Modelling the spatial distribution of Mammals

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Abstract

In this thesis I outline the different processes, operating at different scales, that influence the spatial distribution of mammals and review modelling approaches that have been used to represent these processes. I investigate the application of a selection of modelling approaches operating at different scales.

A model based on the energetics and movements of individual foragers was developed to investigate population spacing patterns and applied to the red squirrel. At high food densities, small, similarly sized, non overlapping ranges were generated, whereas at low food densities ranges were larger, more overlapping and more variable in size. The model is a first step towards investigating the spacing patterns of ranging mammals.

A model representing the positioning of dens was applied to predict the distribution of badger main setts. The model determined how many setts could be placed in suitable habitats while maintaining a pre-defined, minimum inter-sett distance. The representation of badger spacing behaviour and the utility of the approach is discussed.

At a larger scale, a model based upon births and deaths within habitat patches and an explicit representation of dispersal between patches was used to assess plans to reintroduce the beaver. It predicted little or no population spread, in contrast to the application of a generic population viability analysis package that predicted rapid population spread. A difference in the representation of dispersal was identified as the most likely cause of the disparity. A general model based on these approaches was developed to investigate the interaction between dispersal and demographic processes in spatially explicit population models.

The future of models to predict the spatial distribution of mammals is discussed in relation to issues of scale, management applications and modelling philosophies.

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Declaration

A paper containing a large part of the analyses from Chapter 3 is in press with Ecological Modelling.

Chapter 4 was conducted as part of a scoping study to generate proposals for future monitoring of British mammals (commissioned by DETR and JNCC) and some of the analyses appear in Macdonald et al. (1998).

Chapter 5 was co-authored with S.P.Rushton (45%) and D.W. Macdonald (5%). Programming of the custom-built model and initial analyses were conducted by S.P.Rushton. I conducted the Vortex and custom-built model runs and analyses presented. This work has been submitted to Biological Conservation.

Chapter 6 has been submitted to Conservation Biology, and re-submitted following reviewers comments.

1. Chapter 1 : Space and the distribution of mammals

The spatial distribution of animals has been the subject of much recent interest in ecology, both theoretical and applied (e.g. Kareiva 1990; Dunning et al. 1992; deRoos and Sabelis 1995). In this thesis I explore the application of modelling methodologies to the prediction and understanding of the spatial distribution of mammals. In this first chapter, I start by outlining the principal scales at which the spatial distributions of mammals are conventionally considered. I go on to describe the different processes that have been suggested to be responsible for these patterns. In the following chapter, I review modelling approaches based on both pattern and process, that are applicable to the spatial distribution of mammals across the range of scales outlined here.

1.1 Different scales of animal distributions in space

The spatial distributions of mammals are expressed across a range of scales in space, time and the number of individuals (e.g. Addicott et al. 1987; Holling 1992). Three principle areas have received particular attention in the study of mammals (see Fig. 1.1). Firstly, there is individual space use (fig. 1.1a); secondly, the spacing patterns of groups of individuals (fig 1.1b); and thirdly the pattern of occupation of habitat patches within the landscape (fig 1.1c). At a larger scale still, researchers have considered the factors responsible for the geographic distributions of species (e.g. Cox and Moore 1985), but I shall restrict my consideration to the three scales outlined in figure 1.1.

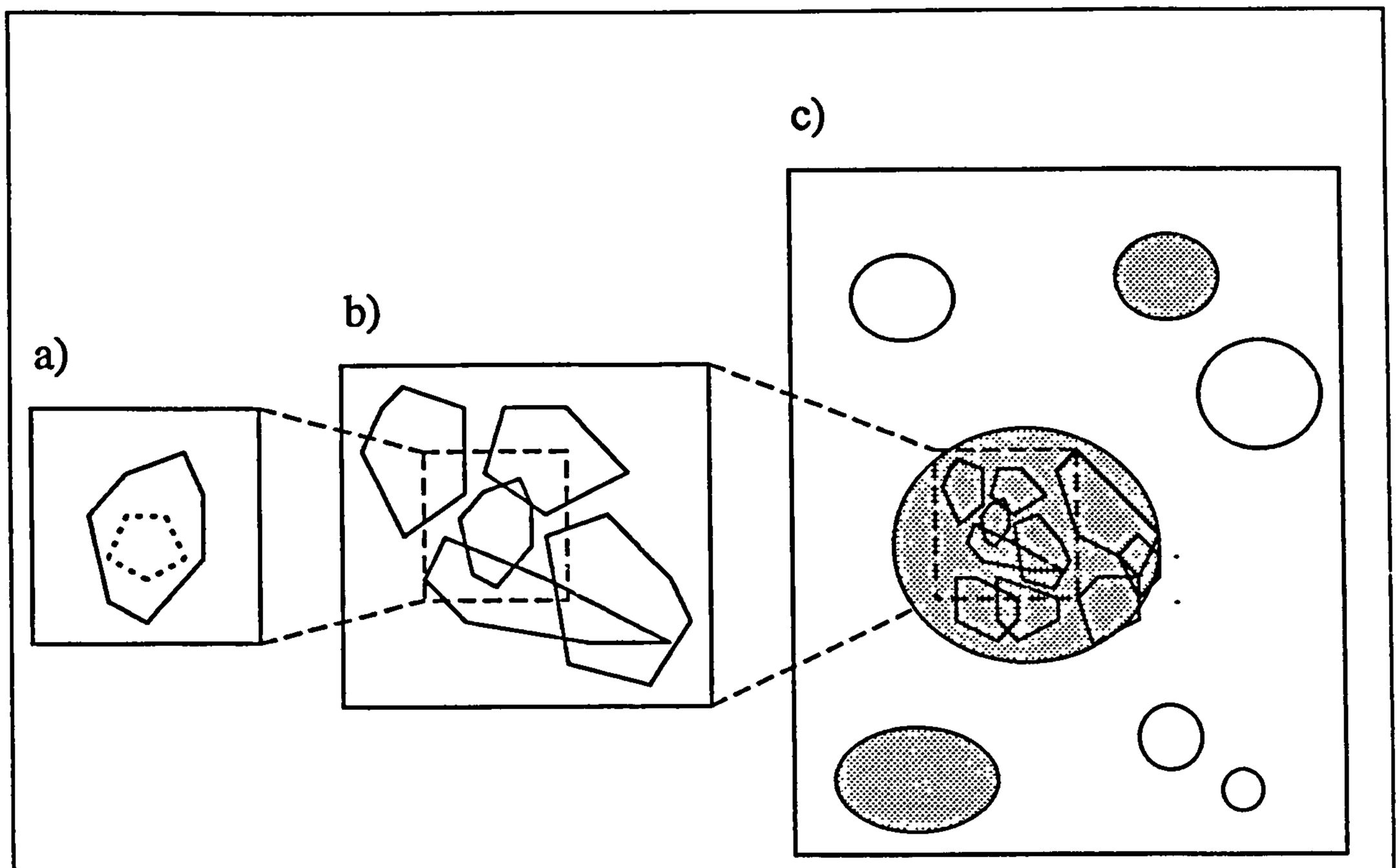

Figure 1.1 The Spatial distribution of mammals at 3 scales. a) Individual space use (solid line = home range, dotted line = core area), b) Population spacing pattern (solid lines = individual home ranges), c) Occupancy of habitat patches (ellipses represent habitat patches, filled ellipses = species present, empty ellipses = species absent).

1.1.1 Individual space use

The movements of an individual within any time period during its lifetime create a pattern of space use. Individual space use can be represented by maps of movement paths (e.g. Siniff and Jensen 1969) but is more often represented by a measure of position and area, termed the home range.

The conventional, often repeated, definition of a home range is : 'that area traversed by the individual in its normal activities of food gathering, mating and caring for the young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range' (Burt 1943). Although attractively simple use of the words 'normal' and 'occasional sallies' render the definition somewhat circular and difficult to apply both conceptually and operationally (Spencer et al. 1990; Gautestad and Mysterud 1995; Powell et al. 1997). Other authors only consider an

individual to have a home range if there is evidence of restriction of movements to a selected area, a process termed sedentarity by Benhamou (1989) and site fidelity by Spencer et al. (1990). Spencer et al. (1990) describe an operational definition of home range based upon comparing observed movements to simulated, random movements.

Although authors have considered that animals have an instantaneous concept of their home range (in terms of the area that it is familiar with) (e.g. Jewell 1966; Powell et al. 1997), the only way that this can be estimated is by recording the individuals movements over time (Powell et al. 1997). In practice home range estimates are derived from a series of location points collected by either radio tracking, trapping or sightings. One of the oldest and still most commonly used techniques for describing an individuals home range is simply to join the outermost locations to create a Minimum Convex Polygon. This has the disadvantages that it may not exclude the 'occasional sallies' of Burts (1943) definition; the area is very dependant upon the positions of the outermost locations, can include large unvisited areas and includes no information about the frequency of use of different parts of the range. There are a number of methodologies that have been developed to confront these difficulties, including identifying 'core areas' of most intensive use (see Kenward 1987; Harris et al. 1990; Kenward and Hodder 1996).

At the simplest level, a home range indicates where an individual is located within the landscape. Home ranges have also been used to indicate habitat preferences (e.g. Aebischer et al. 1993), to compare space use of the same species in different areas (e.g. Kruuk 1989), to compare space use between the sexes (e.g. Powell 1979; Erlinge and Sandell 1986) and as a starting point for looking at interactions between individuals (e.g. Wauters and Dhondt 1992; Koskela et al. 1997).

1.1.2 Spacing patterns

Here I use the term, 'spacing pattern' to represent the spatial and temporal distribution of a group of conspecifics relative to each other (following Sandell 1989). Other terms used to represent similar attributes of populations include social spacing (e.g. Wilson

1975; Mares et al. 1982), social structure (Spencer et al. 1990) and social organisation (Boutin 1990; Powell et al. 1997).

Data can be derived from spacing patterns at different spatial and temporal resolutions. At the lowest resolution measures of density simply consider the number of animals within an area. At greater resolutions, spacing patterns can vary in the overlap of home ranges and core areas, whether this occurs between all individuals, pairs or groups, whether there is any difference between the sexes and what temporal variation there is in the pattern. Patterns of range area and overlap are frequently considered within the framework of behavioural ecology whereas population densities tend to be considered within population ecology.

1.1.3 Occupancy of habitat patches

The structure of most landscapes is such that areas of suitable habitat for many species are distributed as patches within a largely unsuitable matrix (Formon and Godron 1986). Patterns of occupancy of apparently suitable habitat patches have been a source of considerable recent interest in ecology and conservation biology (e.g. Hanski and Gilpin 1991). Studies have documented relationships between the occupancy of patches and their size and position in relation to other patches (see review in Andren 1994). Larger and less isolated patches have been shown to have higher probabilities of patch occupancy in, for example, the bank vole (Geuse et al. 1985) and red squirrel (Wauters et al. 1994; Verboom and Apeldoorn 1990).

Descriptions of these patterns of patch occupancy require two conditions to be satisfied. Firstly, the habitat requirements of the species must be sufficiently narrow (in relation to the habitat available in the whole landscape) to enable patch suitability to be defined independently of species presence/absence. Secondly, the scale of habitat patchiness must be larger than the scale of individual space use. Many large mammals perceive the landscape in a fine grained way (*sensu* Wiens 1976), that is multiple patches of habitat are incorporated within a single home range rather than multiple home ranges existing in a single patch of habitat (Sinclair 1992). For this reason, patterns of patch occupancy have not been described for large mammals.

1.2 Different processes operating at different scales

The three different scales of mammal spatial distributions outlined in the previous section are influenced by processes operating across a corresponding series of scales. Important among these processes are animal movements occurring at the three scales outlined in Figure 1.2. Small scale foraging movements (fig. 1.2a) are the principal determinant of individual space use and also impact upon spacing patterns. Intra-patch dispersal movements (fig 1.2b) alter the positions of individual home ranges and thus influence population spacing patterns. At a larger scale, inter-patch dispersal movements have been implicated as an important contributory factor in patterns of patch occupancy (e.g. Hanski and Gilpin 1991).

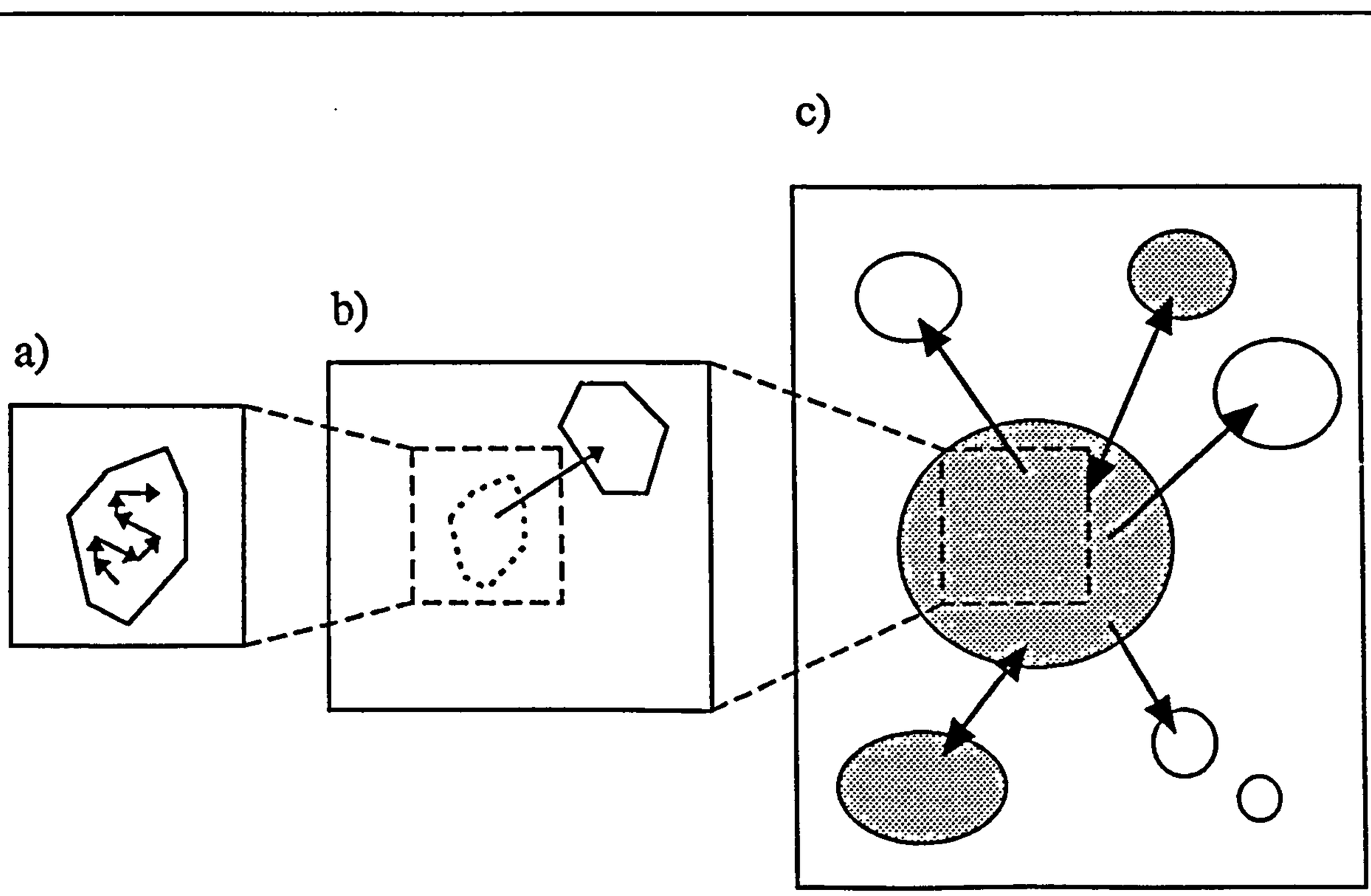

Figure 1.2 Movements of mammals at 3 scales. a) Intra-range foraging movements (solid polygon = home range), b) Intra-patch dispersal movements (dotted polygon = old home range, solid polygon = new home range), c) Inter-patch dispersal movements (ellipses represent habitat patches, filled ellipses = species present, empty ellipses = species absent).

