiebeler 2000), local interactions between individuals (Silvertown et al. 1992), spread of invading species (Sherratt et al. 1997), species co-existence (Grist 1999) and the effects of various landscape structural patterns such as fragmentation levels and habitat loss (e.g. Lancaster et al. 2003, paper V) on species dispersion. Neutral landscape models in particular have been useful in theoretical studies of critical thresholds in landscape connectivity and percolation theory (With 1997, With and King 1997, McIntyre and Wiens 1999, King and With 2002).

Table 1. A generalised overview of the major types of spatial representations used in applied landscape models.

			Patch area	**Patch shape**	**Matrix**	**Environ-mental dynamics**	**Associated species dispersion**	**Thesis reference**
Patch-based		I	uniform	circle	homog.	no	rates	
		II	varies	circle	homog.	no/yes	rates	paper III, paper IV
Raster- and vector-based		III	varies	varies	homog.	no	probabilistic/ rule-based	paper V
		IV	varies	varies	homog./ heterog.	no/yes	probabilistic/ rule-based	
		V	varies	varies	heterog.	no	probabilistic/ rule-based	paper II, paper III
		VI	varies	varies	heterog.	yes	probabilistic/ rule-based	paper I, paper II, paper VI

Both neutral landscape models and GIS-based approaches such as least-cost modelling are attempts to increase the degree of spatial detail taken into account in landscape modelling, without moving too far away from a metapopulation view of the world. Neutral landscape models are, with their binary landscape representation, intuitively closest to a metapopulation space. Approaches such as least-cost modelling move one step further in that they include very detailed landscape- and species-specific information in a highly aggregated manner. Behind an ecological distance calculated using least-cost models, is information on detailed landscape structure and content as well as on species habitat choice. As such, least-cost models appear, as were they just one step down on the information-ladder from spatially explicit movement models (for example the 'Smallsteps' model described in paper III). But there are important distinctions (Adriaensen et al. 2003). Most important of them all is the fundamental recognition of individual variation in movement models.

2.1.2. Simulating individuals in a dynamic environment

The presence of individual variation is the main reason why landscape models are developed with a degree of spatial detail and realism that seems extreme compared for instance to a metapopulation space. The real world is non-uniform, individual organisms are distributed in a non-uniform way and may respond differently to identical environmental conditions depending on sex, age, physical condition and past history. The requirements of an individual organism from the environment may change during the day, season or the lifetime of the individual. These are long-recognised facts in ecology and ecological modelling and the motivation behind the rise of *individual-based models* (IBMs) in ecology in the course of the 1980s and 1990s (DeAngelis et al. 1979, Kaiser 1979, Huston et al. 1988, Judson 1994, Uchmański and Grimm 1996, Lomnicki 1999). The transition from a population-based to an individual-based view of the world is much more than just a step up the information-ladder. It is a fundamental shift in the perception of space and the importance of spatial attributes for population level processes. The individual organism is the natural ecological unit (Huston et al. 1988). Whatever patterns and processes we observe at the population level, they are all emerged from local interactions between individuals and between individuals and their environment. Hence it follows naturally that the spatial representations used when modelling individuals should attempt to portray the world as perceived by the individual organism. This is a tremendous challenge, because how does a roe deer or a field vole perceive the world? Which cues in the environment influence individual decisions? And at which scale? In a forthcoming book Grimm and Railsback (in press) move the individual-based approach one step further by coining a new term *individual-based ecology* (IBE). In doing that the authors not only signal that the individual-based approach is a new way of thinking in ecology and ecological modelling. They also prepare the path for a more rigorous and theory-based research agenda focused on how individuals perceive and use environmental information and consequently how the fate of individuals (growth, survival and reproduction) is affected by environmental conditions. Progress in this field will advance our ability to develop landscape models that are closer to the real world as perceived by the organisms under study.

In agricultural landscapes in particular there is an additional component for which individual variation is relevant and that is human activity. Agroecosystems are complex dynamic entities driven primarily by the activities of man. Temperate agroecosystems are under continuous management and are typically the dominating land-use. Agricultural activities cause changes to land-use and vegetation characteristics at a smaller temporal scale and at a larger spatial scale than most corresponding natural processes. Consequently, in agroecosystems, biological processes and human decision-making interact to create complex, temporally and spatially dynamic entities (Antle et al. 2001, paper VI, synopsis section 2.4). This has fostered an increased interest in the role of human decision-making in shaping land-use and hence species distribution patterns. It has also led to the development of a large number of dynamic landscape models to support management models of animal populations (e.g. Higgins et al. 2000, DeAngelis et al. 1998, Ahearn et al. 2001, Gross and DeAngelis 2002, Wu and David 2002, Mathevet et al. 2003, paper I). Some of these models (see for instance Mathevet et al. 2003, paper I) implement human decision-making (especially farming decisions) in the form of autonomous 'agents' or virtual farmers, that make decisions based on a set of decision-rules and environmental information. In fact this is exactly the same way as animal decision-making is implemented in most IBMs. The individual farmer just pursues a different agenda (growing his crops in the most efficient way) from that of the individual animal (maximising its survival or reproduction). There is ample empirical evidence for the importance of spatial context and short-term landscape dynamics for species survival and distribution. Crop choice and crop allocation affect the connectivity of the landscape for dispersing animals (e.g. Basquill and Bondrup-Nielsen 1999, Ouin et al. 2000, de la Pena 2003), machinery and cultivation practices impose direct mortality on species breeding or foraging in agricultural fields (e.g. Strandgaard 1972, Tew and Macdonald 1993, Jarnemo 2002, Purvis and Fadl 2002), and the adverse effects of agricultural activity and pesticide application on invertebrate populations have been shown to depend both on timing and spatial context (e.g. Sunderland and Samu 2000, Thorbek 2003).

2.1.3. ALMaSS – an individual-based simulation of landscape dynamics (paperI)

Paper I presents the design and implementation of the simulation model framework ALMaSS (*Animal, Landscape and Man Simulation System*), with emphasis on the representation of space and spatio-temporal dynamics. ALMaSS was designed as a decision-support tool for use in answering management and policy questions related primarily to changes in land use and agricultural management (for applications of ALMaSS see also Thorbek 2003, Topping et al. 2003, Bilde and Topping in press, Topping and Odderskær in press, Pertoldi and Topping in press). The primary motivation for developing ALMaSS is pragmatic. Human land use strategies and agricultural practices affect (often irreversibly) the living conditions for wildlife species. Assessments of the potential consequences for wildlife of introducing a given change, e.g. in land use, are required. Extrapolation of results from experimental field studies is often less than straightforward due to the large spatial and temporal scales involved and the complexity of natural landscapes. ALMaSS serves the role of an experimental tool-box in which proposed land use changes can be mimicked under controlled conditions and the impact on animal populations can be evaluated based on the best available knowledge about species ecology and species-environment interactions. As such it is intended as a support during the decision-making process and a complement to field surveys and small-scale experimental trials.

ALMaSS is targeted towards temperate agricultural ecosystems as typically found in North Western Europe. These are highly dynamic ecosystems with two primary driving forces: weather and the activities of man. Agricultural activities cause changes to land use and vegetation characteristics at a smaller temporal scale and a larger spatial scale than most corresponding natural processes. This can have profound impact on the suitability of the agricultural surface as habitat for wildlife species. Hence the backbone of ALMaSS is a temporally and spatially explicit simulation of landscape processes related to land use, farming decisions and vegetation growth. The landscape model supplies the model animals with all the information they require on their surroundings. It is designed with a fine spatial and temporal resolution and a high level of detail in the simulation of agricultural activities. This ensures a high degree of realism in the spatial information supplied by the landscape model. It does however also opens up for a potential information overload when evaluating issues or species less affected by fine scale environmental dynamics. To make the ALMaSS landscape model as versatile as possible, it was constructed so that landscape information can be accessed on several levels of detail according to need and relevance (fig. 1). Time series of real or artificially generated weather data is input in the model. This information can be made available to model animals either directly or indirectly via weather effects on vegetation growth. The coarsest level of landscape information is land cover (fig. 1, level 1). A raster map of land cover types (paper I: table 1) is input in the model and this level is therefore unaffected by landscape dynamics. The next two levels contain information of increasing detail resulting from the simulation of landscape dynamics. The vegetation type (fig. 1, level 2) found in a given field changes between years following crop rotation schemes. Vegetation growth follows crop specific growth curves (paper I: fig. 1, table 2). Vegetation characteristics (fig. 1, level 3) thus depend both on weather, crop type and season. Consequently, there is an increase in realism through landscape level 1 to 3, but also an increase in spatial and temporal heterogeneity.