1.2.1 Processes influencing individual space use

The resources, principally food, that mammals require are separated in space. Food tends to be patchily distributed at multiple scales, for example fruits on a tree, trees within a forest and forested areas within the landscape. The patchiness experienced by a forager will be dependant upon the scale at which it operates (Wiens 1976; Addicott et al. 1987). Movements within patches at certain scales and between patches at other scales are the main components of space use (Wiens et al. 1993). These movements are influenced principally by an interaction between an individuals searching strategy and the spatial distribution of food (Bell 1991).

McNab (1963), working on small mammals, was the first to document a positive relationship between the average home range size and body weight of a species. This was attributed to the greater resource requirements of larger animals. Within mammal species, negative relationships between home range size and food density have also been documented (e.g. Kenward 1985; Tufto et al. 1996; Powell et al. 1997). In addition there is experimental evidence to support the dependence of range size on food availability. Boutin (1990) reviewed 23 studies in which the food supplies of terrestrial vertebrates were supplemented, and in 19 of them home range areas decreased. However, as population density tends to be higher at higher food densities, the extent to which range size is a response to food density itself or to the density of neighbours is not always clear (Don 1983; Kenward 1985; Boutin 1990). The suggestion is that at high population densities range sizes may be smaller as individuals attempt to avoid contact with conspecifics. Kenward (1985) concluded that this latter mechanism was more likely to explain range size changes between seasons in a grey squirrel population as range areas were more closely correlated to population densities than to food abundance. In contrast, Mares et al. (1982) conducted a food supplementation experiment on chipmunks and still found a decrease in range area despite controlling for the effect of increased population densities by removing animals. It is likely that food density and population density have a combined effect on range size.

In a number of cases where female space use has been found to be related to food availability, male space use has not (e.g. Erlinge and Sandell 1986; Powell et al. 1997).

This can be explained by the theory that females are the principle resource determining male spacing behaviour in vertebrates (Erlinge and Sandell 1986; Davies 1991; Sutherland 1996). Although males also have to satisfy food requirements, they can increase their fitness by attempting to gain access to as many females as possible. As such it is likely that it will be more difficult to predict the space use of males than of females.

Many mammals have some form of nest or den that they return to on a daily basis. Foraging movements must be incorporated into moving out from and returning to the den. The relative importance of den sites and foraging habitat as a resource is likely to determine whether the home range could be considered to be formed around the den or the den located within the home range. For example, in the European badger where dens (setts) are large complex underground structures that can be passed on from generation to generation for hundreds of years (Neal and Cheeseman 1996) the home range of an individual is more likely to be a result of the position of the sett than the other way around. In contrast, in the red squirrel where nests (dreys) are relatively small structures built mostly from twigs, it seems more likely that an individuals foraging areas will determine where it locates a drey.

The space use of individual mammals can also be influenced by territorial behaviour. Definitions of territoriality generally include exclusive use of space, active defence or both (Maher and Lott 1995). Territory boundaries may be defined by physical aggression, display or some form of marking. However difficulties in the operational definition of territoriality means that species defined in the literature as being territorial may not necessarily occupy areas of space exclusively (Maher and Lott 1995). In the absence of territorial interactions other mechanisms may favour individuals restricting their movements. Food depletion by neighbouring animals may make it unprofitable to stray into their ranges (Stewart et al. 1997). Alternatively an animal may be less likely to locate food or more likely to succumb to predation within unfamiliar areas, also providing an advantage to restricting home range areas (Benhamou and Poucet 1996).

Temporal variation in food availability can modify space use from what might be expected based upon the previously outlined processes. Garshelis and Pelton (1991) document how black bears fed predominantly on fruits in summer and acorns in autumn, leading to very different summer and autumn ranges, and consequently a larger annual range. A similar situation was observed in red squirrels switching between tree species that cone at different times of year (Lurz 1995).

1.2.2 Processes influencing spacing patterns within populations

Spacing patterns are an emergent property of the individual space use of a group of neighbouring conspecifics (Sandell 1989). Although home ranges are predominantly determined by individual foraging movements, their positioning within the landscape can be determined by dispersal movements occurring over larger temporal and spatial scales. Lidicker and Stenseth (1992 : p22) define dispersal simply as : "one-way movements of individuals away from their home ranges". Dispersal movements can result in the displacement of foraging movements (and thus the home range) from one area to another. Following this logic the spacing pattern within an area can be thought of as a combined result of dispersal movements that cause the approximate positioning of home ranges, and intra-range movements that define the exact locations of home range boundaries. Any effect of social behaviour on spacing patterns, such as attraction or repulsion to or from members of the opposite or same sex will manifest itself via these two scales of movement. It is, however, often difficult to differentiate between spacing behaviour that is motivated by social interactions as opposed to a direct response to food availability (e.g. Macdonald 1983; Stewart et al. 1997).

The number of animals within an area is a fundamental result of survival, reproduction and movements across the boundary of the area. Food availability could determine animal density and spacing pattern by influencing these three processes directly. Alternatively, social behaviour could determine the spacing pattern, limiting density possibly below the level potentially supportable by the available food. This is a restating of the debate as to whether population regulation in mammals is a result of intrinsic (behavioural) or extrinsic (environmental) factors (e.g. Sinclair 1989; Wolff 1997).

Regulation is often attributed to extrinsic factors for large mammals and intrinsic factors for small mammals (Sinclair 1989).

1.2.3 Processes influencing the occupancy of habitat patches

Patterns of patch occupancy are a result of a balance between births and deaths within patches and dispersal between patches. In metapopulation theory (e.g. Hanski and Gilpin 1991) patches are assumed to be linked by limited dispersal such that individual patch dynamics are largely independent. Under this assumption smaller patches are more vulnerable to extinction due to demographic and environmental stochasticity. Limited dispersal between patches can lead to recolonisation of extinct patches, or a 'rescuing' of patches close to extinction (Hanski 1982). If dispersal is distance dependant, the combination of extinction and colonisation predicts a positive relationship between patch occupancy and patch size and a negative relationship between patch occupancy and the distance between patches.

Harrison (1994) and Haila et al. (1990, 1993) point out that patterns of patch occupancy may more often be a result of individual rather than population processes. They suggest that in many patchy landscapes dispersal between patches may be frequent such that individuals in separate patches can be considered to be in the same population. In this case the probability of dispersal between patches is similar to that within patches (i.e. the movements in Figure 1.2b are not qualitatively different from those in Figure 1.2c). Along similar lines, the random sample hypothesis states that lower patch occupancy for small patches is simply a result of them being a smaller random sample of larger patches (Haila 1993; Andren 1996). Andren (1996) demonstrated how in landscapes with a large proportion of habitat, it can be difficult to differentiate between the random sample hypothesis and the results of a model where patch survival was dependant on area and isolation.

1.3 Predicting the spatial distribution of mammals

Predicting the spatial distribution of mammals, both into the future and into unsurveyed areas, is an important applied issue (e.g. Wiens et al. 1993; Starfield 1997). Management decisions relating to land use, nature reserve design, pest control and species

reintroductions all require information on spatial distributions. This information is predominantly needed at the scale of population densities and patch occupancies but the ability to make these predictions may depend upon an understanding of the processes operating at finer scales. The aim of this thesis is to investigate how different spatial processes can be modelled at different scales to predict the distribution of mammals. In the following chapter I review applicable modelling approaches.

2. Chapter 2 : Modelling to predict the spatial distribution and abundance of mammals

There are a great number and diversity of methodologies that have been used, or have the potential to be used, to predict the spatial distribution and abundance of mammals. Subsets of these different methodologies have been outlined in recent reviews, that cover either areas of application (e.g. spatial population dynamics (Kareiva 1990), metapopulation biology (Hanski and Gilpin 1991; Hanski and Simberloff 1997), wildlife modelling for conservation (Norton and Possingham 1993) and landscape ecology (Wiens et al. 1993)) or particular modelling methodologies (e.g. models based on the ideal free distribution (Sutherland 1996), population viability analyses (Mills et al. 1996), individual based models (DeAngelis and Gross 1992) and spatially explicit population models (Dunning et al. 1995)).

These models differ principally in the scale (spatial, temporal and number of individuals) at which they represent causal processes and the scale of predictions. A major difference exists between models that derive correlations from patterns and apply these to generate predictions at the same or lower scales and models that represent processes at one scale to generate predictions at larger scales. The former have been termed associative and the latter process-based (Rushton et al. 1997). Associative models are essentially a 'top down' approach, whereas process based models are essentially 'bottom up'.

2.1 Associative models

Associative models are based on the derivation of correlations between a species distribution and measurable environmental variables. These relationships can then be used to predict the distribution of the species in an un-surveyed area or in a

surveyed area following environmental change. Thus the complex interaction of factors determining the presence/absence or density of a species in an area is modelled indirectly through correlation with environmental variables. Associative models vary in their complexity. The simplest ones use a rule based approach to predict presence or absence of a species based on the presence of certain habitats or habitat features. Aspinall (1993) used this to predict the distribution of red deer in Scotland.

More complex methods involve the construction of a statistical model linking the distribution of the species to explanatory variables, including a random error component to account for variation caused by other factors not included in the analysis. Logistic regression, one such method, can be used to predict presence/absence and has been used for a number of taxa including trees (Lenihan 1993), red deer (Buckland and Elston 1993) and kangaroos (Walker, 1990). It can also be used to predict abundances or densities and has been used to do so for river corridor birds (Rushton et al., 1994) and red squirrels (Lurz et al. 1995). Determining the nature of the response of the species density or probability of occurrence to the explanatory variables is not always straightforward. The response can potentially be monotonic (i.e. a change of the explanatory variable in one direction will lead to a change in one direction of the species distribution), unimodal or complexly non-symmetric and an inability to distinguish between them can limit the accuracy of model predictions (Yee and Mitchell 1991).

The models mentioned so far do not consider the spatial structure of landscapes, such as habitat patch sizes, patterns and connectivity, and the potential effect of this on species abundances. Associative models can, however, be extended to include spatial information (see Upton and Fingleton 1985 and Hainining 1990 for a formal treatment of the incorporation of space into regression models). Bright et al. (1994) included woodland size and distance to other woodlands in a regression to predict the abundance of dormice, and similar approaches have been applied to red squirrels (Verboom and van Apeldoorn 1990; van Apeldoorn et al. 1994; Delin and Andren 1996).

Buckland and Elston (1993) described a more complex modelling approach to predict the probability of a species inhabiting a site in the future, based upon site suitability, present distribution and species mobility. This was based on data derived from surveys conducted at two points in time. It does, however, rely on qualitative judgements as to whether a species is absent in an area because that area is locally 'unsuitable' or because the species has not reached it, either due to surrounding unsuitable habitat or just because the colonisation front has not advanced that far. Any sites judged to fall into the last two categories should not be included in the model construction (Buckland and Elston 1993).

Augustin et al. (1996) pointed out that the methodologies of Buckland and Elston (1993) did not allow for the effects of spatial autocorrelation, i.e. that a species may be more likely to be present in one area simply because it is present in a neighbouring area. They described a method of adding a spatial autocorrelation term to logistic models. This represents, for each square, the mean of species presence within a set of neighbouring squares, weighted according to distance from the square under consideration. For data based on samples rather than a complete census, and for applying the method to new areas, the pattern of occupation of neighbouring squares is of course unknown. This potential problem was avoided by initially applying the ordinary logistic model to generate a starting predicted distribution. They found that adding the spatial autocorrelation component to a logistic model of red deer presence in Scotland (Buckland and Elston 1993) increased the match between predicted and observed at the level of individual 1 km squares, but decreased the match at the level of the whole area.

Associative models rely on correlation and as such do not necessarily increase understanding of the mechanisms determining animal densities. The explanatory variables used may not be causal at all, but simply correlated with causal factors. In such a situation a change in a causal factor independently of the explanatory variable could lead to errors in the predictions of the model. Thus a model that explains most of the variation in the observations that used to construct it may perform poorly when predictions are extrapolated (Buckland and Elston 1993). For example an analysis of watervole distribution on the Thames by Barreto et al. (in

prep.) showed that watervole presence was significantly correlated with water quality, however this was suggested as being a result of a secondary correlation between water quality and the distribution of the American mink. The American mink is currently spreading from the lower reaches of the Thames, and therefore inhabits mostly poor water quality areas. It was suggested that heavy predation in these areas created the correlation between watervole presence and water quality.

Associative models also suffer from the limitation that they are essentially based on interpolation between measured datapoints, thus their predictions are unreliable outside the range of conditions encountered in the areas used to develop the model. This precludes application to very different regions or to predicting the results of radical landscape change.

The amount of species survey data and associated habitat variables necessary to develop and test useful associative models can be very large. For example the red deer predictive models developed by Buckland and Elston (1993) and Augustin et al. (1996) were based on deer survey and habitat data for 256 1km squares, but in order to test the models they used the full deer survey that consisted of 1277 1 km squares. Likewise the bird models developed by Buckland and Elston (1993) were based on data from 395 sites of between 15 and 25 km^2.

2.2 Process based models

The range and complexity of process based models applicable to the spatial distribution of mammals is much greater than that of associative models. Here I subdivide the models principally according to the three scales of mammal use of space, outlined in the first chapter, namely : individual movement, movement of multiple individuals relative to each other and large scale dispersal movements. Summaries of the published models in each category are given in tables 2.1 to 2.3.

Reference	Model aims to predict :	outputs	assumptions / input data	representation of space	theoretical / applied (t/a)
Optimal foraging theory e.g Stephens & Krebs 1986	what foragers should do to maximise their intake, over short time periods	optimal foraging strategy	costs and benefits of feeding in different patches	heterogeneous, aspatial or implicit	t
Optimal territory size e.g Schoener 1983	territory size as a trade off between benefits of access to resources and costs of defence	optimal territory size	costs and benefits associated with territory size	homogenous, implicit	t
Gautestad & Mysterud 1995	null model of home range	individual movement pattern	movement rules	homogenous, realistic	t
Armstrong et al. 1987	the benefits of memory for foragers	food intake, foraging time	movement & feeding rules, energetics, territory boundaries	heterogeneous, explicit	t
Benhamou 1989	mechanistic explanation of home ranging movements based on olfaction	individual movement pattern	movement rules	homogenous, explicit	t
Stillman & Sutherland 1990	effect of different movement rules on resource intake	individual food intake	movement rules	heterogeneous, explicit	t
Stewart et al. 1997	that avoiding entering neighbouring ranges can increase food intake (PRE)	individual food intake	movement rules, den positions, territory boundaries	heterogeneous, explicit	t
Saarenema et al. 1988, Folse et al. 1989	use of Artificial Intelligence techniques for modelling animal-habitat interactions	food intake, movement paths	movement rules, random and memory based	heterogeneous, realistic	t, a

Table 2.1 Summary of models applied to individual space use

Reference	Model aims to predict :	outputs	assumptions / input data	representation of space	theoretical / applied (t/a)
Jones & Krummel 1985	optimal territory size in the presence of neighbours	territory boundaries, optimal territory size	den positions, movement and competition costs	homogenous, explicit	t
Hard core (e.g. Bartlett 1974)	distribution of nests, based on avoidance	spatial distribution of nests	minimum distance between nests	homogenous, explicit	t, a
Ideal Free Distribution (IFD) e.g. Fretwell & Lucas 1970	distribution of foragers between food patches	spatial distribution of animals	optimisation of food intake, perfect knowledge, no travel costs	heterogeneous, implicit	t
Bernstein et al. 1988, Bernstein et al. 1991	distribution of foragers between food patches, under relaxation of assumptions of the IFD	spatial distribution of animals	optimisation of food intake	heterogeneous, explicit (1 dimensional)	t
Ideal despotic distribution Sutherland 1996	effect of patchiness of food availability on relationship between forager competitive ability and territory size	territory sizes	costs of defence, benefits of larger territories	heterogeneous, implicit	t
Turchin 1991	distribution of foragers as an emergent property of movements	equilibrium, spatial distribution of animals	movement lengths and turn angles in different habitats	binomial, explicit	t
Blackwell 1994, Blackwell & Tranmer 1994	whether territories formed to support a single pair of animals can support others	spatial distribution of territories	distribution of resources, territory formation rules	heterogeneous, explicit	t
Ryti & Case 1992	distribution of ant colonies as a result of competition at or following establishment	spatial distribution of colonies of animals	colony formation and competition rules	homogenous, explicit	t