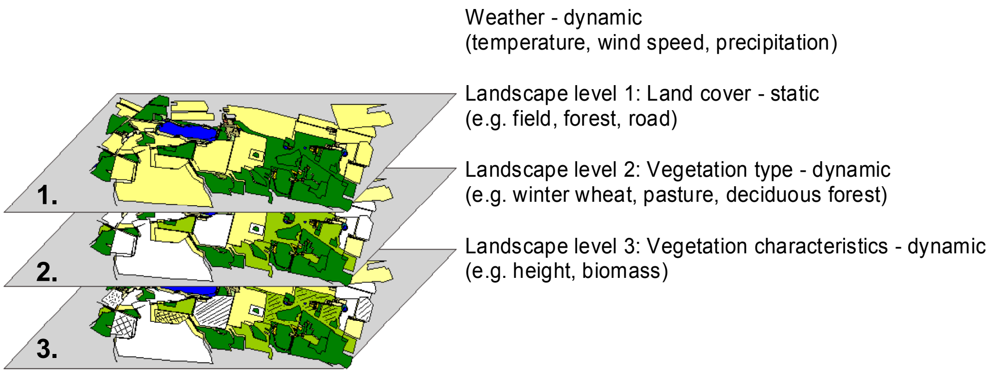


Figure 1. Landscape information availability in the ALMaSS landscape simulation model.

In addition the option exists of switching off the dynamic functionalities of the landscape model altogether. This is equivalent to freezing a snapshot of the model landscape and maintaining it constant throughout a simulation. Consequently, while the ALMaSS landscape model by default is a comprehensive and detailed model it is sufficiently flexible to allow adjustment of the available information to the relevant case. The papers presented in this thesis provide several examples of this. In paper III the full dynamic version and a reduced non-dynamic version of the ALMaSS landscape model are used directly to evaluate the effect of model choice and landscape heterogeneity on predicted dispersal probability of a small mammal. In paper V the realistic landscape representations usually used in ALMaSS are substituted by neutral binary landscapes to study the interaction between woodland fragmentation and behavioural plasticity of roe deer. Finally paper VI utilises the full dynamic landscape model and a range of individual-based species models to discuss the use of multiple-species predictive scenarios in management of agroecosystems.

2.1.4. Looking ahead in landscape modelling

In the absence of sufficiently detailed information on animal perception and the nature of the environmental cues used in animal decision-making, the strategy in many landscape models used for individual-based approaches has been to include as much detail as possible. But landscape modelling is approaching a cross-road, where the rapid advances in computer science, remote sensing and information processing set almost no limit to the level of spatial detail that can potentially be included in landscape models. It is a fact that our ability to capture and represent spatial complexity is progressing much faster, than our understanding of the processes shaping the spatial distribution patterns of species and the ability of individuals to adapt to environmental conditions (paper V). The complexity of the real world can be simulated without great difficulty in a landscape model. But all this information is filtered through eyes that are potentially very different from ours, when an animal decides where and when to forage, disperse or breed. There is a challenge in developing landscape models that reproduce the real world in a more accurate, efficient or detailed manner. Among other things this includes the continued integration of human decision-making in models of landscape change and short-term dynamics. But the main challenge is at the interface between landscape- and species modelling and this is to ensure that the information-level used in landscape models matches the level of detail in the species models (e.g. Lima and Zollner 1996). Meeting this challenge requires an advance in our understanding of behavioural issues such as animal perception and use of environmental cues and adaptive behaviour/behavioural plasticity. And, just as importantly, it requires a continued focus on the consequences of model choice on predictions and recommendations in practical management (Bollinger et al. 2000, Stephens et al 2002, paper III).

2.2. Predicting species distribution

2.2.1. Species distribution models in management and conservation

The terms ‘habitat (distribution) models’, ‘species distribution models’ and even ‘landscape models’, have been used to describe a group of static, probabilistic models that use environmental correlates to predict the distribution of species or communities. As with landscape modelling, large strides in predictive habitat modelling have been taken in the wake of technological developments in GIS software and remote sensing techniques (e.g. Lehmann et al. 2002). Predictive habitat modelling has gained importance both as a research tool and as a method to evaluate possible consequences of changing land use and environmental conditions (e.g. climate) on species distribution and relative abundance (e.g. Buckland and Elston 1993, Pearce and Ferrier 2000, Austin 2002, Lehmann et al. 2002). The dynamic response of many species to changes in environmental conditions is not known. With a predictive habitat model the consequences of changing environmental conditions can, to a certain extent, be evaluated without addressing – or indeed knowing – the in-depth processes shaping the species response to the environment. Habitat models are static and hence assume both equilibrium conditions and a constant response of the species to the environmental variables included in the model. This means that any dynamic behavioural responses (e.g. strong threshold behaviours, behavioural plasticity; paper V) are not easily taken into account.

The most common approach used to develop habitat models is to establish a statistical relationship between a certain number of environmental predictor variables and a response variable, which could be presence-absence, density or relative abundance of a species, or community attributes such as biodiversity or species composition. Generalised regressions are among the most popular statistical approaches, but a multitude of other methods are used more or less frequently (see Guisan and Zimmermann 2000 for a recent review). These include ordination and classification techniques (e.g. Guisan et al. 1999, Eyre et al. 2003), environmental envelopes (e.g. Walker ad Cocks 1991, Bryan 1993), Bayesian techniques (e.g. Wintle et al. 2003), GIS overlay models (e.g. Lauver and Busby 2002), often in combination with rule-based approaches or expert opinion (e.g. Schadt et al. 2002, Chamberlain et al. 2003, Petit et al. 2003, Yamada et al. 2003). Neural networks already have a history in modelling of environmental change especially in remote sensing applications (e.g. Silveira et al. 1996, Cihlar 2000). Only more recently have neural networks been used to predict species distribution with promising results (Özesmi and Özesmi 1999, Bradshaw et al. 2002, Maravelias et al. 2003, Olden 2003).

Information about the presence-absence of a species is generally both cheaper to obtain and associated with less uncertainty, than information on density or relative abundance. But while presence-absence records can at most be seen as an indication of whether or not habitat is suitable for the species, relative abundance or density can be assumed to indicate at least some aspect of habitat quality. This based on the assumption that high density is a result of high survival or reproductive success (e.g. Hobbs and Hanley 1990). It therefore seems obvious to conclude that the additional information content of relative abundance data would improve the predictive ability of habitat models over and above that obtained using presence-absence records. This is not necessarily the case though. In a recent review of a large number of predictive habitat models developed for both plant and animal species, Pearce and Ferrier (2001) concluded that models based on abundance data had no better performance when applied to independent data than models based on presence/absence records. Abundance models with reasonable predictive ability could be obtained for just 12 out of 44 species (Pearce and Ferrier 2001, table 5). For species where a reasonably accurate abundance model was developed, the corresponding presence/absence model performed equally well in indicating relative abundance. There was thus no obvious benefit from using abundance data for developing the predictive models. The authors give two main reasons for this result. Firstly, the assumption that abundance is a good indicator of habitat quality may very well be true for some species, but the relationship is generally unknown. The second reason is related to the increased uncertainty in abundance estimates. Even if a strong relationship exists between abundance and habitat quality, it may be blurred by a poor correspondence between actual and surveyed abundance. Abundance data depends on a uniform detectability of the study objects (and hence on habitat, weather, observer bias etc.) to a much larger degree than presence-absence data.