Table 2.2 Summary of models applied to the relative movements of individuals

Sutherland & Anderson 1993, Sutherland & Allport 1994	distribution of set number of flocking birds between foraging sites due to depletion competition	distribution of foragers between food patches	patch choice rules, number of foragers, no travel costs, perfect knowledge	heterogeneous, implicit	t, a
Sutherland & Dolman 1994	population size and distribution between foraging sites under the effect of interference and depletion competition	number of foragers and their distribution between food patches	patch choice rules, no travel costs, perfect knowledge	heterogeneous, implicit	t, a
Turner et al. 1993	where animals go, survival rates, what is the best movement rule	animal survival	movement rules, number of animals	heterogeneous, realistic	t, a
Moen et al. 1997	effect of foraging strategy on survival and reproduction	body mass, activity times, intake rates	movement & feeding rules, energetic parameters	heterogeneous, realistic	a
Turner et al. 1994, Wolff 1994	response of animals to landscape change	individual survival (and breeding success in Wolff 1994)	movement & feeding rules, energetic parameters	heterogeneous, realistic	a
Milne et al. 1992	interaction between scale dependent foraging activity and landscape patterns	spatial distribution of foragers and forage	home range areas, range movement rules	heterogeneous, realistic	t
Moen et al. 1998	extrapolate from foraging behaviour to population dynamics	individual energy balance, population densities	movement & feeding rules, energetic parameters, reproduction rules	heterogeneous, explicit	a

Table 2.2 Summary of models applied to the relative movements of individuals (continued)

Reference	aim to predict	outputs	assumptions / input data	representation of space	theoretical / applied (t/a)
Metapopulation models e.g. Levins 1969, Hanski 1994	the effect of patch sizes and spatial arrangement on population persistence	equilibrium patch occupancy and persistence	extinction and colonisation rates	binomial, implicit	t, a
Diffusion models e.g. Okubo 1980, Okubo et al. 1989	spread of populations	changing distribution of a population over time	population growth and diffusion rates	homogenous, implicit	a
Spatially implicit population models, e.g. Lindenmayer & Lacy 1995 a,b,c	the influence of habitat fragmentation and dispersal on population persistence	patch occupancy and persistence probability over a defined time period	demographic and dispersal rates	binomial, implicit	t
SEPMs with an implicit representation of dispersal e.g. Lahaye et al. 1994, Rushton et al. 1997	the viability of populations in real landscapes	patch occupancy and persistence probability over a defined time period	demographic and dispersal rates, dispersal rules	binomial, explicit or realistic	t, a
Explict Dispersal models e.g. Gustafson & Gardner 1996, Schippers et al. 1996, Schumaker 1996, Ruckelshaus et al. 1997	the effect of landscape structure and dispersal rules on the dispersal of animals between habitat patches	dispersal probabilities or successes between patches	dispersal movement rules, mortality probabilities	binomial or heterogeneous, explicit or realistic	t, a
SEPMs with an explicit representation of dispersal e.g. Pulliam et al. 1992, Liu et al. 1995	the viability of populations in real landscapes	patch occupancy and persistence probability over a defined time period	demographic and dispersal rates, dispersal rules	binomial, realistic	a

Table 2.3 Summary of models applied to dispersal movements

Within the three scales covered by tables 2.1 to 2.3, each model can be classified according to a variety of attributes including whether they are theoretical or applied, the representation of space, the number of animals represented, the type of movement represented and the amount of landscape information accredited to animals. In most cases these model attributes fit into some form of continuum but putting them into distinct categories facilitates an understanding of how the different models relate to each other.

Models can be classed as theoretical (or strategic, Holling 1966) if they are designed to develop general principles or rules, and applied (or tactical, Holling 1966) if they are designed to address a particular management scenario. The former tend to exclude as much detail as possible while capturing the desired processes (e.g. May 1974) whereas the latter tend to include as much detail as is available, or possible to model, in order answer a particular applied question.

Two aspects of the representation of space within models can be recognised. Firstly there is the representation of the spatial separation of objects or processes. Models can be classed as either aspatial, spatially implicit, spatially explicit or spatially realistic (Hanski 1994; Hanksi and Simberloff 1997). A similar classification into island models, stepping stone models and continuum models is described by Kareiva (1990). In spatially implicit models, spatial subdivision is represented but no consideration of relative positioning is considered. Thus, objects and processes are separated in space, but all are equally separated. For example, in the original metapopulation model of Levins (1969), extinction and colonisation probabilities are equal for each patch. The theory of the ideal free distribution of foragers, developed by Fretwell and Lucas (1970) is also based upon patches that are separated in space but their spatial positions are not considered. In contrast, spatially explicit models do represent the relative positioning of objects and processes, such that the interactions between different locations are not equal. Generally locations that are closer together are represented as having a greater interaction than those that are further apart. For example, Bernstein et al. (1991) developed a model to investigate the effect of incorporating an explicit representation of space and non negligible travel costs on the ideal free distribution.

Spatially realistic models are a special case of spatially explicit models, where the interactions between locations are based on their positions in real landscapes. Such models have recently become popular as a means of representing population dynamics in real landscapes (e.g. Liu et al. 1995; Rushton et al. 1997).

Secondly, there is the representation of the attributes of different spatial locations. Space can be represented as homogenous, with equal attribute values for each location, binomial, where there are just two potential attribute values and heterogeneous, where a range of attribute values are represented. For example, Okubo et al. (1989) used a homogenous representation of space to model the spread of the grey squirrel in Britain. Most models that predict the occupancy of habitat patches by populations use a binomial representation of space that differentiates only between habitat and non-habitat (e.g. Lahaye et al. 1994; Lindenmayer and Lacy 1995c). Studies simulating small scale foraging movements have tended to use a heterogeneous representation of space (e.g. Turner et al. 1993, 1994; Moen et al. 1997).

Although all of the models described here represent processes that are emergent from the behaviour of individuals, they differ in the number of individuals represented and whether processes are represented at the individual level or not. Possibly the simplest models represent the behaviour of a single individual, for example the home ranging models of Gautestad and Mysterud (1995) and Benhamou (1989). At larger scales, more complex models simulate the interaction of multiple individuals (e.g. DeAngelis and Gross 1992, Liu et al. 1995). At larger scales still, processes are often represented at the population rather than individual level (e.g. Lahaye et al. 1994).

All of the models described here include some representation of animal movements. They differ in the type of movements that are represented and the way in which those movements are represented. Types of movement represented include : 1) nomadic movements, where daily foraging paths are not constrained to a sub-section of the landscape (e.g. Turner et al. 1993, 1994; Moen et al. 1997), 2) home ranging movements, where foraging paths are constrained (e.g. Gautestad and

Mysterud 1995; Benhamou 1989), 3) territorial movements, where animals are excluded from areas used by others (e.g. Sutherland 1996), 4) dispersal movements within a population, where an animal disperses but remains within the same population or sub-population (e.g. Milne et al.1992) and 5) dispersal movements between populations, where an animal moves to a different population (e.g. Levins 1969; Rushton et al. 1997). These different movements can either be represented implicitly or explicitly. In an implicit representation only the beginning and end points of the movement are considered, whereas in an explicit representation the movement path itself is considered. For example Fretwell and Lucas (1970) implicitly represented the movement of foragers between food patches, others have represented it explicitly (e.g Turchin 1991; Turner et al. 1993). Similarly the dispersal of animals between populations has been represented implicitly (e.g. Levins 1969; Lindenmayer and Lacy 1995c) or explicitly (e.g. Gustafson and Gardner 1996; Schippers et al. 1996).

The representation of movements may be based upon a response to the structure of the landscape or not. Lima and Zollner (1996) coined the term 'informational continuum' to describe the range of levels of knowledge of the landscape accredited to animals within movement models. At one extreme animals are represented as moving randomly effectively having no information about the landscape (e.g. Gautestad and Mysterud 1995); and at the other extreme animals are assumed to have perfect knowledge of potential food intake rates in different parts of the landscape (e.g. Sutherland and Dolman 1994) and to be able to calaculate the most efficient routes between resource cells (e.g. Gross et al. 1995). In between these extremes animals may be accredited with information about areas within a perception range of their present location (e.g. Turner et al. 1993) or some form of learning and memory may be represented (e.g. Folse et al. 1989). It has been suggested that due to the lack of behavioural information at the landscape scale, the only justification for any of these rules is a 'standard of plausibility' but that until more behavioural knowledge is gathered this is perhaps the only option (Lima and Zollner 1996).

Bearing in mind these general differences I will now go on to review models applicable to the spatial distribution of mammals. For clarity I divide the review into 3 sections, similar to the 3 scales of mammal spatial distributions and movements outlined in chapter 1. These three sections are : 1) Modelling individual space use, 2) Modelling foraging movements of multiple individuals, and 3) Modelling long distance dispersal movements.

2.2.1 Modelling individual space use

Individual space use has been modelled in two fundamentally different ways. In one the emphasis is on the actual movements of the foragers, which are modelled explicitly. In the other the emphasis is placed on the size of ranges or territories resulting from such movements, but the movements themselves are not modelled explicitly.

2.2.1.1 Foraging movement models

Most foraging movement models are based on simulation at the level of the individual. For each of a number of time steps the movement of the individual through a representation of the landscape is simulated using a rule base. Published models differ in both their objectives and in the methods employed to achieve those objectives. Issues addressed by this type of model include attempting to determine what movement rules animals follow (Andersen 1996; Gross et al. 1995; Garber and Hannon 1993), investigating the mechanisms of home range formation (Gautestad and Mysterud 1995; Gautestad and Mysterud 1993; Benhamou 1989; Siniff and Jessen 1969) and investigating the efficiency of different foraging rules in different landscapes (Cain 1985; Andersen 1996; Moen et al. 1997; Stewart et al. 1997).

To investigate what foraging rules animals follow, simulation models based on plausible movement rules have been compared to animal movement patterns observed in the field. Garber and Hannon (1993) simulate the foraging paths of tamarins searching for fruit and compare these simulations to field observations. Tamarin behaviour in the field was consistent with the animals utilising a spatial memory map and it was concluded that this is likely to be used in conjunction with

other sensory cues. A similar approach has been applied at a smaller spatial scale to herbivores foraging for visible prey (Gross et al. 1995). The movements of bighorn sheep in experimentally constructed food plant mosaics (100m square) was compared to simulations following a number of different rules-of-thumb. The rules simulated included a random walk, movement towards the nearest food patch and calculation of the most efficient movement path by solution of the 'travelling salesman' problem. They came to the conclusion that modelling herbivore foraging using a random walk is 'clearly inappropriate' and that a 'move to nearest food patch' rule should be more realistic for herbivores with visible prey.

Similarly a number of studies have developed simulation models in an attempt to explain how animals restrict their foraging movements to a home range. Siniff and Jessen (1969) developed a model in which movements are biased towards previously visited points, the initial pattern of space use being either derived from telemetry data or from an initial simulation period based on empirically derived movement parameters. Benhamou (1989) developed a model based on olfactory stimuli that enables an animal to stay within its home range without having to be aware of distance from the den. Gautestad and Mysterud (1995) developed a simple simulation model aimed to represent the conventionally accepted picture of a home range where movement at the edge of the range tends to be back towards the centre. They indicated that the results of this model corresponded poorly to telemetry data for sheep and foxes. A multi-scaled random walk model (Gautestad and Mysterud 1993) which is equivalent to one random walk being super-imposed upon another was claimed to be more consistent with field data (Gautestad and Mysterud 1995).

These studies and others indicate uncertainty on the part of biologists and modellers regarding the foraging rules or cues that animals follow (Lima and Zollner 1996). Studies simulating animal foraging with other objectives than simply determining what movement rules the animals are following, have thus still tended to use either a number of plausible rules (e.g. Moen et al. 1997) or vary parameters within the foraging rule (e.g. Andersen 1996; Cain 1985). The results from the different foraging rules then tend to be compared to investigate the range of potential behaviour, and to avoid reliance on a single movement rule that is possibly a poor

representation of reality. The conclusions from such studies can be divided into those that refer to the performance of a single foraging rule under different conditions and those that refer to the relative performance of different foraging rules under the same conditions.

In the former category Cain (1985), simulating insects searching for a single hostplant, concluded that at low plant densities success increased with plant aggregation, and at high densities aggregation had a negative effect. Andersen (1996), simulating pocket gophers using visual cues to search for food plants, came to the unsurprising conclusion that a higher concentration and density of food increases forager success. Comparing the relative success of different foraging rules under the same conditions Stillman and Sutherland (1990) demonstrated an increase in food intake if forager movement in good patches is slower than that in poor patches. Folse et al. (1989) described how search paths based on a rule incorporating memory of food locations were shorter than random ones. Stewart et al. (1997) found that food intake of group living foragers was greater for animals that spend more time in areas mid way between neighbouring dens. Moen et al. (1997) demonstrated that simulated moose using non-random foraging rules achieved a higher body mass than those using random rules, and that this difference was greater at lower food densities.

2.2.1.2 Predicting the size of ranges or territories

There has been much theoretical work on predicting the optimal size of territories by determining the size at which the difference between costs of defence and benefits of access to resources is greatest (reviewed in Schoener 1983). These models are particularly simplified, dealing with uniform environments and with simple functions to describe changes in costs and benefits. Schoener (1983) showed how their predictions can differ according to the assumptions made, for example whether animals are modelled as time minimisers or energy maximisers.

2.2.2 Modelling foraging movements of multiple individuals

Models of the relative movements of individuals can be divided into 3 categories. Firstly there are those that model the distribution of foragers between food patches based on the optimisation of individual resource intake, but with little or no representation of the actual movements between patches. Secondly there are those that model territoriality and the pre-emption of space, with only an implicit representation of the ranging movements of individuals within those territories. Thirdly there are those that use an explicit representation of the small scale movements of individuals to generate emergent behaviours at larger scales.

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2.2.2.1 Modelling the distribution of foragers between food patches

This group of modelling approaches is based on optimisation of individual behaviour, and on the assumption that the optimal behaviour of one individual will be dependant on that of other individuals. This has been used to predict the distribution of competing consumers between patches differing in resource abundance. The ideal free distribution (IFD) (Fretwell and Lucas 1970) is based on assumptions that all individuals are equal, act to maximise their resource consumption, have perfect knowledge of the resource landscape, are free to move between patches and travel costs are negligible. Under these assumptions the prediction is that consumers will locate between patches such that all individuals gain equal reward over time, and this is termed the IFD. If the intake of individuals in one patch is lower than that in others, the theory predicts that animals would move away, increasing the intake of those remaining in the patch, decreasing the intake of those in the patches that gain individuals and thus act to equalise the intake of all individuals and move the population towards the IFD. This type of approach can be used to predict the distribution of animals within ranges or when applied at a larger scale the distribution of ranges within the landscape.

The accuracy with which the IFD predicts the distribution of consumers has been the subject of much debate. Some authors suggest it is robust to the violation of its assumptions (e.g. Milinski 1988) others that it consistently over-predicts the use of the best sites (e.g. Sutherland et al. 1988). A recent review (Kennedy and Gray

1993) comes to the conclusion that : 'in its current form the IFD does not accurately predict the distribution of foraging animals. The hope that the IFD would prove a simple, accurate and robust model does not seem justified'. However, it is suggested elsewhere that the principle utility of the IFD is as a null model to which the effect of more realistic factors can be added (Sutherland 1996).

Sutherland and Anderson (1993) and Sutherland and Allport (1994) develop models to predict the distribution of consumers between food patches under the effects of depletion. The number of consumers, depletion rates and the resource densities of patches are the principal inputs to the models that base consumption rate on a type 2 functional response (Holling 1959). Consumers initially concentrate on the richest patches until these have been depleted to the extent that other previously poorer patches are now of equal quality. Thus as depletion continues the number of patches used by the consumers will increase. The representation of space is implicit as the relative positioning of patches is not considered. Assuming that there is a threshold resource density below which consumers starve or migrate, the number of consumers that can be sustained by a location over a particular time period can be calculated (Sutherland and Anderson 1993). This approach has been applied to predict the numbers of bean geese that can be supported at a particular site in Norfolk (Sutherland and Allport 1994). Interference and depletion models have been combined with population dynamics to predict the consequences of habitat loss for migratory bird species (Sutherland and Dolman 1994). The interference and depletion models are used to predict the distribution of consumers between sites. Population change within sites is calculated from density independent mortality and density dependant breeding and starvation. It does not work strictly at an individual level but models a population as a number of phenotypes differing in their competitive ability.