Introducing a recent special issue on ‘Regression models for spatial prediction’ (*Biodiversity and Conservation* 11, 2002) Lehmann et al. (2002) list the following characteristics required for (regression) models used in biodiversity and conservation assessments: i) Ecologically sensible, meaningful and interpretable, ii) General across space and time, iii) Fully data-defined (e.g. empirical basis for all variables) and iv) Expressed in a spatial framework. This short list summarises many of the important methodological concerns when developing and applying predictive habitat models in management and conservation. For a model to be ‘ecologically sensible, meaningful and interpretable’ it should not only be in agreement with current ecological theory (as argued by Austin and Gaywood 1994, Austin 2002). It is also important that the chosen predictor variables have a clear basis in the biology of the species in question. For example, variables such as ‘moss coverage’ and ‘minimum altitude’ have been shown significant components of regression models describing where badgers place their breeding setts (Macdonald et al. 1996, Good et al. 2001). The causal relationship between these variables and badger habitat choice is not obvious. The significance of such variables may be a result of co-variation between several variables, or simply that they are ‘secondary indicators’ i.e. they indicate certain conditions that directly influence badger habitat choice. Predictor variables with unclear causal relationships with the response variable should always be included with extreme caution, since they are unlikely to be spatially consistent and add little or nothing to our understanding of the environmental mechanisms shaping species distribution. Temporally and spatially consistent variables are prerequisites for obtaining a model that can be extrapolated. The higher the consistency in predictor variables, the larger the environmental space within which the predictive model is valid. The only way to test the generality of the model is through various validation procedures (see below), preferably including validation against independent data. An additional point that also relates to the generality of the predictive model, is the availability of the predictor variables. In species distribution models it is quite common to find variables that describe detailed attributes such as vegetation height or understory plant cover. However, for a model to be useful in prediction on a large scale, the predictive variables must be easy to obtain. This means that they should preferably be obtainable from digital map sources. Variables that require a substantial field effort cannot be obtained on a large spatial scale, and therefore place a severe limitation on the utility of a habitat model in predictive management. The issue of predictive ability is, perhaps surprisingly, not on the list. How accurate a predictive habitat model should be in order to be useful in management will always, to a certain extent, depend on the conditions in which it is to be applied, the types of questions asked and the alternatives available. A rule-of-thumb is outlined in Pearce et al. (2001) based on a common measure of model accuracy (the discriminating capacity (DC) derived from a ROC curve; see below). On a scale from 0.5 to 1, they classify regression models with DC < 0.6 as ‘poor’, with DC = 0.6-0.7 as ‘marginal’, with DC = 0.7-0.9 as ‘good’ and DC > 0.9 as ‘excellent’ (table 2 in Pearce et al. 2001).

The performance of a predictive regression model based on presence-absence data is evaluated based on the ability of the model to discriminate between positive and negative records (e.g. ‘used’ and ‘unused’ sites). Traditionally this has been done using a confusion matrix (e.g. Lindenmayer et al. 1990, Fielding and Bell 1997) shown in fig. 2. In order to determine whether observations have been ‘correctly’ or ‘incorrectly’ classified a threshold must be defined. This threshold separates suitable habitat (where you would expect most of the known presences to be recorded) from unsuitable habitat (where most known absences should be recorded). A threshold can only rarely be deduced from ecological knowledge and is often an arbitrary choice (e.g. 0.5). Threshold independent methods have therefore more recently been introduced into ecology from other fields and are now the recommended approach to evaluating model performance. The most common approach for presence-absence models is to use ROC-plots (Receiver Operating Characteristics plots; Fielding and Bell 1997). A ROC plot is obtained by plotting the sensitivity of the model (= the proportion of used sites correctly predicted to be used, ‘C’ in fig. 2.) against the false positive fraction (= the proportion of unused sites incorrectly predicted to be used, ‘D’ in fig. 2) over a large number of threshold probabilities. The area under the resulting curve (AUC; either calculated directly from the data points or from a fitted Gaussion curve; Pearce and Ferrier 2000) then indicate the probability that the model will distinguish correctly between two observations. For a model with no discrimination capacity the area under the ROC curve will be 0.5, while for a model with perfect discrimination capacity the area will be 1 (see section 2.2.2. for an example ROC plot).

		Recorded		
		Present	Absent	
Predicted	Absent	A	B	A+B
	Present	C	D	C+D
		A+C	B+D	A+B+ C+D

Figure 2. A confusion matrix. A, B, C and D represent the number or proportion of observations. The ‘accuracy’ or ‘matching coefficient’ of the model is the total proportion of correctly classified cells = (B+C)/(A+B+C+D). Redrawn from Pearce and Ferrier 2000.

2.2.2. The case of the European badger (paper II)

The importance of landscape structure and habitat characteristics for the spatial distribution of the European badger has received considerable attention in recent years (e.g. Clements et al. 1988; Thornton 1988; Macdonald et al. 1996; Feore and Montgomery 1999; Virgos and Casanovas 1999; Wright et al. 2000; Hammond et al. 2001; Good et al. 2001; Revilla et al. 2001; Johnson et al. 2002; Revilla and Palomares 2002). From a management perspective the species attracts interest partly due to conservation concerns and partly due to its possible role in transmitting wildlife diseases to domestic animals. From an ecological perspective the badger is intriguing due to its flexible social behaviour expressed through social group sizes in excess of 15 adult individuals in high-density populations in the UK (Johnson et al. 2001) and strict pair-living in low-density areas in Southern Europe (Rodríguez et al. 1996; Revilla et al. 1999). The elusive behaviour of the badger renders direct censuses of population sizes difficult even on a small scale. The density of breeding setts is therefore frequently used as a surrogate for badger population densities.

A number of statistical models are available describing the choice of sett habitat by badgers across the species’ European range (see references in paper II). Some of these models are developed from sett density data, but most are – like the present – based on presence/absence data. Characteristic for almost all of these studies is that they identify significant variables related to forest cover and terrain (slope, aspect, “hilliness”). Variables indicating preferred feeding habitat (pasture, semi-natural grassland, orchards etc.) and soil type have been shown significant in some studies, though not all. The majority of models include a combination of map- and field-measured variables.

The overall aim of the presented case study of the European badger (paper II) was to develop estimates of densities of badger setts in a region of Denmark. The information available to us came from surveys of three different study areas for the presence of badger setts (used sites) and a sample of control sites where no badger sett were present (unused sites). We therefore chose to use a step-wise procedure. Firstly, we developed a statistical habitat model using data from one of the study areas. Secondly, we extrapolated this model to a larger region including all three study areas. Thirdly, we validated the predictions of the model against data from the remaining two study areas and finally we attempted to translate the predictions of the habitat model into estimates of sett densities.

In our choice of parameters we attempted to optimise the model for predictive management. This means that only parameters with a clear basis in badger biology were considered. In addition we limited our choice to information that was available on a nation-wide digital format. This was done even though certain variables, traditionally described, as important cues for badger sett site choice (most noticeably soil type), would have to be ignored. Instead, the effort was directed towards investigating the effect of scale of the chosen parameters and towards developing an automated index that could capture the terrain attributes believed to be important for the suitability of a site as sett habitat. The final model was simpler than previously published models of badger sett site selection. It contained just three variables related to forest cover, terrain heterogeneity and proximity of infrastructure (paper II: table 3).

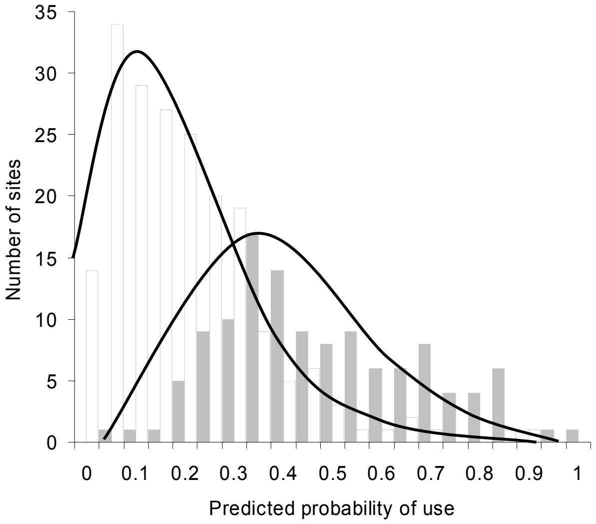


Figure 3. The frequency distribution of predicted probabilities for all sites in the two validation areas. White bars are unused sites, grey bars are used sites. The large overlap between the two distributions illustrates the difficulty in determining a fixed probability threshold separating used from unused sites. The curves were drawn for illustrative purposes and are not fitted to the data.

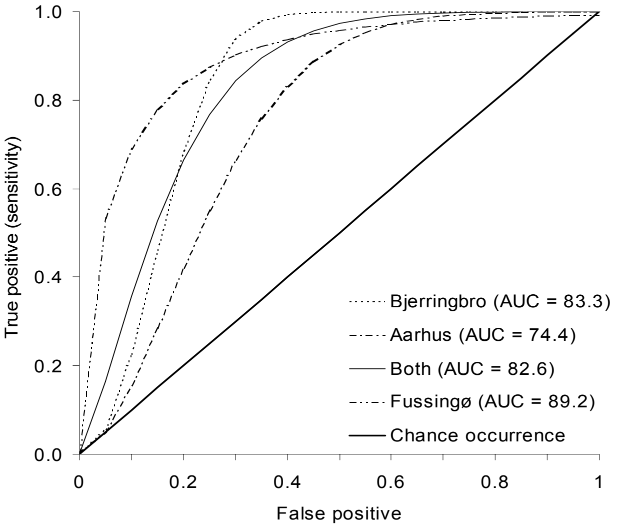


Figure 4. The ROC curve (Gaussian distribution) of the final model for the model development data set (Fussingø) and the two validation data sets (separate and pooled). 'AUC' is the area under the ROC curve. The 45° line indicates the relationship for a model with no discriminating capacity (chance occurrence).

The ability of the final model to discriminate between used and unused sites in the model development area and the two validation areas was initially inspected using a frequency distribution plot of the predicted probabilities associated with used and unused sites (fig. 3, see also Pearce and Ferrier 2000). From these plots it was clear that the two distributions were overlapping and that any fixed threshold would result either in used sites being erroneously classified as unused or vice versa. Hence we evaluated the performance of the model using the threshold-independent ROC plots (Fielding and Bell 1997). ROC plots (Gaussion curves) for all areas are shown in fig. 4. The final model had a predictive ability in excess of 80% as judged against independent validation data (paper II: table 4). This indicates that a predictive model that is sufficiently accurate for use in predictive management can be obtained using easily accessible digital map sources and presence-absence data. This is a very encouraging result.

The habitat model indicates the probability that a given cell contains a badger sett. To predict the distribution of setts in an area in which total sett density is unknown, an extrapolation algorithm is needed that is able to place setts in accordance with the probability map. We chose to do this by developing an algorithm that calculates a minimum acceptable distance (*D*) between a given sett and all of its neighbours, based on the probability score. This mimics the presence of an exclusive territory around each sett – a reasonable assumption for a territorial species such as the badger. We aimed at developing an algorithm that i) was able to reproduce observed patterns of sett densities in different probability classes in the Fussingø study area, ii) was functional over the whole range of probabilities, to avoid a predefined probability threshold for use and iii) required a minimum of additional information. The sett distribution algorithm that came closest to meeting all the criteria above was one assuming a logistic relationship between inter-sett distance (*D*) and probability of use (*P*) at a given site. The predictions of the sett distribution algorithm were evaluated against three different observed patterns in the Fussingø study area. The three patterns were: i) the total density of setts, ii) the density of setts in different probability classes (e.g. 0.1-0.2, 0.2-0.3 etc), and iii) the relative number of setts in different probability classes (paper II: fig. 5). An independent validation against the estimated main sett density in the Bjerringbro area (paper II: table 5) indicated a good correspondence between model prediction (0.75 ± 0.18 setts/km^2) and observed density (0.88 setts/km^2).

Several aspects of badger ecology renders predictive habitat modelling a useful tool in management of the species. Firstly, badgers follow a fairly consistent pattern when selecting sett habitat. This is the first requirement for developing a general model suitable for regional or national extrapolation. Secondly, badger setts are long-lived structures that are easy to locate in the field. In addition, access to a sett is a requirement for successful breeding in the badger. The actual relationship between sett densities and badger densities is poorly documented (Macdonald et al. 1996). The validity of sett densities as a surrogate for badger densities should therefore be the subject of more attention in the future. But the fact remains that very often sett surveys are the only type of information available indicating the distribution and density of badgers. The case study presented is an attempt to make the most of this information.

2.3. The trade-off of complexity

2.3.1. The trade-off of complexity

Natural ecosystems are complex systems. When we observe a certain characteristic distribution pattern of a species in nature, we can be sure that this particular pattern has been influenced, to a smaller or larger degree, by cultural, economic, evolutionary, phenotypic and environmental processes. The purpose of building an ecological model is to create a tool that can help distinguish the influence of one process from the other. It does not take more than a rudimentary understanding of ecological systems to see why ecological models sometimes develop into reasonably complex entities as well. A model that is uncritically complex can be very

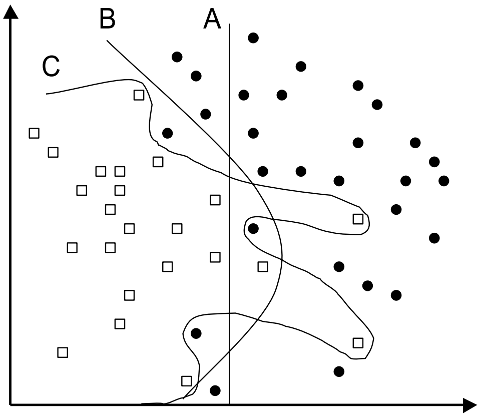


Figure 5. The modeller's dilemma. Redrawn after Eliosoff and Posse 1999.

difficult to understand, while a model that is too simple will fail to reproduce the relevant patterns. This trade-off of complexity is the modeller's dilemma. The problem is sketched in fig. 5. In this case the task of the ecological modeller is to find a solution that in the simplest possible way separates the black dots from the white squares. Solution A is cheap, simple and straightforward, but the associated error is very high. Solution B performs much better, but is already much more complex in that it involves a non-linear relationship. Still it can probably be described in reasonably simple mathematical terms. Finally solution C gives a perfect separation of the two samples. But the required solution is complex and highly specific for this particular case. It is not likely to perform very well if applied to a different sample of dots and squares. The modeller's dilemma consists of choosing the simplest possible solution that lives up to the requirements. This is also referred to as 'Occam's razor[1]' (Grimm and Railsback in press, ch. 3).

It is a common opinion in ecology that no model can simultaneously meet the requirements for simplicity, realism and precision (e.g. Levins 1966, Gilpin and Hanski 1991). In the same breath is often the accusation that complex spatial models are of no use in advancing understanding or ecological theory, because they are too specific, contain too many interacting parameters and cannot be evaluated using traditional statistical approaches. Wennergren et al. (1995) stated directly that, "*To a large extent, spatial models seem to represent either loose metaphors with little justification for their complexity, or highly specific descriptions that could never be adequately parameterized*." (Wennergren et al. 1995, p. 354). This criticism has especially been targeted towards explicit individual-based models. There is no doubt that the community of researchers developing and applying individual-based models to a large extent has brought this criticism on themselves. Individual-based ecology is challenging the classical modelling world. Individual-based modelling was launched as somewhat of a panacea to ecology in a few very visionary papers (Huston et al. 1988, Judson 1994) and have in some areas failed to live up to the high expectations (see review by Grimm 1999). Important reasons for this have been a lack of a theoretical framework for IBMs and an uncritical increase in information-load and complexity in attempts to obtain 'realism' (Hogeweg and Hesper 1990, Grimm 1999, Grimm and Railsback in press). But individual-based modelling is slowly recovering from its childhood maladies and finding its place in ecology as consensus develops on parameterisation and evaluation methods (Fahse et al. 1998, Grimm et al. 1996, Wiegand et al. 2003, Wiegand et al. 2004), integration of theory, and a conceptual framework for model design (Railsback 2001, Grimm and Railsback in press).

The view on simplicity and precision as mutually exclusive attributes in an ecological model is also being challenged by recent advances in studies of adaptive behaviour and rationality theory (see for instance Gigerenzer and Todd 2000). This has shown that adaptive choices can be made based on simple heuristic principles and a minimum of knowledge about the environment. In many real-life cases this so-called 'fast and frugal heuristics' performs at least as well as decision rules assuming that individuals have a very detailed knowledge about their environments and the consequences of their decisions (Davis et al. 1999, Gigerenzer and Todd 2000, Todd 2000). Input from rationality theory is likely to be useful for designing and improving decision rules for behavioural models of animals in heterogeneous environments. This illustrates well that the way forward in modelling complex ecological systems is not to make complex models 'simpler'. It is a mistake to believe that simplicity and generality in an ecological model is obtained simply by substituting explicit implementations by generalised assumptions. Better models of complex systems can only come from an advance in our ability to master complexity; to identify the relevant processes behind ecological patterns and improve our understanding of the motivation behind individual choice.

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[1] After the 14th century British philosopher William of Occam (or Ockham) who stated *"plurality should not be assumed without necessity"*.