Bernstein et al. (1988) develop an individual based simulation model that relaxes the assumption of omniscience implicit in the ideal free distribution. Animals are simulated as learning and moving on from a patch when their intake rate declines below their perception of the mean intake rate across the whole area. In a later paper this model is extended (Bernstein et al. 1991) to incorporate the effects of

non-negligible travel costs between patches in a one dimensional, explicit representation of space. These models indicate how departure from the assumptions of the IFD leads to departures from its predictions. The first paper (Bernstein et al. 1988) showed that at high depletion rates, foragers were unable to keep track of prey availability and thus the IFD was not reached. The second paper (Bernstein et al. 1991) showed that the addition of travel costs made foragers less likely to move, and this again prevented the population from reaching the IFD.

2.2.2.2 Territorial, space pre-emption models

Jones and Krummel (1985) criticised models of individual territory size that do not explicitly consider the spatial behaviour of neighbouring individuals (e.g. Schoener 1983). They develop an analytical model to predict the spatial distribution of individuals in a population context, but it was still restricted to a uniform environment.

The effect of territorial interactions on the spacing of animals has been addressed using hard-core models that simulate the pre-emption of space (Upton and Fingleton 1985). This group of approaches are based on the idea that individual animals and plants occupy a certain amount of space to the exclusion of conspecifics. This has been modelled statically by generating a random distribution of points and then removing pairs of points that are closer than a certain distance (Matern 1960) and sequentially by generating the points one at a time and only retaining those points not too close to a previously generated (Matern 1960) or retained point (Diggle et al. 1976) (reviewed in Upton and Fingleton 1985). In these each point is effectively surrounded by a circular area termed a 'hard-core' from which other points are excluded. Such a model has been used to describe the positioning of nests in gull colonies (Bartlett 1974).

These hard-core approaches are based on linear distances between neighbours irrespective of how many neighbours there are, thus the hard-cores are all circles of identical size. A consideration of the interaction with all neighbours would seem more biologically meaningful. Such an approach has been applied to plants by firstly dividing space into Thiessen polygons around each individual (Kenkel 1991).

Thiessen polygons have the property that each point within that polygon is closer to the individual around which the polygon was constructed than to any other. It was shown that plants with a very close neighbour may still be able to acquire enough resources if their polygon extends far enough in another direction. For territorial animal species territory boundaries might be expected to conform to Thiessen polygons as individuals might only be able to defend space closer to their home than that of any other individuals (Jones and Krummel 1985). There is some evidence to suggest that this is the case in high density badger populations (Doncaster and Woodroffe 1994) although this has been questioned (Blackwell and Macdonald 1997).

A combination of hard-core and tessellation type approaches could offer new possibilities for predicting space pre-emption in mammals. Ryti and Case (1992) developed a model that contained elements of these two approaches to predict the spacing of ant colonies. It represented the effect of neighbourhood competition on either or both of colony establishment and colony persistence. In the former, new colonies were not allowed to establish within a pre-defined distance of existing colonies. In the latter, the survival and reproductive output of existing colonies was set to be dependent on the number and proximity of existing colonies. It was found that when the effect on colony establishment was included, nest spacing became increasingly regular with increasing densities, but when competition between established colonies only was included the resultant nest spacing was random.

Although the previous series of methods considered the relative positions of individuals in space, the space that they considered was homogenous. Blackwell (1994) and Blackwell and Tranmer (1994) developed simple models of territory formation in heterogeneous landscapes. They represented the landscape as a series of randomly located points with resource values drawn from a statistical distribution. Territories are constructed by randomly selecting an initial point, then selecting additional points around this until the territory reaches a defined minimum richness. This process is repeated until no more contiguous territories can be constructed. A function based on the construction of Thiessen polygons around resource points simulates the interaction between neighbouring territories and

prevents the formation of territories that are non contiguous. This approach was used to show that territories formed to support a single pair of animals often contain sufficient resources to support additional animals. Constructing Thiessen polygons around the resource points within a territory is however less biologically meaningful than constructing them around dens. A Thiessen polygon formed around a den defines the area that is more accessible to that animal than any other, constructing polygons around food sites does not have such ecological relevance (Blackwell pers. comm.).

A theoretical model, related to the IFD, the ideal despotic distribution (Fretwell and Lucas 1970), has been constructed to predict the distribution of territorial consumers between patches. It considers each patch as containing a number of territories of varying quality, as individuals arrive they occupy the best remaining territory. Thus, the patch containing the best territory will be occupied first, subsequent patches will be occupied when territories within them are of a higher quality than those remaining in the best patch. This has also been termed the ideal pre-emptive distribution (Pulliam and Danielson 1991). Assumptions made in these models include perfect knowledge over the area of investigation and ability to move freely to un-occupied territories.

Sutherland (1996, chapter 6) develops a model based on the ideal despotic distribution that predicts the size of territories in an environment with patches of varying quality. This takes into account differences in competitive ability, patch quality and the size of the population but the representation of space is only implicit as it does not consider the relative locations of territories or patches. A simple relationship between the costs of defence and territory area was assumed and this was balanced against the benefits of holding a larger territory, which were assumed to be exponentially related to territory area and patch quality. Under these assumptions superior competitors ended up with larger territories when patches were equal in quality, but not necessarily when patches differed in quality.

2.2.2.3 Individual movement models

In the following series of models, the implicit representation of foraging movements used in the models outlined in the previous section, is replaced by an explicit representation. Turner et al. (1993) simulated the movements of large numbers of individual herbivores in Yellowstone National Park under a range of movement rules and food availabilities. They demonstrated that the spatial arrangement of food had a greater influence on foragers with limited movement or detection abilities. They also showed that this difference between the performance of different foraging rules decreased at high food densities. Despite simulating multiple foragers in a representation of a real landscape they did not produce any predictions of the spatial distribution of animals, but they did indicate that this was a potential output. In a subsequent paper (Turner et al. 1994) the same model was applied to predict the effect of fire and winter severity on ungulate survival, also within Yellowstone. This also concentrated on outputs of foraging and performance, but did produce some predictions of the spatial distribution of foragers.

An analytical model approximating the individual-based simulation approach was described by Turchin (1991). It predicted the population density of organisms across an area based on the frequency distributions of move speed, duration and turning angle in the different habitat types that make up that area. Although this is less cumbersome than simulation it relied on a number of assumptions (e.g. that movement is largely random and that there are a large number of organisms moving around in the same way without interacting) that restrict its application beyond the insects to which it was applied in the paper.

Also modelling at the individual level, Milne et al. (1992) concentrated on the results of home range movement at the population level. Home range movement was modelled by movement in a random cardinal direction for a distance less than 1.5 times the width of the home range. The availability of food across the landscape was described from satellite data. Animals foraged randomly within this landscape and if they achieved a negative energy balance over a defined time period they were

made to move range. Thus, the dependence of range movements on movements within ranges was explicitly considered.

Moen et al. (1998) used a somewhat more complex methodology to extrapolate from individual level behavioural processes to landscape and population level outputs. They linked a moose foraging model that runs for a single individual in a single year (Moen et al. 1997) to population and plant growth models that run over multiple years. The change in body mass of the individual foraging animal was used to determine the survival and natality rates used in the population model. As the simulated landscape was too small to represent the home range of a moose, the effect of moose food depletion was actually represented by some fraction of an animal foraging on the landscape (R. Moen pers. comm.). Thus, moose density (calculated in the population model) fed back to the availability of food in the landscape by influencing the 'size of the fractional animal' simulated in the foraging model. An increase in moose density increased the size of the fractional animal simulated and thus increased levels of food depletion. This framework was used to show how different foraging strategies influenced the availability of forage and moose population densities. The approach combined explicit and implicit representations of space to achieve these objectives. Although the spatial distribution of food was represented explicitly in the foraging simulations, the use of fractional animals and the way that the simulated forager was restarted at random positions when it reached an edge, are essentially implicit representations of space.

2.2.3 Modelling long distance dispersal movements

Models of long distance dispersal movements can be divided into 4 categories. Firstly, there are diffusion models that represent the spread of populations through homogenous space. Secondly, there are metapopulation models that describe the occupancy of spatially separated habitat patches as a balance between extinction and colonisation. Thirdly, spatial population simulation models represent demographic processes within habitat patches and dispersal between them. Fourthly, explicit dispersal models that simulate actual dispersal paths between patches.

2.2.3.1 Diffusion models

The spread of animal populations has been described using analytical diffusion models (e.g. Okubo et al. (1989). These models consist of two parts: firstly population growth and secondly movement. Movement is based on Fickian diffusion whereby the movement of a large number of independent random walkers in a homogenous environment can be described using a diffusion equation (Okubo 1980). These assumptions are violated in real mammal populations in real landscapes and this limits the utility of the method. However diffusion models may provide useful null models for the behaviour of populations in the absence of spatial complications (Kareiva 1990).

2.2.3.2 Metapopulation models

Most other process-based models at this scale assume a simple division of the landscape into habitat patches that are able to support populations, and the matrix, that is unsuitable for long term occupation but through which animals can disperse. The simplest of these models are the analytical metapopulation models that represent populations of populations (Levins 1969). Within these patches are represented in a similar way to individuals in conventional population models, in that they can be born (colonised) and die (go extinct). In Levins (1969) original metapopulation model each patch is considered as either occupied, and if so has a defined probability of going extinct, or un-occupied in which case it has a defined probability of being colonised. This formulation allows an analytical solution of the proportion of patches occupied at the equilibrium between colonisation and extinction.

In more complex, structured models (e.g. Hastings 1991, Hanski and Thomas 1994, Verboom et al. 1991), intra-patch dynamics are explicitly modelled. Rather than describing patches as simply occupied or unoccupied, such models describe the changing numbers of individuals within patches. Structured metapopulation models can also be extended to include the age structure of local populations (e.g. Hastings 1990) although models including both spatial and age structure become 'unwieldy' (Wennegren et al. 1995).

Local dynamics can be modelled using logistic type models (e.g. Hastings 1991, Hanski and Thomas 1994) or a simpler Markov chain model (e.g. Lankester et al. 1991, Verboom et al. 1991). In the latter there are a finite number of states that a patch can exist in, corresponding to the number of individuals perhaps dividing them into different sex and age classes. A matrix of transition probabilities determines changes in the probability of a patch existing in a particular state from one time step to the next. Verboom et al. (1991) compared the results of a Markov chain model explicitly considering local dynamics and a Levins type 'winking patches' model. They concluded that the simpler model was 'a sufficiently accurate representation of the complex model'. Lankester et al. (1991) suggested that simple Levins type models can be calibrated by construction of detailed models for single patches.

Source-sink population modelling is an extension of the metapopulation concept that concentrates on the consequences of differences in intra patch processes between areas of differing habitat suitability. The models are based on the theory that dispersal from one area of high habitat suitability to another area of low habitat suitability may sustain a population in the latter area (Pulliam 1989). Pulliam's (1989) model is of the simple analytical type. Source-sink type behaviour, if it was going to occur in a particular situation, would be expected to be an emergent property of the more complex simulation models described later.

Hanski (1994(b)) outlined a practical model of metapopulation dynamics, in which mechanistic equations representing extinction and colonisation were derived from patterns of patch occupancy observed in the field. In contrast to the previously described approaches this included an explicit representation of space in the form of patch areas and inter-patch distances. These were used as inputs together with a parameter describing the distribution of migration distances, and assuming the population was at an extinction/colonisation equilibrium, maximum likelihood techniques were used to derive a model to predict patch occupancy in the field. This approach was thus intermediate between the analytical models described previously and the spatial simulation models I will describe next.

2.2.3.3 Spatial population simulation models

Spatial population simulation models differ principally according to whether they represent space implicitly or explicitly and whether they represent demographic processes at the level of the individual or the patch. Lahaye et al. (1996) described the application of a spatially explicit model to the Spotted Owl in southern California, in which demographic processes were represented at the level of the patch. This was undertaken using the RAMAS/space software package (Akçakaya and Ferson 1992). Within-patch population growth was simulated using a stochastic, age structured population model, sampling survivors from a binomial distribution and fecundity from a poisson distribution to represent demographic stochasticity. Habitat patches were identified as forested mountain tops within the arid matrix that makes up most of southern California and patch carrying capacities were estimated based on field surveys. No dispersal was observed in the field, in the model dispersal was simulated as occurring only between selected patches, but the criteria upon which this connectance was based were not explained. For the connected patches a range of distance dependent dispersal rates were simulated. Model runs were also conducted under a range of correlations in population growth rates. Predictions of population change were shown to be particularly sensitive to the level of correlation with increased correlation levels leading to increased risks of population decline. A similar approach was applied to the helmeted honeyeater, an endangered Australian bird, by Akçakaya et al. (1995). They firstly used a logistic habitat suitability model to create a binomial habitat suitability map. Dispersal between patches was represented using an exponential distance-dependant dispersal model such that the probability of individuals moving between two patches was higher the closer they were.

Rushton et al. (1997) also used a spatially explicit, population based approach to simulate the interaction between red and grey squirrels in Norfolk, UK. Habitat patches were defined according to woodland cover derived from satellite imagery. Patch carrying capacities were calculated as the number of average sized home ranges that could be accommodated, multiplied by a 'packing factor' of 1.1 to allow for range overlap. Within each run, demographic processes were represented by

applying constant mortality and fecundity rates to each patch. In contrast to Lahaye et al. (1996) and Akçakaya et al. (1995), dispersal was represented as only occurring once a patch reached carrying capacity, at which point all excess animals were dispersed. Individuals were dispersed to the nearest patch that was below carrying capacity as long as this was within an estimated maximum dispersal distance. Runs were conducted under a range of demographic, dispersal distance and carrying capacity parameters.

Application of an individual-based spatially implicit population model has been described by Lindenmayer and Lacy (1995 a,b,c). They used Vortex, a population viability analysis software package (Lacy 1993). They investigated the likely impact of population subdivision on the mountain brushtail possum in south-east Australia (Lindenmayer and Lacy 1995 c) and looked at the differences between the predicted response of this species and two other arboreal marsupials (Lindenmayer and Lacy 1995 a). Vortex simulates the births and deaths of individuals as sequential events governed by separate probabilities, the outcomes determined by a random number generator (Lacy 1993). Lindenmayer and Lacy (1995 c) simulated hypothetical populations of 100, 200 and 400 animals divided into 1-10 subpopulations. Dispersal was simulated as the probability, for each individual, of moving to each other sub population and values of 0.01 and 0.05 were used. The results indicated a predominantly negative effect of population subdivision on patch occupancy and population persistence. The effect of dispersal rate was dependent upon patch size. At patch sizes in excess of 40 individuals increased dispersal rate lead to increased persistence and population growth. The opposite effect was demonstrated at patch sizes below 40 individuals.

2.2.3.4 Explicit dispersal models

In all of the patch models described above dispersal between patches is represented only implicitly. Another group of modelling approaches have explicitly represented dispersal movements between habitat patches (e.g. Gustafson and Gardner 1996; Schippers et al. 1996; Schumaker 1996; Ruckelshaus et al. 1997). Schippers et al. (1996) used a random walk with assigned probabilities of entering different habitat types, to estimate connectivity between habitat patches for the badger in the

Netherlands. They suggested that these estimates could usefully be incorporated into the metapopulation models of Verboom et al. (1991) and Lankester et al. (1991). However they acknowledged that there is very little available data to test their representation of dispersal.

Gustafson and Gardner (1996) simulated dispersal movements between woodland patches in artificial and satellite data derived landscapes. For each patch they conducted 10000 runs in which a random walker was started at the patch, and moved until it reached another patch or had moved 1000 steps, in which case it was assumed to die. They calculated, for each patch, the proportion of dispersers successfully locating any other patch and the proportion of dispersers arriving in the patch. They investigated changing the probabilities of entering each land cover type, from a homogenous representation where all probabilities were equal to a heterogeneous representation in which probabilities of entering certain land cover types was higher than others. They found that this had unpredictable effects on dispersal success due to the different landscape structures.

A similar approach was followed by Schumaker (1996), but in this case the aim was to determine the ability of a range of landscape indices to predict dispersal success. Satellite data for forest cover in the western USA was used to provide the landscapes on which the dispersal simulations were run. A hexagonal grid was superimposed on the satellite data with each cell the size of a potential territory, those cells that contained larger than a threshold proportion of woodland were classed as suitable for occupation. At the beginning of each simulation half of the suitable territories were initialised with animals. Offspring of these animals were simulated as moving randomly between cells with a predefined per time step probability of stopping, that was set to give a mean path length of 25 steps. Individuals not locating a vacant territory before stopping were assumed to have died. A 'linearity parameter' was included that allowed movement paths to be made more directional in some model runs. Dispersal success, namely the fraction of individuals that successfully located vacant territories, was used as the main output. It was found that all of the conventional landscape indices tested were poor

predictors of dispersal success, but that a newly developed one performed slightly better.

Dispersal success was also used as the main output by Ruckelshaus et al. (1997). They described a spatially explicit model of animal dispersal in which individuals were simulated as moving randomly within randomly generated fragmented landscapes. For each replicate a single animal was positioned at a randomly chosen patch and moved until it located another patch. This framework was used to show how changing the values of three model inputs (proportion of suitable habitat, maximum dispersal distance and dispersal mortality) effected dispersal success, calculated as the fraction of dispersers that successfully located a habitat patch.

Explicit representations of spatial population dynamics and dispersal paths have been combined in a model applied to the Bachman's sparrow (Pulliam et al. 1992; Liu et al. 1995). The model represented space as a hexagonal grid with each cell approximating the size of a breeding territory. A habitat map was derived from a forest compartment map and this was used to classify the suitability of potential territories. Survival and fecundity probabilities were applied to individuals within territories. Dispersal of juvenile females only was simulated, but not if the female parent died in which case the natal territory was inherited. Dispersers chose randomly from adjacent suitable cells, or if no adjacent cells were suitable moved to a randomly chosen unsuitable cells. If the cell moved to was unsuitable and surrounded by unsuitable cell, the individual continued to move in a straight line. A fixed, per time step, dispersal mortality probability was imposed and individuals continued to move until a vacant suitable cell was found or the individual died. Pulliam et al. (1992) also conducted additional simulations in which a memory effect was incorporated in the dispersal representation, stopping individuals from entering previously visited cells, and showed how this lead to predictions of increased population size.

2.3 Assessment of models used to predict the spatial distribution of three mammals : the red squirrel, European badger and European beaver

There are in excess of 40 species of terrestrial mammal that are endemic within the United Kingdom. These species differ widely in their life history patterns and ecological status. Some like the grey squirrel and mink are pests and are currently expanding their range; others such as the red squirrel and dormouse are considered to be of high conservation value and are declining (Bright 1993). I chose three species, which differed in terms of their ecology and status, to which a range of models have been applied to predict their spatial distributions. These were the red squirrel, a declining species with restricted habitat requirements; the badger, an almost ubiquitous species with more general habitat requirements and the beaver, a species that may be reintroduced into the United Kingdom some 500 years after it became extinct. In the following sections I review methodologies used in past modelling research on these species, with a greater emphasis on the applied predictions than in the previous sections.

2.3.1 Models to predict the spatial distribution of the red squirrel

The red squirrel (*Sciurus vulgaris*) is a medium sized rodent that feeds predominantly on tree seeds and inhabits coniferous and deciduous mixed woodland (Corbet and Harris 1991). Individuals are largely solitary and exhibit a spacing pattern of overlapping home ranges (Lurz 1995). Red squirrels spend the night and rest periods during the day in tree nests termed dreys. Dreys are constructed from twigs, leaves and moss and individuals tend to have more than one. Historically the red squirrel was present across the whole of Britain, but presently is absent from most of central and southern England, a fact that has been attributed to the spread of the introduced grey squirrel (*Sciurus carolinensis*) (e.g. Okubo et al. 1989).

In the context of Britain the red squirrel can be considered as a habitat specialist as areas of habitat that are capable of supporting the species form a minor part of the landscape as a whole and are relatively easy to differentiate from unsuitable areas. This makes it amenable to a patch based, population modelling approach as followed by Rushton et al. (1997). The availability of conifer seeds, the red squirrels main food source, is relatively easy to measure and predict (e.g. Lurz 1995) and this

makes the species relatively amenable to the development of models based upon food availability.

An associative model to predict red squirrel densities based upon forest composition was described by Lurz et al. (1995), and applied to a plantation of Sitka spruce, Norway spruce and Lodgepole pine. They found that presence or absence of a Norway spruce cone crop, the area of Norway spruce and Lodgepole pine relative to that of Sitka spruce, and the size of the plantation explained 75% of the variance in trapping results. They extrapolated these relationships to make management recommendations but acknowledged that the results could not reliably be applied to plantations larger than 60 ha or with different species compositions.

Most of the associative approaches applied to the red squirrel have included larger scale factors principally related to the size and spacing of habitat patches (Verboom and van Apeldoorn 1990; van Apeldoorn et al. 1994; Delin and Andren 1996). Verboom and van Apeldoorn (1990) studied an area in the Netherlands with 7 large woods (30-200 ha) permanently occupied by red squirrels and 60 small woods (0.5-14 ha) that were assumed not to be permanently occupied. The aim was to predict the presence or absence of red squirrels in the small woods according to their size, quality and position in the landscape. Ten were excluded from the analysis as they consisted of habitat considered unsuitable for red squirrels. Of the remaining 50 woods, 52% were found to be occupied by red squirrels. In a logistic regression the area of conifers in the wood (considered to be an index of habitat quality), and the total area of the wood explained 35% of the variation in patch occupancy. Addition of variables relating to isolation of the woods from other small woods, large woods or hedgerows increased the variance explained to just over 50%.Van Apeldoorn et al. (1994) repeated the analysis for the same area with an additional 3 years field data and found this pattern to change slightly as the population increased over the study period. They found that as patch occupancy increased the predictive ability of habitat quality decreased, the effect of distance to the nearest large wood also decreased but the effect of the distance to the nearest small wood increased. Delin and Andren (1996) performed a similar analysis in Sweden. They used habitat quality (percentage of spruce), wood size and distance to nearest wood greater than

30ha as independent variables in regressions against the occupancy by red squirrels. Over 4 years they found only 3 significant relationships, size of wood explaining 28% of the variance in one year and habitat quality explaining 33% and 35% of the variance in two other years. The lack of an effect of isolation was attributed to generally low distances between woods and low hostility of the matrix, relative to the Dutch study area of Van Apeldoorn et al. (1994).

In a recent review of this type of approach, published models were applied to different areas from those in which they had been developed (Rodriguez and Andren in prep.). The authors concluded that the models had little general utility to predict squirrel distributions outside of their training areas.

Two process based approaches to predicting the spatial distribution of red squirrels have been published (Okubo et al. 1989; Rushton et al. 1997). Both have been applied to the geographic replacement of the red squirrel in Britain by the North American grey squirrel. Okubo et al. (1989) described an analytical reaction diffusion model, in which the reaction part was used to represent competition between red and grey squirrels and the diffusion part to represent the diffusion of the greys. They found that within a certain range of parameters competition between the reds and greys could explain the national pattern of replacement of the reds. The model assumed an homogenous distribution of squirrel habitat within Britain, thus ignoring any likely regional or local effects of habitat on the distribution of squirrels. As such the approach would appear to have little utility as an applied tool to predict squirrel distributions at anything other than a very general national level.

In contrast Rushton et al. (1997) describe a spatially explicit population model of red and grey squirrel interaction that is explicitly based upon the distribution of habitat. A map of suitable habitat patches was derived from satellite imagery. The carrying capacity of habitat patches was calculated from their size and published estimates of squirrel range sizes. Within patch population dynamics and between patch dispersal were simulated for both species. The model was applied to Norfolk, UK and compared to independently obtained survey data (Reynolds 1985). Model

outputs were closest to the field data when assuming high natality and low mortality for the grey squirrel, relative to estimates derived in the field. It was acknowledged that correspondence between certain of the model predictions and observations was almost inevitable across the range of parameter values simulated and that the model needed to be tested in other areas before it could be used as a general tool.

2.3.2 Models to predict the spatial distribution of the badger

The badger (*Meles meles*) is a large carnivore that, in the UK, commonly lives in social groups inhabiting a single den called a main sett (Kruuk 1989; Neal and Cheeseman 1996). Main setts are large underground structures that take years to build and are most commonly located in woodland (Neal and Cheeseman 1996). Badgers feed predominantly on earthworms, that are most available in areas of pasture. The highest densities of badgers are found in regions where the landcover is dominated by pasture and deciduous woodland (Neal and Cheeseman 1996). The badger is widespread throughout most of the UK.

In contrast to the red squirrel, the badger in Britain can be considered as a habitat generalist as it is capable of surviving in most habitats and it is more difficult to differentiate between areas that are suitable and those that are not. This is also partly a result of the scale of badger space use relative to the scale of landscape structure in Britain. Badgers use space at a scale that means that individuals can utilise multiple habitat fragments, thus blocks of habitat that do not provide all of an individuals requirements can still form an important part of its home range. The inability to identify habitat patches within an unsuitable matrix makes a patch based population modelling approach unsuitable. Availability of the badgers main food, earthworms, is much more difficult to measure and predict than that of the red squirrel. For example availability can change considerably over short time periods or distances due to variation in microclimatic conditions (e.g. Kruuk 1989). This limits the ability to construct fine scale models based upon food availability.

The most extensive attempt at predicting the spatial distribution of badgers has been the national badger survey of Britain set up by the then Nature Conservancy Council in 1985 (Cresswell et al. 1990). Between 1985 and 1988, 2455 1km squares

were surveyed for badger signs, largely by volunteers. The sample squares were stratified according to the Institute of Terrestrial Ecology's land classification that assigns each 1km square in the country to one of 32 land classes based on numerous factors including topography, climate, soils, land-use and native vegetation (Bunce et al. 1983). For all but four of the land classes at least 40 squares were surveyed. The survey was repeated between 1994 and 1997 (Wilson et al. 1997).

The mean main sett density per km was calculated for each land class and this was used to extrapolate to an estimate of badger densities in each of 11 regions of Britain. The standard errors about these mean values provide some indication of the confidence associated with these predictions but they have not been independently tested. The method should not be applied at a finer scale than the regional level due to the variability within the land classes that will not be fully represented by a small sample (Cresswell et al. 1990).

Extensive habitat data were also collected for each of the 1km squares. Discriminant analysis was applied within land classes to attempt to differentiate between squares with and without main setts. For each land class the percentage of correct classifications varied between 66 and 100%, however the small number of squares with setts in many of the land classes means that percentages of correct classifications very close to this can be obtained simply by classifying all squares as not containing setts. When all of the land classes were used, 2400 squares were included of which 2026 were without a main sett. From the discriminant analysis a percentage of correct classifications of 68.2% was obtained. If all squares were predicted to contain no setts the percentage of correct classifications would be 2026/2400 x 100 = 84%. Thus, the percentage of correct classifications from the discriminant analysis was less than the percentage of correct classifications if all squares were predicted empty. As such the discriminant analysis would appear to have little potential utility for predictive purposes.

Reason et al. (1993) reanalysed the data of Cresswell et al. (1990) and divided 1km squares into those that were 'good' or 'poor' for badgers, the criteria for a successful division being : "if any subset of the data could be divided into two

categories with significantly higher active main sett densities in the 'good' category, and where the numbers of squares in the two categories were not widely disproportionate". Using this approach it was found that 'good' squares could be classified as those containing at least 5 of the following : hedgerows, treelines, semi-natural broadleaved woodlands, semi-natural mixed woodlands, mixed plantations, parkland, tall scrub, low scrub, bracken, running natural water, lowland unimproved grassland, semi-improved grassland and improved grassland (but the grassland categories were not allowed to count for more than 2). Badger densities were shown to be significantly higher in the 'good' squares.

Wilson et al. (1997) performed a discriminant analysis on the results of the second national badger survey and expressed the results as the percent of 1km squares correctly predicted as having a main sett. They showed that it was possible to classify correctly 40% to 72% of the squares with a main sett. They grouped habitats into 3 categories: specific habitats predicted the presence of main setts and commonly acted as sett sites, general habitats predicted the presence of main setts but seldom acted as sett sites and avoided habitats predicted the absence of main setts. Although some significant relationships between the amounts of these habitats and main sett densities were found in some land classes, no simple relationship could be derived. It is not clear whether these data could form the basis of a useful model to predict main sett densities in unsurveyed areas.

Cresswell et al. (1990) also applied a multiple regression approach, using number of setts per 1km square as a response variable. The habitat data collected in the survey and mean values of habitat variables for each land class (Bunce et al. 1981) were used as predictor variables. This was applied only to the squares containing setts and the following equation explaining 88% of the variation ($P<0.0001$) was obtained:

Active main sett density = 0.502(area of tall scrub) + 0.024(area of semi-natural broadleaved woodland) - 0.130(area of parkland) - 0.217(area of running natural water) + 0.000023(length of hedgerows in m) - 0.483(area of canals) + 0.012

Although this equation explains a large amount of the variation it has little utility in extrapolating badger densities to un-surveyed areas as it was only derived from those squares that contained setts. As a result of this and the small size of the sample squares relative to badger range size there was very little variation to explain; over 78% of the squares contained just one sett and over 94% of the squares contained 1 or 2 setts.

Over a smaller area Thornton (1988) used regression approaches to develop a predictive model of the density of badger social groups within 2x2km squares (tetrads) in south west England. 42 randomly located tetrads in Devon and Cornwall were surveyed for main setts. 14 habitat variables were derived from field surveys and map data. Social group density was predicted using hilliness, hedge length, altitude, number of woodland units greater than 1ha and diggability of soils. It explained 64% of the variation, 70.8% of the predicted values were within 1 main sett per tetrad of the observed values. For 24 test squares the model performed less well with 50% of the predicted values within 1 main sett of the observed. In both cases the model consistently overestimated in areas of low density and underestimated in areas of high.

A similar, local scale, approach was applied to East Sussex by Macdonald et al. (1996). They used multiple linear regression to compare the power of the following variables to predict main sett density (MSD): 1) ITE land classes, 2) Map read variables 3) Ordinated map read variables, 4) Map read and field-measured variables 5) Ordinated map read and field-measured variables. Sett data for the entire 1835km^2 was collected by E.D.Clements between 1968 and 1978, 31 map read variables were derived for each 1km square. Forty 1km squares, stratified according to land class, were re-sampled and 22 habitat variables were measured in the field. At this scale sett density did not vary significantly between the eight land classes present. The best predictive power was obtained using just three map read variables: number of contours, minimum elevation and height of nearest hill, but this only accounted for 13.7% of the variation in MSD. All other methods explained less variation than this. There was more success in predicting outlier sett density but

as their relationship with badger density is unknown this is of little practical utility (Macdonald et al. 1996).

The performance of the associative models developed by Cresswell et al. (1990), Macdonald et al. (1996) and Wilson et al. (1997) has not been assessed by application to areas not used in their development. In Thornton's (1988) application of her model to new areas, performance decreased but a modest amount of predictive ability was retained. This latter model was, however, restricted in its application to SW England. The prospects of being able to predict at local scales on a national level using these approaches do not appear good.

Very simple process based models have been applied to the badger to investigate the spread of bovine tuberculosis (Anderson and Trewhella 1985; Swinton et al. in prep). These deliberately use a very limited number of parameters to enable the dynamics of the disease to be investigated and therefore have little utility to predict anything other than very general trends in badger population size. Models including an implicit representation of the spatial dimension have been applied to the badger in the Netherlands where the population is in decline (Verboom et al. 1991; Lankester et al. 1991). These are based on the metapopulation concept, representing individual clans as sub-populations, modelling demographics within clans and dispersal between them. They do not represent the actual locations of patches and as such only offer the potential of predicting general trends in density as a result of fragmentation. Schippers et al. (1996) simulated badger movement between areas of suitable habitat in the Netherlands and suggest that such an approach could be coupled with the previously described metapopulation models to predict the spatial population dynamics of the species in real landscapes. However, badgers in Britain are able to live in most habitats and as such are unlikely to conform to the metapopulation template of multiple, semi-isolated populations.

White and Harris (1995a) developed a spatially explicit simulation model to investigate the dynamics of bovine tuberculosis in Britain. The model was used to investigate the effect of different TB control strategies (White and Harris 1995b). It did not, however, directly address the relationship between population density and

the nature of the landscape. The representation of the landscape was homogeneous, with territories modelled as equal sized cells in a regular grid, each able to support the same, disease free equilibrium group size. Thus habitat effects on population densities were not included.

From this it can be seen that the process based models that have been applied to the badger to date are as yet unable to predict population densities in real landscapes.