2.3.2. The best of all possible models?

As clear from the previous section, there is no such thing as the perfect model of an ecological system. The type of model and the spatial representation that is most suitable for a given case will always depend on the type of questions the model is expected to answer. A model that is found suitable in one context might be entirely unsuitable in another, despite an apparent identical ecological framework. The choice of structural design of the model determines the types of ecological processes that can be simulated, and the amount and quality of available data limits the degree of detail that can be incorporated in the model. Nevertheless there will be a number of possible models that will appear suitable for every specific management case. This may appear trivial, but is in fact far from it. Spatial models developed with similar objectives, but with varying complexity, can produce very different predictions and hence result in different management recommendations (e.g. Bollinger et al. 2000, Hokit et al. 2001, Stephens et al. 2002, Goss-Custard et al. 2003, paper III). The choice as to which type of model to employ in a particular situation, is often governed by logistic constraints and the personal preferences of the modeller. Still the consequences of model choice are rarely addressed in ecological literature, despite the obvious usefulness of such information for managers and researchers alike.

In the following, I summarise the two included case studies (paper III and IV). They address two different issues related to the consequences of model choice. Paper III is a direct comparison of the performance of three common spatial simulation models developed with a shared objective, namely to predict dynamics of individuals or populations in space given a specific spatial configuration of habitat patches. Paper IV is an evaluation of a specific published metapopulation model (Frank and Wissel 2002), with the purpose of highlighting the consequences that the structural simplifications necessary in mathematical frameworks may have when applied to real systems.

Case study 1. A comparison of three spatially explicit modelling approaches (paper III).

The aim of this case study was to investigate the consequences of model choice on estimates of dispersal probabilities and hence, corridor efficiency, through a habitat network. To achieve this, we employed three existing spatially explicit modelling systems including a varying degree of spatial and behavioural complexity. The three models were chosen as representatives of three common types of spatial models:

- incidence function models or patch-based metapopulation models (hereafter “IFM”)
- individual-based movement models (hereafter “IBMM”)
- individual-based population models including movement (hereafter “IBPM”)

The incidence function model, Corridor (Hans Baveco, unpublished[2]), is based on classical metapopulation theory (Hanski 1994, 1999). The probability of individuals arriving at a certain patch is derived from patch geometry and dispersal attributes of the species and is thus independent of matrix properties. The movement model, Smallsteps (Vos 1999[3]) was developed as a versatile tool to assess functional landscape connectivity at different temporal and spatial scales. It generates animal movement paths across a spatially heterogeneous landscape using a Correlated Random Walk (CRW) algorithm and a matrix of boundary transition probabilities. The individual-based population model used was ALMaSS (paper I). The temporal heterogeneity in the ALMaSS landscape model can be switched off yielding a static (hereafter “IBPM_st”) and a dynamic (hereafter “IBPM_dyn”) version of the landscape model. The main properties of the three systems (four versions) are summarised in table 2 (= paper III: table 1).

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[2] The CORRIDOR model can be accessed online on the authors home page (http://purl.oclc.org/NET/alterra/corridor)

[3] The SMALLSTEPS model can be accessed online on the authors home page (http://purl.oclc.org/NET/alterra/movement)

Table 2. Summary of the models.

	Spatially explicit	Individual-based	Explicit movement	Demo-graphics	Time step	Spatial information	Matrix heterogeneity	Matrix dynamics
CORRIDOR (IFM)	yes	no	no	no	year	area and location of patches	no	no
SMALLSTEPS (IBMM)	yes	yes	yes	no	hour	polygon-vector map	yes	no
ALMaSS_static (IBPM_st)	yes	yes	yes	yes	day	raster map	yes	no
ALMaSS_dynamic (IBPM_dyn)	yes	yes	yes	yes	day	raster map	yes	yes

The IBPM is the most complex model and can cope with the most detailed spatial information. For comparing the models we therefore derived the parameters for the other two from the IBPM by simplification. The models were parameterised for the field vole (*Microtus agrestis*; paper I). A set of hypothetical landscape templates was developed consisting of two large habitat patches connected by either 3 larger (paper III: fig. 1a) or 6 smaller (paper III: fig. 1b) patches. This was defined as the *core network*. The degree of connectivity was varied over these templates by adding either a large number of stepping stone patches or a continuous corridor (paper III: fig. 1c-f). The core network + stepping stones was defined as the *total network*. High and low connectivity versions of all landscapes were constructed by surrounding every field polygon in the matrix by a grassy field margin. This provides high-quality movement habitat without affecting patch area. All patches consisted of optimal breeding habitat for the field vole. Each model produced an asymmetrical matrix of predicted dispersal probabilities to and from each patch in the total network. Network connectivity was summarised in two measures: i) The aggregated dispersal probability (= the probability that a disperser leaving from anywhere in the network will successfully reach another patch) and ii) the annual number of successful immigrants in the core network (see paper III for details). Based on these measures all habitat networks were ranked from best to worst.

The results and conclusions to be drawn from this study can be summarised as follows.

- All models made similar predictions regarding the relative ranking of the habitat networks, but large discrepancies existed in quantitative estimates of network connectivity.

- Connectivity estimates from the two simpler models (IFM and IBMM) were 20% - 230% higher than IBPM estimates in well-connected networks and approx. an order of magnitude higher in poorly connected networks.

- The predicted consequences of adding a realistic behaviour and demography (going from IBMM to IBPM_st), on dispersal probability, were much larger than the predicted consequences of adding landscape dynamics (going from IBPM_st to IBPM_dyn).

- Both the two simpler models reach a limit of applicability as network connectivity decreases. The IFM because it ignores the increasingly important matrix properties and the IBMM because it does not consider local demography.

- The applicability of the IBPMs is limited mainly by data availability. They are suitable when evaluating habitat networks for a limited number of species (or ecological profiles; paper VI) and have their strength where local dynamics is shaping larger scale patterns.

In conclusion, this case study indicates that caution needs to be taken in the choice of model. In addition it places strong emphasis on the need to critically compare models based on different formulations in order to pinpoint the consequences of using one or the other, and - when possible - evaluate the performance against independent data. Even when suitable independent data is not available, model comparisons increase our understanding of model behaviour and allow us to define crude limits of applicability.

Case study 2. Evaluating a formula for decision-support in metapopulation management (paper IV).

This case study was conducted in direct response to a recent contribution made by Frank and Wissel (2002). In this paper the authors present a mathematical approximation formula for the mean lifetime T_m of a stochastic, spatially realistic metapopulation. This is an important advance. If the mean lifetime of a stochastic metapopulation can be approximated in mathematical terms, based on patch characteristics and species attributes, it means that the survival probability to time t (S(t)) of a population in alternative habitat networks can be calculated and compared directly, without tedious model simulations. Hence, the approximation formula represents a stochastic pendant to the deterministic metapopulation capacity (Hanski and Ovaskainen 2000). The authors were able to show that the approximation formula successfully reproduced the results of a stochastic, spatially realistic metapopulation model (Frank and Wissel 1998). In addition they supplied a 7-step recipe illustrating how species attributes and landscape data should be combined to estimate the survival probability of a given real population (Frank and Wissel 2002, p. 544).

Even a sophisticated metapopulation model is a gross simplification of reality. To capture the stochastic and spatial attributes of a metapopulation model, such as Frank and Wissel (1998), in a mathematical framework requires additional simplifying assumptions. Given the high potential applicability of the approximation formula as a decision-support tool, and a simplifying short cut in metapopulation management, we felt that a thorough evaluation of the performance of the formula was necessary. We chose to do this 'from a manager's perspective'. Consequently, we were interested in i) the performance and structural behaviour of the formula, ii) the uncertainty of formula output in relation to input data, and iii) the possibilities for parameterisation.

The approximation formula is outlined in detail in paper IV (table 1). The required input in the formula is landscape data (area of all patches and a matrix of inter-patch distances) and four parameters ($\varepsilon_{\max}$, $ext_{\min}$, d_a, d_ρ). $\varepsilon_{\max}$ is the annual number of emigrants from the largest patch, $ext_{\min}$ is the extinction rate of the largest patch, d_a is the mean dispersal distance of the species, and d_ρ is the correlation distance. The importance of the last parameter, d_ρ, requires further explanation. It is well known that spatial correlation in environmental fluctuations (e.g. climatic conditions) can act as a synchronising factor in population dynamics (e.g. Grenfell et al. 1998, Bjørnstad et al. 1999, Lande et al. 1999, Post and Forchhammer 2002). In other words, local populations that are close together in space are affected in a similar way by environmental conditions. Hence they will have more similar population dynamics than local populations that are separated by large distances. Most metapopulation models ignore within-patch dynamics and consider only whether patches are occupied or extinct at a given time. A common way to include the effect of environmental fluctuations in a patch-based metapopulation model is therefore to assume a distance-dependent spatial correlation of extinctions between any pair of patches ($\rho_{ij,}$

paper IV, eq. 2). This can also be thought of as the probability that a pair of patches go extinct simultaneously. The parameter d_ρ is the mean distance over which this correlation acts.