2.3.3 Models to predict the spatial distribution of the European beaver

The European beaver (*Castor fiber*) is a large, semi aquatic, herbivorous rodent. It lives in small colonies, in a burrow or lodge constructed beside a river, lake or swamp (Macdonald et al. 1995). Historically the beaver was distributed across most of Europe including the UK, but went extinct in many areas, including the UK, due to a combination of hunting pressure and habitat loss. There have been a series of successful reintroductions across Europe, resulting in large healthy populations (Nolet and Rosell 1998).

The beaver is closer to the red squirrel than the badger in the breadth of its habitat requirements, requiring a combination of deciduous woodland and some form of water body (Macdonald et al. 1995). This relatively simple classification of suitable and unsuitable habitats facilitates application of a patch based population modelling approach. Determining more precise habitat requirements in Britain is somewhat difficult as the beaver has been extinct for more than 500 years and the landscape has changed considerably over that period. Food availability for the beaver, principally deciduous trees and herbaceous vegetation, should be relatively easy to measure and predict. In addition beavers impact considerably on their own environment and food supply (e.g Hartman 1996). As such, the interaction between beaver foraging behaviour and the landscape, and the potential effects of this on populations, are likely to be eminantly modellable.

Relative to the badger and red squirrel the European beaver appears to have been the subject of few attempts to predict its spatial distribution. Four papers have been published in English, one relating to habitat selection in Sweden (Hartman 1996),

the other 3 related to reintroduction programs (Macdonald et al. 1995; Nolet and Baveco 1996; Macdonald et al. 1997).

Hartman (1996) compared the habitat attributes of 10 beaver territories with randomly chosen unoccupied areas using multivariate analysis techniques. The tortuosity of streams and the presence of grasses and forbs in the ground layer were found to have the greatest positive effect on potential territory occupancy. This study was conducted in a region recently colonised by the beaver, where densities are still well below carrying capacity. The aim was to determine habitat preferences rather than to determine attributes of areas suitable for occupation. As such its potential utility for predicting the spatial distribution of beavers into the future or in areas closer to carrying capacity is limited.

Macdonald et al. (1995) outlined the potential application of Vortex, population viability analysis software (Lacy 1993) to the proposed reintroduction of the beaver to Scotland. They considered only a single population and thus included no representation of space except for the largely arbitrary values used for population carrying capacity.

Nolet and Baveco (1996) described the application of a custom built population viability analysis model to a reintroduced beaver population in the Netherlands. The model was firstly applied to the current population, the representation of space being restricted to the carrying capacity estimate that was derived from an estimate of the area of available habitat and average territory size. Data on survival and reproduction were derived from the German source population and the recently translocated Dutch population where natality rates were lower. The model predicted a low probability of persistence when it was assumed that the low natality rates were a permanent result of poor habitat, and a high probability of persistence when it was assumed that natality rates would return to high levels for the offspring of the original founders. They also investigated the effect of a further reintroduction to another nearby area by simulating 2 or 3 populations with an implicit representation of dispersal between them. This analysis showed that the establishment of the additional sub population could increase viability of the population as a whole.

An explicit representation of dispersal in the fragmented Scottish landscape was used by Macdonald et al. (1997) to assess the likely spread of animals from 3 selected reintroduction sites. It was predicted that populations would persist, but that spread to new areas would be low. This was a preliminary analysis and the consequences of uncertainty in model structure and parameters were not explored.

2.4 Assessment of modelling approaches

> 'The different ways of representing space, keeping track of populations, dealing with environmental variability, describing dispersal, and portraying dynamics within patches, together combine to yield an assortment of models that is overwhelming in its variety.' Kareiva (1990).

From this overwhelming variety of approaches it is necessary to identify the ones that offer the greatest potential to increase firstly our understanding of mammals interactions with space and secondly our ability to predict spatial distributions into the future and to unsurveyed areas. The different scales at which mammals interact with space, and the variation between different species means that no single approach will be suitable for all situations. A hierarchical approach to understanding the role of space has been called for (Murdoch et al. 1992; de Roos and Sabelis 1995). This advocates using detailed models to investigate processes at small scales and from these generating parameters summarising the influence of space for less detailed models at larger scales. If such a hierarchy were adopted for mammals, the important question is : which of the modelling approaches reviewed here could best fit into it ?

Associative approaches are non-mechanistic and exhibit poor generality. Norton and Possingham (1993) suggested that associative approaches may be best used for exploratory data analysis, to be followed, when more information is available, by process based modelling approaches. Wiens (1989, p317) described eleven factors that limit the predictive power and understanding generated by associative models applied to birds. These include the effects of predators and competitors, events in

different parts of individual or population ranges, historical events and measuring habitat variables at the wrong scale. These factors are also pertinent to mammals.

The use of process based models does not automatically overcome these problems, indeed most of the problems are potentially shared by both approaches, but a process based modelling approach does allow the problems to be addressed and their consequences investigated. Process based models can be used to investigate the complex interactions of ecological processes in a way that is not possible using purely associative approaches. This is particularly the case for higher animals such as mammals that exhibit complex behaviours.

Process based models are not without their problems. Models based on behavioural optimisation and the ideal free distribution often rest on assumptions about costs and benefits that are difficult to test, and tend to assume perfect knowledge of resource availability. Simulations of foraging and dispersal movements are mostly based on rules that are little more than plausible. Models representing territoriality tend to be based on a poor understanding of the mechanisms governing territory formation. Metapopulation models assume the existence, often doubtful, of identifiable, semi-isolated sub-populations, existing at an equilibrium between extinction and colonisation.

Bearing in mind these potential difficulties, in the following four chapters I investigate the use of a range of process based models to predict the distribution of mammals across the range of scales outlined in chapter 1.

2.5 Modelling approaches employed in the thesis

In chapter 3, I develop a framework for extrapolation from simple movement rules based on memory, to investigate whether these can explain individual space use and population spacing patterns in the red squirrel. This represents an attempt to extrapolate from the fundamental process of food acquisition to the relative movements of individuals, while making as few assumptions as possible. Patch based population models have been used to predict the distribution of red squirrels

between habitat blocks (Rushton et al. 1997), but these include little mechanistic representation of the processes going on within blocks.

In chapter 4, I compare the ability of 1) an associative model and 2) a simple model based on habitat suitability and space pre-emption, to predict the density of badger main setts. The positioning of main setts was the focus of the second model as they are large, costly relatively permanent structures and their positioning is thought to be an important component of the spacing behaviour of the badger. Foraging behaviour is not represented explicitly due to the difficulty in representing food availability for the badger. Patch or metapopulation type models were not used as there is no evidence that badger populations are structured this way.

In chapter 5, I outline two approaches used to predict the spread of the beaver in Scotland following a proposed reintroduction. Both approaches are based upon the births and deaths of individuals within habitat patches and dispersal between them. The first is a custom built model with an explicit representation of dispersal through the habitat matrix and the second a generic population viability analysis package in which dispersal is represented implicitly. The inevitably small size of a reintroduced population means that stochasticity and dynamic processes will play an important role in the fate of a population, these are best represented by the individual based approaches used here.

In chapter 6, I investigate the interaction between demographic parameters and the representation of dispersal within spatially explicit population models, such as those used in the previous chapter. Such models are frequently used to address applied questions, but knowledge of the dispersal process is recognised as being limited. Despite this there have been few attempts to investigate the consequences of different representations of dispersal.

3. Chapter 3 : Extrapolating from individual movement behaviour to population spacing patterns in a ranging mammal

3.1 Introduction

Mammals move to exploit spatially separated resources. Individual space use and population spacing patterns are emergent from these movements and the way that these patterns of space use are generated is fundamental to the interaction between mammals and the landscape (Lima and Zollner 1996).

Mammal space use is commonly described by the area of an individuals home range. The home range is conventionally defined as " that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943). More recently the restriction of home ranging movements to a smaller area than could potentially be covered has been highlighted (e.g. Benhamou 1989; Gautestad and Mysterud 1993). A spacing pattern of overlapping home ranges is exhibited by many mammal populations (e.g. European red squirrels, Lurz 1995; Wauters and Dhondt 1992; grey squirrels, Kenward 1985; black bears, Powell et al. 1997; bank voles, Koskela et al. 1997). Range overlap can also occur in populations defined as being territorial (Maher and Lott 1995). A number of studies have shown negative relationships between range sizes and food density (e.g. in roe deer, Tufto et al. 1996; grey squirrels, Kenward 1985; and black bears Powell et al., 1997). Within such systems, however, it is not clear to what extent spacing behaviour is dependant upon a direct response to food availability, mutual avoidance of conspecifics or active defence of an area (e.g. Stewart et al. 1997; Kenward 1985). In addition, for mammals with overlapping ranges, populations exhibiting the same distribution of range sizes can potentially exhibit very different spacing patterns as a result of the degree of range overlap. The degree of range overlap is an important component of such spacing patterns yet few of the mammalian studies that have documented range size have addressed it. Authors that have addressed range overlap (e.g. Wauters and Dhondt 1992; Koskela et al. 1997; Powell et al. 1997) have concentrated on behaviour, using

overlap as a measure of the degree of territoriality (less overlap taken as evidence of more territoriality).

Economic models that have been developed to assess the evolutionary costs and benefits of territoriality versus home range overlap (e.g. Carpenter and MacMillen 1976; Powell et al. 1997) predict either exclusive territories, overlapping home ranges or a combination of the two, but they do not generate quantitative predictions regarding the expected degree of overlap. There appears to have been little attempt to develop models to investigate the quantitative degree of range overlap and the response of this to food availability.

There have been numerous models applied to the space use of foragers (see chapter 2). Highly mobile animals, such as birds, can be assumed to have an accurate knowledge of food availability across very large areas (e.g. Sutherland and Anderson 1993). In such a situation extrapolation from individual behaviour to space use can be based upon principles of optimisation and the ideal free distribution (Sutherland 1996). For less mobile animals decisions are likely to be made at a more local scale (Armstrong et al. 1997), based on limited available information ad thus the ideal free distribution may not be appropriate. Tyler and Hargrove (1997) develop a simulation that relaxes some of the assumptions of the ideal free distribution and use this to predict the spatial distribution of foragers, but they include no spatial memory and assume that foraging does not deplete food resources.

Predicting patterns of mammal space use is limited by a lack of understanding of the behavioural mechanisms involved (Lima and Zollner 1996). In this paper I outline a simulation model used to address two principle aims. The first aim was to develop a methodology to extrapolate from individual foraging behaviour to individual space use and population spacing pattern. This methodology confronts the uncertainty regarding animal movement behaviour by allowing alternative plausible movement rules to be simulated to generate testable predictions. I describe a series of simulations based on one set of such rules. These simulations address the second aim which was to predict how the spacing pattern of a population might be expected to respond to changing food density when the predominant interaction between individuals is food depletion.

I develop further an individual based foraging model parameterised for female red squirrels (*Sciurus vulgaris*) in a Scots pine (*Pinus sylvestris*) plantation (South et al. 1997). In the model individual foragers explore to gain knowledge of food availability and use this information to direct subsequent foraging movements. The mechanisms causing the emergent relationships and the prospects for this approach are discussed.

3.2 The Simulation Model

3.2.1 Overall Structure

The model is based upon the movement of individual foragers. Time is represented as a series of days, each composed of a series of time steps. Space is represented as a hexagonal grid, each grid cell has an associated food value and some cells also contain a nest. Foragers cannot move outside of the grid (any edge effects generated are likely to be equivalent to those occurring in real habitat patches in real landscapes). Each forager starts and finishes each day at a nest, builds up a 'memory map' of food availability and gains or loses weight in each time step according to simplified energetics equations. In the plausible scenario simulated here foragers initially explore previously unvisited cells chosen by minimising the distance moved in each time step and the distance moved away from the nest. Subsequently foragers re-visit food cells that they have experienced to contain food. On reaching satiation foragers stop consuming food and switch to exploring until a 'knowledge threshold' is reached, at which point they return to the nest. The model was written in the programming language 'C' and run on a UNIX system.

3.2.2 Forager actions within each time step

At each time step, each forager acts in turn, in a random order to prevent any one forager having a consistent advantage over any other as a result of the sequence in which it appears in a model run. Within a time step a forager either consumes a single cone, moves (up to a defined maximum distance), assesses a previously unvisited cell or remains in a nest (see Fig. 3.1). Foragers switch between the following behavioural states : hungry exploring, movement towards food, eating, satiated exploring, movement towards a nest, and remaining in a nest.

3.2.2.1 Hungry exploring

Foragers start the season with no knowledge of food availability in the landscape. At this stage and at any other time during the simulation when a forager has no knowledge of food availability it switches to the 'hungry exploring' state. In this state the forager moves to the closest cell (to the presently occupied cell) that it has not yet visited. If there are two or more equidistant cells the forager moves to the one that is closest to the nest it started from that day. On arriving at a cell that it has not previously visited a forager spends a defined number of time steps (assess time) assessing the food value of the new cell. After this, if the cell contains food, the forager switches to the 'eating' state, otherwise it remains in the 'hungry exploring' state and moves to another unvisited cell in the next time step. In previously unvisited areas this creates spiral type patterns of exploration.

3.2.2.2 Movement towards food

A forager with knowledge of available food in the landscape (and not currently occupying a cell containing food and not satiated) moves towards the nearest food cell in its memory. Foragers can move a maximum number of cells per time step, determined by a maximum travel speed parameter. On reaching the food cell the forager switches to the 'eating state'.

3.2.2.3 Eating

In the 'eating' state a forager consumes one cone per time step. This simulates, at the scale of a single cell, an abrupt type 2 functional response, in which consumption rate is 0 if there are no cones and 1 if there are any cones. A more gradual functional response relating consumption rate to cone density could have been incorporated into the model but evidence from studies of captive fox squirrels (*Sciurus niger*) suggests that consumption rate does not vary considerably with cone density (Steele and Weigl 1992). In the eating state a forager remains in the occupied cell until one of the following conditions is satisfied : a) the food is depleted to zero, b) the forager reaches daily satiation, c) the forager reaches maximum bodymass, or d) there are ten time steps left in the day (the latter giving the forager time to reach a nest prior to the end of the day).

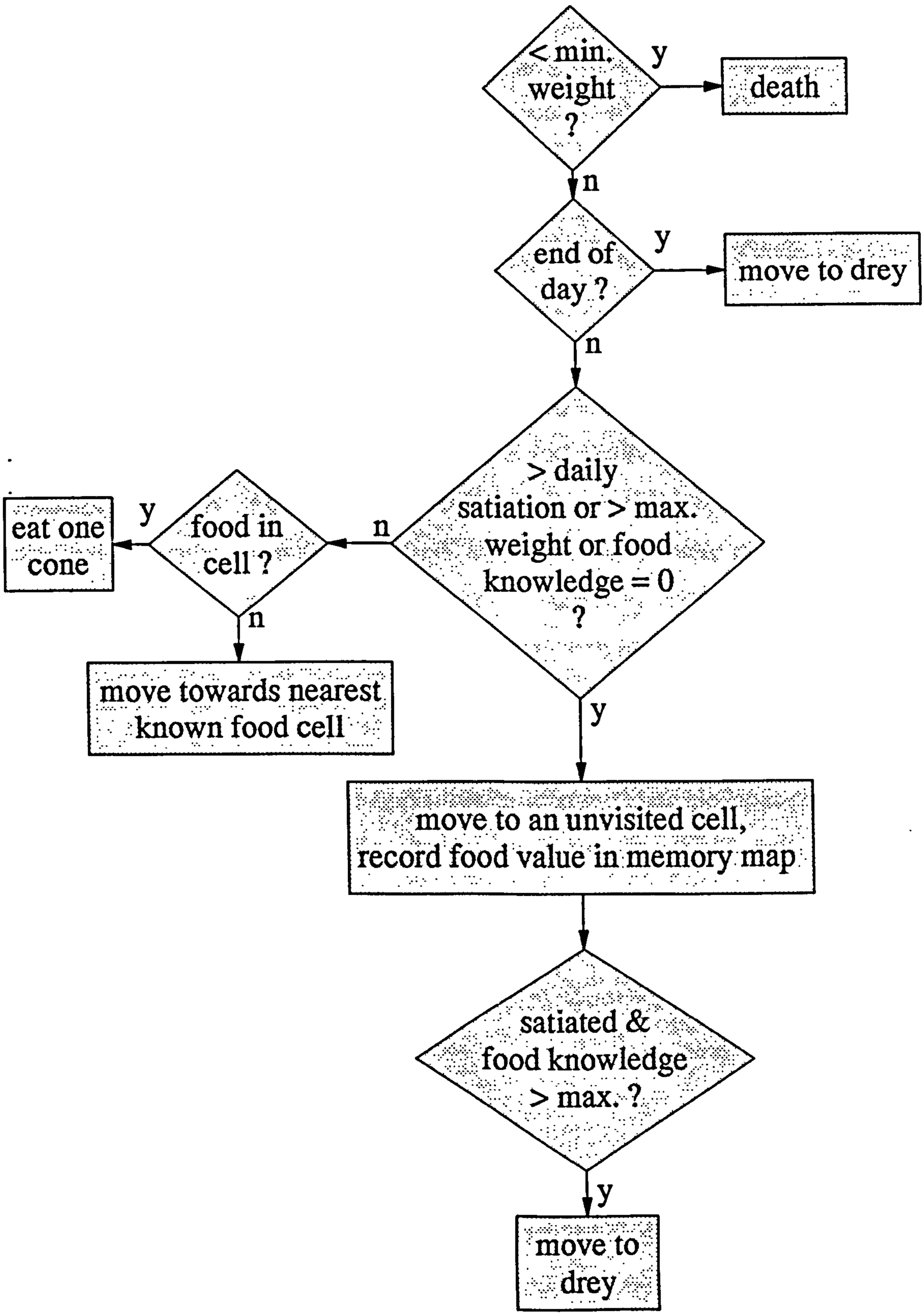


Figure 3.1 : Sequence of events for each forager in each time step of each day. Each forager effectively works through the chart and enters the next time step when it can proceed no further. At each time step each forager acts in turn in a random order to prevent any one forager having a consistent advantage as a result of the sequence in which at acts in each time step.