In order to evaluate the performance of the formula we first chose a common spatial framework (paper IV, figure 1). It consisted of a well-connected habitat network containing between 5 and 10 circular habitat patches of varying size. Patches 1-5 were always included, while patches 6-10 were added sequentially yielding a total of 6 different habitat networks. We then conducted a set of Monte Carlo simulations in which we varied the input values of the four parameters ($\varepsilon_{\max}$, $ext_{\min}$, d_a, d_ρ) within reasonable ranges (paper IV, p.3). One set of 10,000 simulations was done for each habitat network. For each case we calculated the survival probability S(t) of the network at t=100 years. The results and conclusions of the evaluation can be summarised as follows:

- The structural behaviour was evaluated by analysing the effect of adding a patch within the existing connected network. Our assumption was that this should have a non-negative effect on the survival probability of the network (see paper IV for a discussion of this assumption). Our analyses show that this expectation is met in most cases. A proportion of runs, however, predicts the survival probability of the network containing n patches to be higher than the network containing n+1 patches (paper IV: table 2). In other words, an adverse effect of adding habitat. A closer look revealed that this mostly happens when the viability of the network as a whole is low (paper IV: table 3).
- The structural problem only occurs when the environmental correlation is included and when the ratio between the dispersal distance and the correlation distance (d_a / d_ρ) is below 6. As the ratio decrease below 6 more erroneous cases occur (paper IV, table 4). This indicates that there is a clear limit of applicability to the formula when environmental correlation is important.
- It can be concluded that the cause of the structural problem is either the implementation of correlation in the original model (Frank and Wissel 1998) or the distance-dependent submodel used for the correlation (paper IV: eq. 2). The most likely candidate is the submodel (but see a thorough discussion of the implementation of correlation in the original model in paper IV: p. 4). The environment assumed in the submodel is conflicting with reality in that every patch is a source of critical effects that may cause extinction in nearby patches (paper IV: fig. 3a). This causes small patches to be direct drivers of extinction and this is not a realistic implementation of environmental stochasticity such as weather. This highlights an urgent need for further research on correlation in the context of metapopulations.
- The uncertainty profile of the formula indicates that two situations have to be distinguished (paper IV: fig. 4). When mean S(t) is close to the extreme values (0 or 1) the range of formula output (=uncertainty) is very low. This means that for distinguishing a 'viable' from an 'endangered' metapopulation, formula results are robust. Approximately 2/3 of all runs falls in this category. The last (and critical) third however, may be associated with very high uncertainty. An uncertainty analysis should be performed prior to every application of the formula on real habitat networks.
- Certain problems exist regarding parameterisation of the formula. Most noticeably this relates to the local extinction rates. The parameter ν in the formula represents the extinction rate caused by local effects only, and hence has no empirical equivalent. The formula strongly depends on the availability of suitable submodels to estimate input parameters.

2.3.3. Concluding remarks

The two case studies presented here illustrate both some of the consequences of the trade-off of complexity and the importance of model choice. Every choice made regarding model structure and the level of model complexity closes some doors and opens others with regard to the applicability of the model. An open door, however, draws much more attention than a closed one and this is why a critical evaluation of the consequences of model choice is so important. The implementation of environmental correlation that causes so many headaches in the context of metapopulations could be implemented as a patch-independent effect without great difficulty in a spatially explicit simulation model. That choice would, however, mean that the obvious advantages of working in the empirically and theoretically well-founded metapopulation framework would be lost. So would probably the option of using mathematical formulations. This is precisely what the trade-off of complexity is all about.

2.4. Evaluating impacts of long-term landscape planning on wildlife

2.4.1. Integrating behaviour and explicit decision-making in landscape ecology

A recent 'Top 10 List' of priority research topics in landscape ecology lists i) non-linear dynamics and landscape complexity, ii) causes, processes and consequences of land use and land cover change and iii) the integration of humans and human activities, as three of the ten top research priorities in landscape ecology (Wu and Hobbs 2002). It is tempting to add another point advocated strongly in the often-cited paper by Lima and Zollner (1996). This is the integration of a 'behavioural ecology of ecological landscapes' which includes advancing the behavioural component of landscape ecology, as well as a landscape-conscious component of traditional behavioural ecology (Lima and Zollner 1996). Landscape ecology is a multi-disciplinary science aspiring to become inter-disciplinary (Wu and Hobbs 2002). There is a broad and obvious interface between landscape- and behavioural ecology and with the advance of individual-based ecology (*sensu* Grimm and Railsback in press) and behavioural modelling, the importance of merging the two disciplines becomes increasingly obvious. Hence, the four research priority listed above are also a good reflection of some of the major challenges in the endeavour towards better spatial models for use in landscape and species management.

Section 2.1.2. (*Simulating individuals in a dynamic environment*) summarises some of the complex properties of agricultural ecosystems that, firstly, make predictions of the effects of landscape properties on wildlife an immense challenge, and, secondly, renders dynamic, individual-based modelling an indispensable tool in landscape and species management. Temperate European landscapes are temporally and spatially dynamic and highly affected by the continuous interference by man. Hence their dynamics is driven as much by socioeconomic as by ecological forces. Consequently, it is often necessary to take multi-disciplinary considerations into account when trying to forecast consequences of management policies on wildlife. In many cases this requires that human interests or explicit decision-making is included in the model. Strong conflicts of interest may exist between economic yield (e.g. hunting or agricultural production; Musacchio and Grant 2002, Mathevet et al. 2003), environmental concerns (e.g. nutrient loss to ground water or pesticide spray drift; Cryer et al. 2001) and conservation interests (e.g. conserving habitats or species diversity; Steiner and Köhler 2003, Tattari et al. 2003). The use of comprehensive spatially explicit models is common practise in attempts to predict future land-use change as a consequence of management policies (Bell and Irwin 2002, Musacchio and Grant 2002, Luitjen 2003, Schneider et al. 2003, Topp and Mitchell 2003) and the consequences of land-use change on for example economy (Irwin and Geoghegan 2001) and soil properties and erosion (Schoorl and Veldkamp 2001). The next step – to evaluate the implications of future land-use change for wildlife – has typically been based on various GIS-overlay (e.g. Murray et al. 2003) and multivariate statistical models (e.g. Jeanneret et al. 2003). More comprehensive applied decision-support tools are, however, becoming increasingly common (e.g. DeAngelis et al. 1998, Pettifor et al. 2000, Ahearn et al. 2001, Cramer and Portier 2001, Stillman et al. 2001, Hof et al. 2002, paper I). Most of these models – and other models attempting to assess ecosystem consequences of land-use change – share the dilemma that detailed species-level information often is needed in order to evaluate the impact of land-use strategies on target species with reasonable accuracy. At the same time, it is necessary to address species on multiple trophic levels and with various life history characteristics to pinpoint ecosystem consequences. The result is that the evaluation, generalisation and communication of the results of these models represent a real challenge.

2.4.2. Case studies

In the following, I summarise two case studies (paper V and VI), related to the use of individual-based behavioural models in evaluating consequences of landscape structure and management on wildlife. The first case study (paper V) is a comment on the implications of behavioural plasticity in the response of a species to landscape structure, for predictions made based on a behavioural model. The second case study (paper VI) is an example of a multiple-species assessment of land-use change scenarios using the modelling frame work ALMaSS described earlier (paper I, III). This paper comments specifically on generalisation and communication of results of complex behavioural models.

Case study 1. Roe deer behavioural strategies in a gradient of forest fragmentation (paper V)

The ability of a species to exhibit behavioural plasticity to environmental conditions has wide ranging consequences for its success in modern fragmented landscapes. It may affect its ability to deal with for instance predation pressure (e.g. Lima and Dill 1990), habitat alterations (e.g. Boydston et al. 2003) and environmental and resource dynamics (e.g. Maher and Lott 2000, Brashares and Arcese 2002). The roe deer (*Capreolus capreolus*) is one of the foremost examples of behavioural flexibility among ungulate species. In the course of the twentieth century the roe deer has increased rapidly in range and density across Europe, and spread from its original forest-mosaic habitat into open agricultural plains (Hewison et al. 1998). Roe deer populations living in open land habitat show distinct differences in spatial and social behaviour, including larger group sizes and less association with wooded structures, than forest living roe deer. Traditionally, grouping in ungulates has been viewed as an adaptive response to predation pressure (Hewison et al. 1998, Brashares and Arcese 2002, a recent review in Caro et al. in press). The increased vigilance in a large group is suggested to reduce predation pressure and increase foraging time for the individual (e.g. Childress and Lung 2003). Hence, increased group size act as a buffer for the lack of protective cover in the form of tall vegetation or woodland. The speed, at which the transition from forest to field behaviour has happened in the roe deer, suggest that the behavioural strategies observed, are probably a result of behavioural plasticity rather than natural selection. This is supported by theoretical model studies (Gerard and Loisel 1995, Gueron et al. 1996).