3.2.2.4 Satiated Exploring

A forager that reaches daily satiation, determined by the maximum number of cones that can be consumed in a day, or reaches the maximum defined body weight, switches to the 'satiated exploring' state. This is equivalent to the 'hungry exploring' state except that the forager does not switch to 'eating' on encountering food. Instead, it continues to explore until an upper threshold to food knowledge is reached. In the scenario presented here this upper limit is set at the amount of food necessary to support the forager until the end of the season. Once the threshold is reached the forager stops exploring and moves to an unoccupied nest. The rationale behind the 'satiated exploring' state is that it allows foragers to build up a knowledge of food availability in the landscape. Without this component foragers tend to die at low food densities as they experience extended periods when they are unable to find food. During the 'satiated exploring' state each forager develops a unique memory map of food availability in the landscape dependant upon where it has been. At each time step the memory map of each forager is not complete and also contains inaccuracies due to depletion by other foragers. This was thought to be a more accurate representation of the information stored by an animal than perfect knowledge. Once the upper threshold to food knowledge is reached a forager switches to the 'movement towards a nest state'. The food knowledge threshold was incorporated to represent the balance between the costs of activity (e.g. predation risk) and the benefits of knowledge. It stops foragers in the model from being active for every hour of available daylight on every day, behaviour that is seldom observed in the field (Reynolds 1985; Lurz 1995).

3.2.2.5 Movement towards a nest

If a forager is still active ten time steps before the end of daylight (although as mentioned above this seldom occurs) it switches to the 'movement towards a nest' state. In this state the forager moves towards the nearest nest, moving up to the defined maximum number of cells as in the movement towards food state . If the nest is already occupied the forager moves to the next nearest until it finds one that is unoccupied. Each forager can stay in any one of the nests in the landscape providing it is unoccupied on arrival. This is based on observations that a number of red squirrels will use the same nests but not on the same night (Lurz 1995). Once in a nest a forager remains there until the beginning of the next day.

3.2.3 Parameterising the model

3.2.3.1 Space

A landscape of 25 ha (500m x 500m) was represented as a grid of 10000 hexagonal cells (25m^2 per cell). At the beginning of each run each, all cells were assigned the same food value according to a cone density parameter. This created a uniform, non-renewing, food landscape that was depleted through the season by the actions of the foragers. Nests were positioned randomly in the landscape at the beginning of each run. There has not been a comprehensive analysis of the spatial distribution of squirrel dreys. Positioning the nests randomly allowed multiple simulation runs to be conducted without dependence on one spatial pattern of nest locations.

3.2.3.2 Time

The length of each time step was set to represent the approximate time taken for a red squirrel to find and consume a single pine cone within a pine tree (about 2 minutes, Moller 1983). The number of time steps available in each day was determined using a function that calculated daylight hours from the day of the year and latitude (Arnold et al. 1990). This was used because red squirrels are diurnal foragers (Tonkin 1983; Wauters et al. 1992).

3.2.3.3 Energetics

Energetic costs of red squirrel movement, activity and remaining in the drey were estimated from the literature and converted to changes in bodymass (see appendix 1). During each model time step each forager changes bodymass according to the balance between these costs and the energetic value of a cone, if one is consumed. Minimum and maximum limits to bodymass were derived from field studies (Lurz 1995). At the beginning of each season the body mass of each forager was set midway between the maximum and minimum values. If a foragers body mass reaches the maximum the forger consumes no more food that day to prevent the limit from being exceeded. If the bodymass reaches the minimum limit the individual is removed from that simulation run. In the runs described here, however, parameter values and movement rules were set such that the minimum bodymass was not reached.

3.2.4 Numbers of foragers, length of simulation runs and starting food densities

Ten foragers were simulated representing a population density of 0.4 squirrels per ha. This is approximately equivalent to densities of 0.33 and 0.42 measured in areas of Scots pine in Northumberland (Lurz 1995) and Scotland (Moller 1986) respectively, but lower than densities of 0.8 - 2.2 squirrels per ha measured in East Anglia and Belgium (Reynolds 1981; Wauters and Dhondt 1992; Wauters and Lens 1995). At the start of each simulation run each forager was positioned at a randomly chosen nest (without allowing more than one forager to occupy the same one). Each simulation was set to 300 days representing the period from June to March at a site on the same latitude as Northumberland (North England). In scots pine forests around this latitude the new 'green' cones become available to squirrels in June and are the predominant food supply until March the following year (Tittensor 1970; Wauters and Dhondt 1987; Wauters et al. 1992). Cone densities were varied between 3 and 14 cones per m^2. The lower limit is higher than cone densities of 1 cone per m^2 estimated in Northumberland (Lurz 1995), the upper limit corresponds to cone densities of 10 -20 per m^2 measured in Belgium (Wauters *pers. comm.*) but lower than the 30 cones per m^2 estimated for 'good' areas (Wauters and Lens 1995). Lower cone densities were not used as this leads to high forager mortality in the model (South et al. 1997) and complicates the relationship between model outputs and food density by introducing variation in forager density. The high mortality of foragers in the model at these low food densities is not inconsistent with field data as Lurz (1995) observed a high turnover of individuals.

3.2.5 Model runs and Uncertainty analysis

Two sets of 100 model runs were conducted using the depletion mechanism. In the first set of 100 runs food density was varied but all other parameters were kept at a constant value (Table 3.1). In the second set of runs the values of all the major parameters were varied within estimated bounds of uncertainty, derived from the literature. This uncertainty analysis (Turner et al. 1994) was designed to complement the series 1 runs by determining whether responses to food density were robust to changes in the values of other parameters. The variation in parameter values was achieved using a Latin Hypercube Sampling methodology (Blower and Dowlatabadi 1994; Turner et al. 1994), selecting integers from a discrete distribution and other parameters from a uniform distribution (Table 3.1).

Description of Parameter	Parameter name	Value used in series 1 runs	Range of values used in series 2, Uncertainty analysis runs.	Sources (see legend)
Energetic costs (kJ/hour) :				
in nest	nest_cost	12.63	11.37 - 13.89	1, 2
active	active_cost	15.79	14.20 - 17.37	
travelling	move_cost	25.26	22.73 - 27.78	
Energy content of a single scots pine cone (kJ)	cone_energy	3.34	2.85 - 3.84	3, 4, 1
Max. travel speed (cells per time step)	max_speed	20	18 - 22	5
Daily satiation, the max. no. of cones that an animal can consume in a day	day_satiation	150	135 - 166	1
Min. body mass, below which a forager dies (g)	min_mass	260	234 - 286	5
Max. body mass, above which a forager stops feeding for the day (g)	max_mass	350	315 - 385	5
No. of time steps to assess the no. of cones in a newly visited cell	assess_time	5	4 - 6	estimate
No. of nests in the landscape	num_nests	30	20 - 45	6, 7
Timestep length, the time to find and eat a cone. (minutes)	tstep_length	2	1.8 - 2.2	8
Cone density (cones per m^2)	food_density	3 -14	3 -14	6, 9

Table 3.1 : Parameter Values use in the Model . Sources : 1) Grönwall (1982), 2) Gurnell (1987) , 3) Grodzínski and Sawicka-Kapusta (1970), 4) Wauters, Swinnen and Dhondt (1992), 5) Lurz pers. comm., 6) Lurz (1995), 7) Wauters and Dhondt (1988), 8) Moller (1983), 9) Wauters pers. comm.

3.2.6 Model Outputs

The location of each forager was sampled at a fix interval of 45 time steps. A home range analysis software package (Ranges V, Kenward and Hodder 1996) was used to generate 100% Minimum Convex Polygons for each forager in each run. Range edges were exported to the GIS GRASS (Westervelt et al. 1997) for display purposes and to analyse range overlap. For each run a mean range area was calculated from the range sizes of each of the 10 foragers. Range overlap for each forager was calculated by summing the percentage of its range (100% MCP's) that coincided with the range of each other forager (Wauters and Dhondt 1992). Thus, if 50% and 75% respectively of a foragers range was shared by two other foragers, the range overlap value would be 125%. A mean overlap value for the run was calculated from the range overlap of each of the 10 foragers. The variance in range area and overlap within each run (i.e. between individual foragers) was also calculated. Rank correlation analysis was used to analyse the relationship between food density and the model outputs (mean range area and mean range overlap) in both series of runs. Partial rank correlation analysis was used to determine the sensitivity of the model outputs to changes in the values of all parameters within the uncertainty analysis series of runs (following the methodology of Blower and Dowlatabadi 1994). This quantifies the effect of each parameter in turn while holding all other parameters constant. These non parametric analyses were used because outputs were not normally distributed within each food density value, and the variance in outputs was not equal between food density values.

3.2.7 Comparison with an alternative mechanism based upon interference

An alternative mechanism based predominantly upon interference rather than depletion was also programmed. In this foragers build up a memory map of food availability, as in the previous mechanism, but in addition they were simulated as avoiding cells that had been visited and explored by others. Scent-marking behaviour has been observed in squirrels and been suggested as playing a role in home ranging behaviour (Gurnell 1987). This mechanism represents a scenario where foragers avoid areas scent marked by others.

3.2.8 Comparison of model results to field data

The quantitative predictions of the depletion and interference mechanisms were compared to limited available field data from the literature as a preliminary test. Model predictions were only compared to range areas for females as in vertebrates females tend to be distributed according to the distribution of resources whereas the distribution of males tends to be related to the distribution of females (Davies 1991; Sutherland 1996). In red squirrels, male ranges tend to be much larger than those of females, apparently as a result of sexual activity (Wauters and Dhondt 1992; Lurz et al. 1997).

3.2.9 Application of the model to detailed food availability data

I have taken initial steps in applying the model to an area of coniferous woodland for which drey positions, food availability and space use data have been collected (Lurz 1995). The model was run to simulate 1 month (July) for 13 females that were studied within a 4km^2 area of conifer plantation. Tree seed availability across the area was estimated from cone transects conducted by Lurz (1995) and a forest stock map. As female red squirrels lactate at this time of year, estimated costs of lactation were added to the energetic requirements and individuals were made to use a single drey. At the start of each simulation run, each female was placed in a randomly chosen drey.

3.3 Results

Figure 3.2 shows an example of the daily outputs of the model for one run and one forager. In this example the forager gained mass rapidly at the start of the season and remained close to maximum body mass for most of the season, with the exception of a period around day 200 (Fig. 3.2a). At this time a drop in cone consumption (Fig. 3.2b) was followed by a decrease in bodymass and a peak in the daily movement distance (Fig. 3.2d). This was likely a result of the forager being unable to locate any cones as they had been depleted by another individual.

Maps of forager home range boundaries output from the model showed a general pattern of small, equally sized, non overlapping ranges at high food densities, and large, different sized overlapping ranges at low food densities (Fig. 3.3).

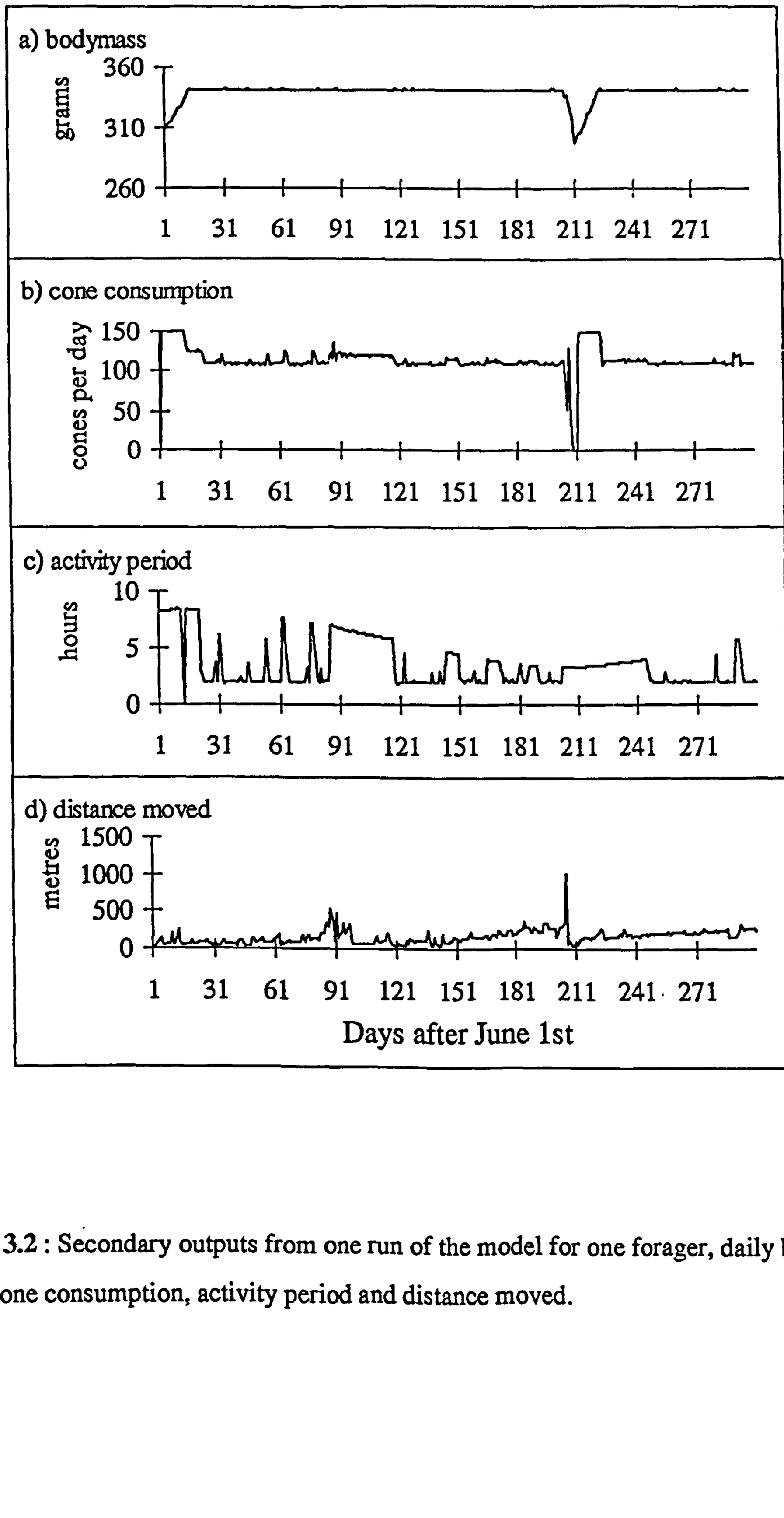


Figure 3.2 : Secondary outputs from one run of the model for one forager, daily body mass, cone consumption, activity period and distance moved.