The presence of behavioural plasticity in species response to landscape structure suggests that behavioural flexibility should also be a concern in models attempting to describe effects of landscape change on species distribution. To date this issue has received very little attention (Komers 1997, Henein et al. 1998, Hewison et al. 2001). We used an individual-based model of roe deer spatial behaviour and demography to evaluate the consequences of including behavioural plasticity for predictions made regarding population response to woodland fragmentation. More specifically we wished to address how the inclusion of an alternative behavioural strategy, under which the company of conspecifics was allowed to buffer insufficient availability of woodland habitat, affected model predictions regarding population persistence, spatial distribution and social structure. We used a roe deer simulation model developed under the ALMaSS framework (paper I, III). We contrasted two rather extreme behavioural strategies both based on the assumptions that cover is a necessary resource for roe deer. In the default strategy the spatial behaviour of all individuals is fixed to a certain environmental cue (proportion of woodland habitat). In the buffer strategy, all individuals have the option of switching to an alternative cue, not determined by landscape attributes (presence of conspecifics). We used artificial neutral landscape models (section 2.1.1, paper V: fig. 1) to illustrate a fragmentation gradient from 0 (all woodland habitat in a single patch) to 100 (random allocation of woodland habitat).

We found that the presence of behavioural plasticity had a very large impact on model predictions regarding the effects of woodland dispersion on roe deer spatial distribution and group size. The difference between the two behavioural strategies was most pronounced when average woodland cover was low. The inclusion of a flexible behavioural strategy resulted in significantly higher estimates of population size, population persistence and the ability to cope with fragmentation (paper V: fig. 2 and 3). A very clear low optimal level of fragmentation was evident in the absence of behavioural plasticity, and the population was not able to persist at the highest levels of woodland fragmentation. Whilst the two contrasted behavioural strategies are obviously less flexible than the plastic response shown by a real species, they are useful for demonstrating the potential implications of ignoring plastic behaviour for our ability to accurately predict the response of species to landscape change and fragmentation.

Case study 2. Evaluating consequences of land-use change for wildlife (paper VI)
This case study address a common dilemma in comprehensive models designed to evaluate broad ecosystem consequences of land-use change. The dynamic and complex nature of agroecosystems require a fairly large degree of realism in spatial representation and species description, in order to capture the local dynamics with reasonably accuracy. This usually means that individual-based models with a fine temporal and spatial resolution are preferred. Simultaneously, it is necessary to address many species or groups of species to identify potential trade-off between species; management actions beneficial to one group of species will very often have adverse effects on others. This calls for generalised measures that are meaningful for species across trophic levels.

We used the ALMaSS framework to perform a multiple-species assessment of land-use change scenarios related to ground water protection and pesticide use in a Danish landscape. ALMaSS was originally designed for addressing questions related to the local response of species to fine-scale spatial and temporal environmental heterogeneity (paper I). The two scenarios involve very different land-use changes. The regional strategy for ground water protection in Denmark involves assigning areas hitherto used for agricultural production to forest or permanent setaside. Hence, it results in large structural modifications of the landscape. The second scenario is based on the agricultural changes predicted to take place upon a complete ban of pesticides in Danish agriculture. This involves modifications in the composition of crops as well as a change in crop management (e.g. increased use of mechanical weed control). This scenario results in a limited structural change of the landscape, but large modifications in short-term habitat characteristics on the agricultural surface.

Our aim was to use these scenarios to address the dilemma of detail and generality described above. We took the following approach:

- Firstly, we based our analysis on a selection of species, chosen to represent five characteristic ecological profiles in a NW European agricultural landscape (paper VI: table 2). This approach is consistent with other attempts to bridge the gap between single-species ecology and ecosystem response, for example the concept of ecologically scaled landscape indices (ESLI; Vos et al. 2001). We chose to maintain descriptions of real species, rather than stylised or generic species (e.g. Hemelrijk 2002, Parrott and Kok 2002). The use of ecological profiles allows a fairly comprehensive description of a broad range of species response patterns based on a limited number of species.

- Secondly, we calculated a spatially differentiated index of the relative impact of each scenario in 16 sub-squares across the landscape (paper VI: fig. 3). This allows a quick visual evaluation of the impact of a large number of scenarios across multiple species. Based on this diagram the broad response patterns can be established, i.e. does conflicting response patterns exists between species, are impacts seen in directly affected areas only or is there generation of neighbourhood effects, etc.

- Thirdly, we aggregated the numeric response (predicted change in total population size compared to a baseline situation) and the spatial response (predicted change in deviation from a random distribution) for each species under each scenario (paper VI: table 4). In conjunction these two numbers indicate the change of conditions experienced by a species. For example a '- 0' response indicates a uniform decrease in density ('thinning out') as would result from a general decrease in habitat quality, while a '- -' response indicates that the decrease in density primarily occurred in previously high density areas. This approach makes it possible to classify large numbers of species according to their general response and possibly even to determine *a priory* rankings depending on a specific case.

The use of indices to integrate environmental attributes and single-species ecology is an advancing approach in ecosystem analysis, well in line with landscape metric approaches used in landscape ecology (e.g. Vos et al. 2001). We consider the use of descriptive spatial impact indices a promising approach to aggregate and communicate the results of complex behavioural models, and encourage further development and application.

2.4.3. Concluding remarks

An adequate description of a complex dynamic system sometimes requires complex models, which in turn can produce rather complex results. As highlighted in the section above and several other places in this synopsis, this is no reason not to develop complex models. Models should be simplified only so far depending on the questions we wish to answer. A better strategy is to learn how to build better complex models and how to communicate the description and results of complex models in a better way. To be able to accurately predict the effects of large-scale land-use changes on wildlife is perhaps a remote goal. Nevertheless, decisions influencing the management and conservation of species have to be made, very often based on a less than optimal information. Limited available resources or urgency in the need for answers, means that improving our abilities to produce reasonable answers based on current knowledge of the system is high priority. Predictive behavioural models are important tools in achieving this.

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3. Abstracts of papers I – VI

Paper I

Topping, C.J., Hansen, T.S., Jensen, T.S., **Jepsen, J.U.**, Nikolajsen, F. & Odderskær, P. 2003. ALMaSS - an agent-based model for animals in temperate European landscapes.

Ecological Modelling 167: 65-82.

The animal, landscape and man simulation system (ALMaSS) was designed as a predictive tool for answering policy questions regarding the effect of changing landscape structure or management on key species in the Danish landscape. By combining agent-based models of animals with a comprehensive and dynamic landscape simulation, it aims to improve predictive ability. The landscape model comprises detailed mapping, weather, farm management, and vegetation growth. Each vegetated area has its own growth model and in the case of farmed areas, management is modelled in detail. Animal models are agent-based, designed using the state-transition concept and are rule-based. Each animal may interact with others and directly with its local environment. Field vole (Microtus agrestis) is used as an example of the extent to which dynamic landscapes can influence the population dynamics. Simulations of crop diversity and rotation demonstrate significant effects of spatial and temporal heterogeneity on population sizes, population fluctuations and landscape permeability. These two factors interact and thus different responses to temporal factors occur at different levels of spatial heterogeneity. Spatial and temporal heerogeneity in both model and the real world are often related to changes in land-use and management. Consequently, the impact of landscape changes on any population can be enormous and heavily spatially influenced. Therefore the use of dynamic andscapes is seen as an important addtion to the modeller's toolkit.

Paper II

Jepsen, J.U., Madsen, A.B., Karlsson, M. & Groth, D. Predicting distribution and density of European badger (*Meles meles*) setts in Denmark.

Submitted to Biodiversity and Conservation.

The European badger attracts interest as a model species both for conservation reasons and because of the important role the species is playing in understanding carnivore sociality. We developed a statistical habitat model based on presence/absence data on badger setts. To maximise the utility of the model in management, we limited the choice of model variables to those that had a clear basis in badger ecoogy and could be obtained on a nation-wide digital format. We extrapolated the habitat model to a region in Denmark and developed a threshold-independent sett distribution algorithm to estimate sett densities. The habitat model was simpler than previously published models of badger sett habitat selection, but nevertheless had a predictive ability in excess of 80% judged against independent data. The sett distribution algorithm was able to simultaneously reproduce several observed patterns of sett density an distribution over the probability gradient. It thus represents a significant improvement over threshold-dependent methods to discriminate between suitable and unsuitable habitat predicted by resence/absence models. Our approach demonstrate that a model of badger sett habitat suitability with high predictive power can be obtained using easily accessible map-variables and presence/absence data. This is a prerequisite for using habitat models as predictive tools on a larger scale. The use of a simple sett distribution algorithm circumvents the common problem of subjectively fixing a threshold to discriminate between suitable and unsuitable habitat. In conjunction the models presented here constitute an important contribution to the management of the badger in Denmark and, upon further validation, possibly to similar regions in Northern Europe.

Paper III

Jepsen, J.U., Baveco, J.M., Topping, C.J., Verboom, J. & Vos, C. Evaluating the effect of corridors and landscape heterogeneity on dispersal probability - a comparison of three spatially explicit modelling approaches.

Ecological Modelling in press.

Spatially explicit models of varying degree of complexity are increasingly used in landscape and species management and conservation. The choice as to which type of model to employ in a particular situation, is however, far too often governed by logistic constraints and the personal preferences of the modeller, rather than by a critical evaluation of model performance. We present a comparison of three common spatial simulation approaches (patch-based incidence-function model (IFM), individual-based movement model (IBMM), individual.based population model including detailed behaviour and demographics (IBPM)). The IBPM was analysed in two versions (IBPM_st and IBPM_dyn). Both assumed spatial heterogeneity of the matrix, but the IBPM_dyn in addition included temporal matrix dynamics. The models were developed with a shared minimum objective, namely to predict dynamics of individuals or populations in space given a specific confguration of habitat patches. We evaluated how the choice of model influenced predictions regarding the effect of patch- and corridor configuration on dispersal probabilities and the number of successful immigrants of a simulated small mammal. Model results were analysed both at the level of the entire habitat network and at the level of individual patches.

All models produced similar rankings of alternative habitat networks, but large discrepancies existed between absolute estimates of dispersal probabilities and the number of successful immigrants predicted by the different models. Generally, predicted dispersal probabilities were highest in the IBMM, intermediate in the IFM and the IBPM_st and lowest in the IBPM_dyn. Observed differences in predictions were due both to differences in implementation (e.g. raster versus vector based movement algorithms), the chosen level of detail in landscape representation (e.g. matrix complexity) and the degree of behavioural realism included in the models (e.g. demography, differentiated mortaity). The advantages and disadvantages of the three modelling approaches are discussed, as are the implications of the results for the recommended use of the three types of models in practical management.

Paper IV

Knauer, F., **Jepsen, J.U.**, Frank, K., Pouwels, R., Wissel, C. & Verboom, J.**.** Approximating reality? Evaluation of a formula for decision support in metapopulation management.

Submitted to Oikos.

Conducting reliable estimates of survival probabilities for metapopulation systems is a great challenge. In metapopulation management a variety of models from rules fo thumb and simple analytical models to complex individual-based and spatially explicit approaches are in use. But so far no models are perfect solutions for management applications, either because it is impossible to get the necessary data, or because the time required for developing or running the model is too long, or both.

Frank and Wissel (2002) recently published a formula to estimate the survival probability of metapopulations, which is relatively easy to apply and deals with data, which are possible to collect in the filed or derive from simple models. Because of its potential usefulness for applocations we tested the structural behaviour of the formula, the uncertainty of the output in relation to the input data and the posibility for parameterization. We found the following results: (1) The applicability of the formula is limited in cases where spatial correlation of extinction is reælevant. (2) In cases of intermediate values for the survival probability of the metapopulation, the formula produces very high uncertainty in the outputs. (3) Parameterization is problematical since the local extinction rate used in the model cannot be determined from empirical data, but has to be estimated from submodels.

From these results we conclude that this formula should only be used within strict limits and not without an extended uncertainty analysis.

Paper V

Jepsen, J.U. & Topping, C.J. Roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: Behavioural plasticity and choice of cover.

Submitted to Canadian Journal of Zoology.

The ability of a species to exhibit behavioural plasticity to environmental conditions has wide ranging consequences for its success in modern fragmented landscapes. The roe deer (*Capreolus capreolus*) is one of the foremost examples of behavioural flexibility among ungulate species. During the twentieth century the species has increased rapidly in range, and spread from its original forest-mosaic habitat into open agricultural plains. Roe deer populations living in open land habitat show distinct differences in spatial and social behaviour, including larger group sizes and less association with wooded structures, than forest living roe deer. This is traditionally viewed as an anti-predator strategy with large group sizes acting as a buffer for the lack of habitat cover.

The presence of strong behavioural plasticity in species response to landscape structure suggests that behavioural flexibility should also be a concern in models attempting to describe effects of landscape change on species distribution. To date the implications of behavioural plasticity for modelling species' response to environmental conditions has received little attention.

We used an individual-based model of roe deer spatial behaviour and demography to evaluate the consequences of including behavioural plasticity for predictions made regarding population response to woodland fragmentation. We found that the inclusion of a flexible behavioural strategy, where an increased group size was allowed to buffer lack of woodland cover, resulted in significantly higher estimates of population size, population persistence and the ability to cope with fragmentation. This clearly demonstrates that behavioural flexibility in species response to landscape structure may affect our ability to accurately predict the effects of landscape change and should be a concern to modellers.

Paper VI

Jepsen, J.U., Topping, C.J., Odderskær, P. & Andersen, P.N. Assessing impacts of land use strategies on wildlife populations using multiple species predictive scenarios.

Submitted to Agriculture, Ecosystems and Environment.

Agroecosystems are complex dynamic entities driven primarily by the activities of man. Agricultural activities cause changes to land-use and vegetation characteristics at a smaller temporal scale and a larger spatial scale than corresponding natural processes. Simulation models have become important tools in attempts to predict future land-use change as a consequence of management policies and in advancing our understanding of the behaviour of complex managed ecosystems. In order to capture the temporal dynamics and the non-equilibrium properties of agroecosystems and to deal with multidisciplinary trade-offs between e.g. economic and conservation interests, it is often necessary that models are both spatially and temporally explicit and incorporate some component of human decision-making. In this paper we present a multiple-species assessment of land-use change scenarios related to a ground water protection and pesticide use in a Danish agroecosystem. We use a spatially explicit simulation model that incorporates the temporal dynamics (driven by weather and farming decisions) of a real agricultural landscape in great detail. Our aim was to address how the numeric and spatial outcome of multiple-species predictive scenarios based on real landscapes and realistic simulations of species behaviour and demographics can be captured in simpler spatial impact indices. We advocate the use of ecological type species selected for a range of attributes relevant for the specific case, to allow for a comprehensive description of a broad species response based on a limited number of species. Our results are based on 5 ecological type species (a carabid beetle (*Bembidion lampros*), a linyphiid spider (*Oedothorax fuscus*), a small farmland bird (skylark, *Alauda arvensis*), a small mammal (field vole, *Microtus agrestis*) and an ungulate (roe deer, *Capreolus capreolus*). We chose to aggregate simulation results into two numbers indicating the overall numeric response (mean population size) and the overall spatial response (Ripley's *L*) of each type species. In conjunction these two numbers indicate the change of conditions experiences by a species and thus make it possible to classify large numbers of species according to their general response. The use of indices to integrate environmental attributes and species ecology is an advancing approach in ecosystem analysis and landscape ecology, but one that has so far rarely been used to aggregate results of complex behavioural models. We consider this a promising approach that encourages to further development and application.

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This thesis deals with four main subjects related to the use of spatially explicit models in landscape and species management. These subjects are i) Landscape modelling and the representation of space, ii) Predicting species distribution and abundance, iii) The trade-off of complexity and the choice between simple and complex models, and iv) The importance of individual behaviour and the use of complex behavioural models in evaluating impact of long-tern landscape planning on wildlife. Each subject, and most of the questions raised dealing with it, are of general concern when using simulation models as tools in management and conservation anywhere in the world. The general discussion is illustrated by a set of case studies focused on North-Western European agricultural landscapes..

Spatially explicit models in landscape and species management

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