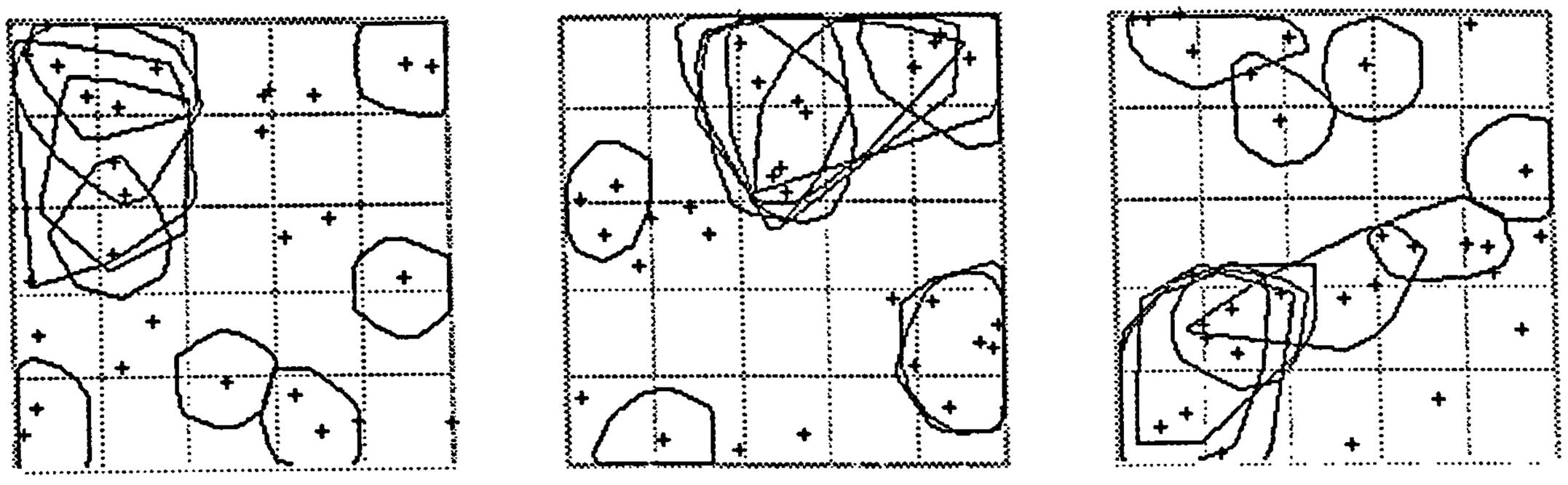


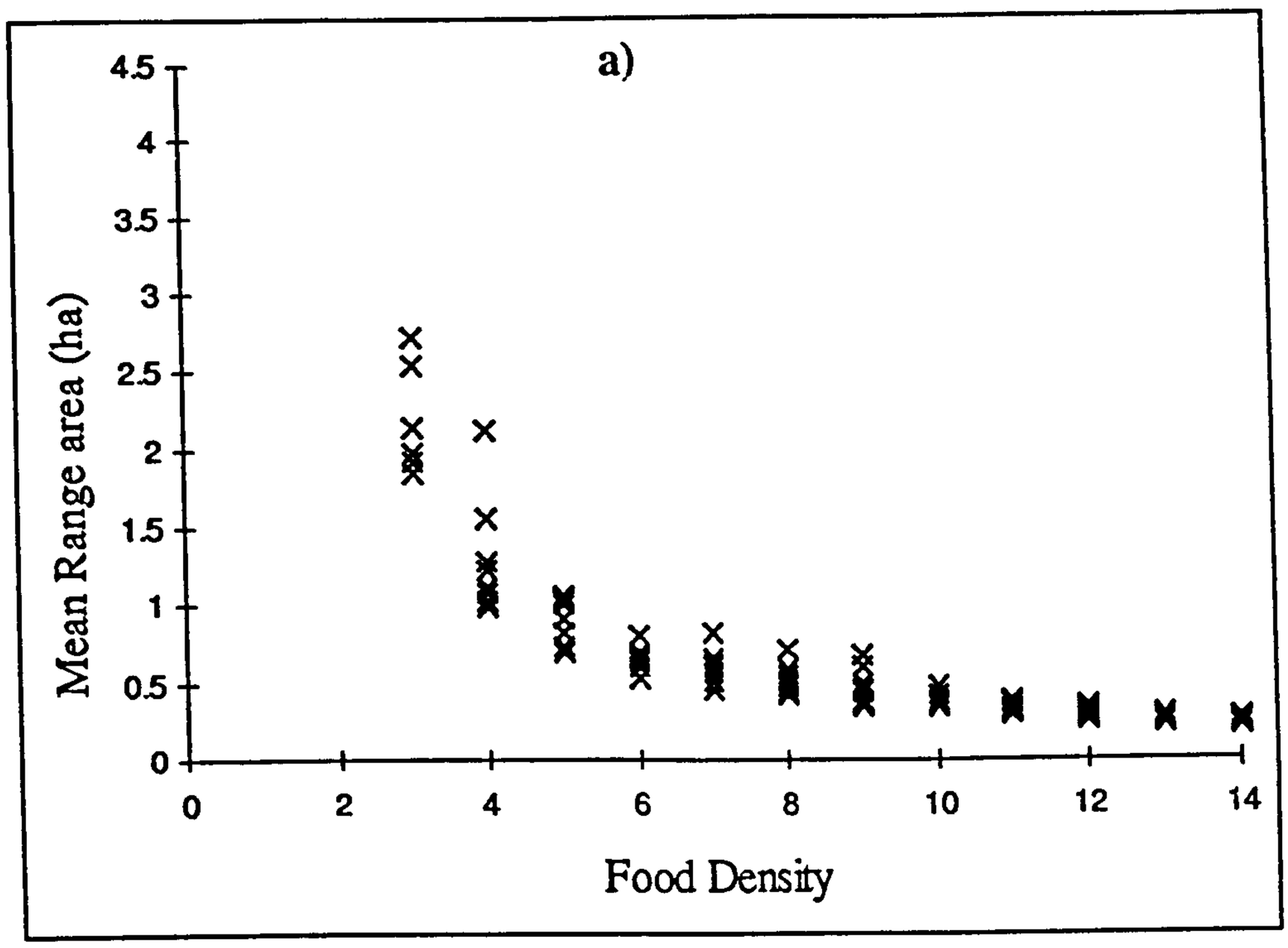
Figure 3.3 : Ranging Patterns (Minimum Convex Polygon estimates) generated by 9 runs of the model from the series 1 runs (depletion scenario). (+ = refuges, each grid square = 100m x 100m). (a) - (c) Food density = 3, (d) - (f) Food density = 8, (g) - (i) Food density = 14.

3.3.1 Mean range area and mean range overlap

Mean range area decreased with increasing food density in a similar way in both series of runs (Fig. 3.4). The magnitude of the correlation was only slightly less in the series 2 runs, in which all parameters were varied, (Spearman rank correlation coefficient, $r_s = -0.918$) than in the series 1 runs in which food density alone was varied ($r_s = -0.969$). The decrease in range area in response to a unit increase in food density was greater at higher food densities as represented by the curvilinear relationships in Figure 3.4.

Calculating the reciprocal of range area linearised the curve and lead to a better fit in a simple linear regression against food density (Series 1: mean range area $R^2 = 63\%$, 1/mean range area $R^2 = 94\%$, Series 2: mean range area $R^2 = 53\%$, 1/mean range area $R^2 = 84\%$). The negative relationship between range area and food density was largely a result of foragers having to visit fewer cells to satisfy their energy requirement when food densities were higher. The underlying mechanism that the number of cells a forager needed to cover was equal to a food requirement divided by food density (i.e. $y = 1/x$) explains the better linear fit of the reciprocal of range area to food density.

The response of mean range overlap to increasing food density was also negative (Fig. 3.5) and also differed little in strength between the series 1 runs ($r_s = -0.668$) and the uncertainty analysis series of runs ($r_s = -0.514$). This change in range overlap was also seen in the proportion of ranges that were overlapped. At the highest food density the number of ranges overlapped within each simulation run varied between 0 and 4, at the lowest it varied between 7 and 9. These patterns can be explained by the fact that at lower food densities the foragers covered larger areas and thus their movements were more likely to overlap with the movements of others. In addition food depletion will tend to lead to foragers obtaining less food from the cells that are overlapped. Therefore if a foragers range contains overlapped cells its range is likely to be larger to compensate for this depletion competition. This generates a positive feedback; as ranges get larger overlap tends to increase, increasing the potential for depletion competition and thus increasing range areas further.



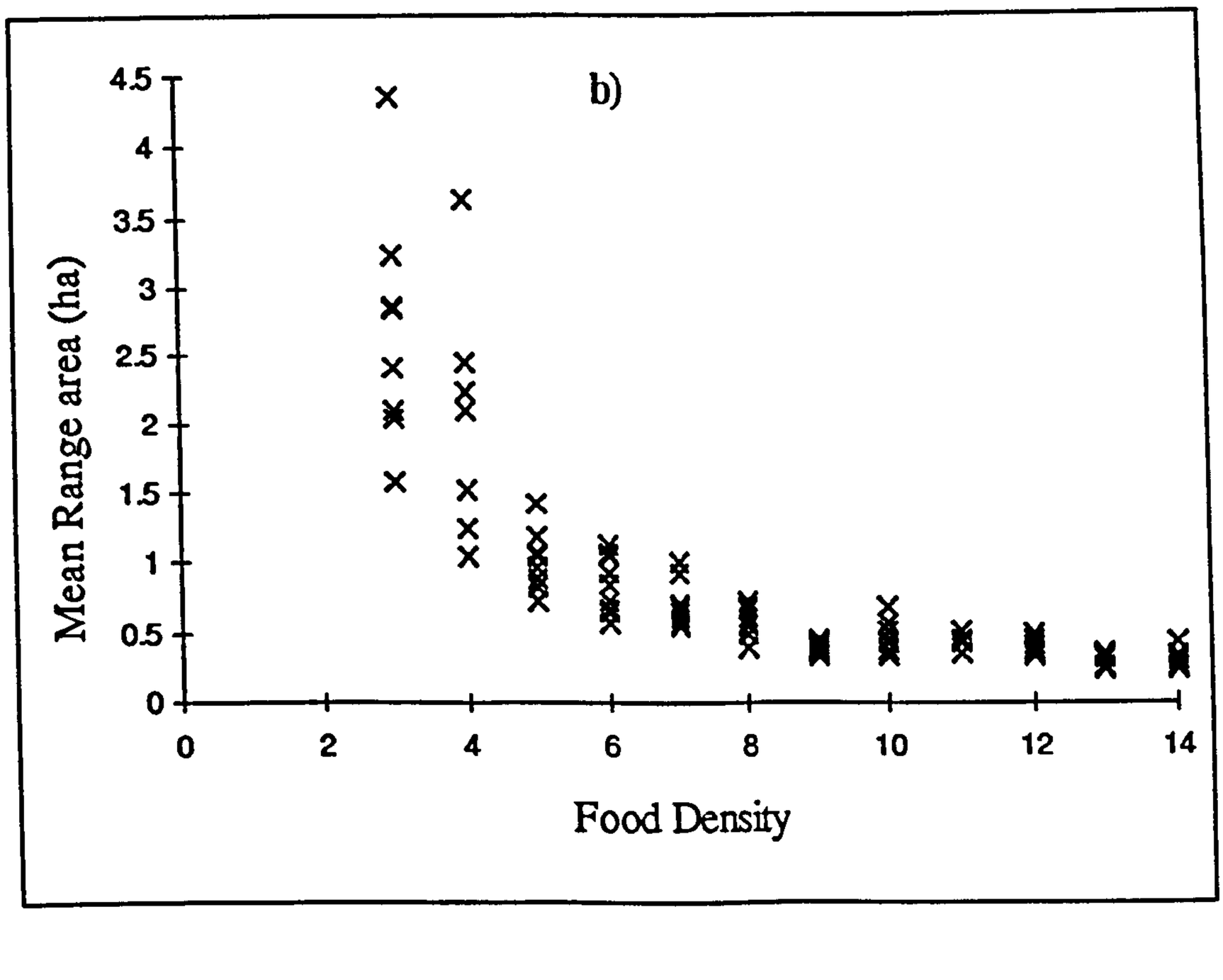
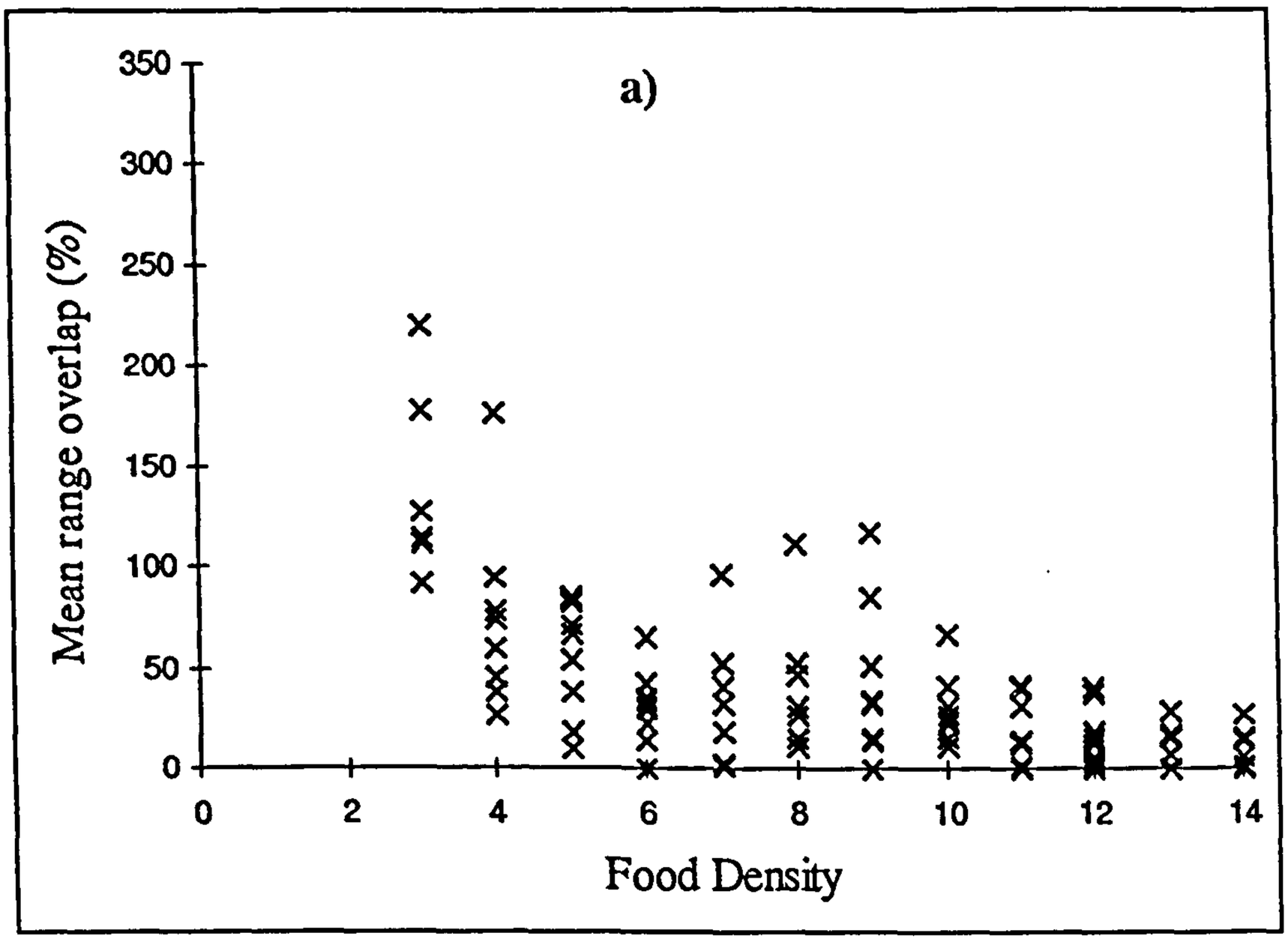


Figure 3.4 : Relationship between mean range area generated by each model run and food density, for the depletion scenario. **(a)** Series 1, food density alone varied. (Spearman rank correlation, $r_s = -0.969$, $p < 0.001$) **(b)** Series 2, uncertainty analysis, all parameters in Table 1 varied. (Spearman rank correlation, $r_s = -0.918$, $p < 0.001$).



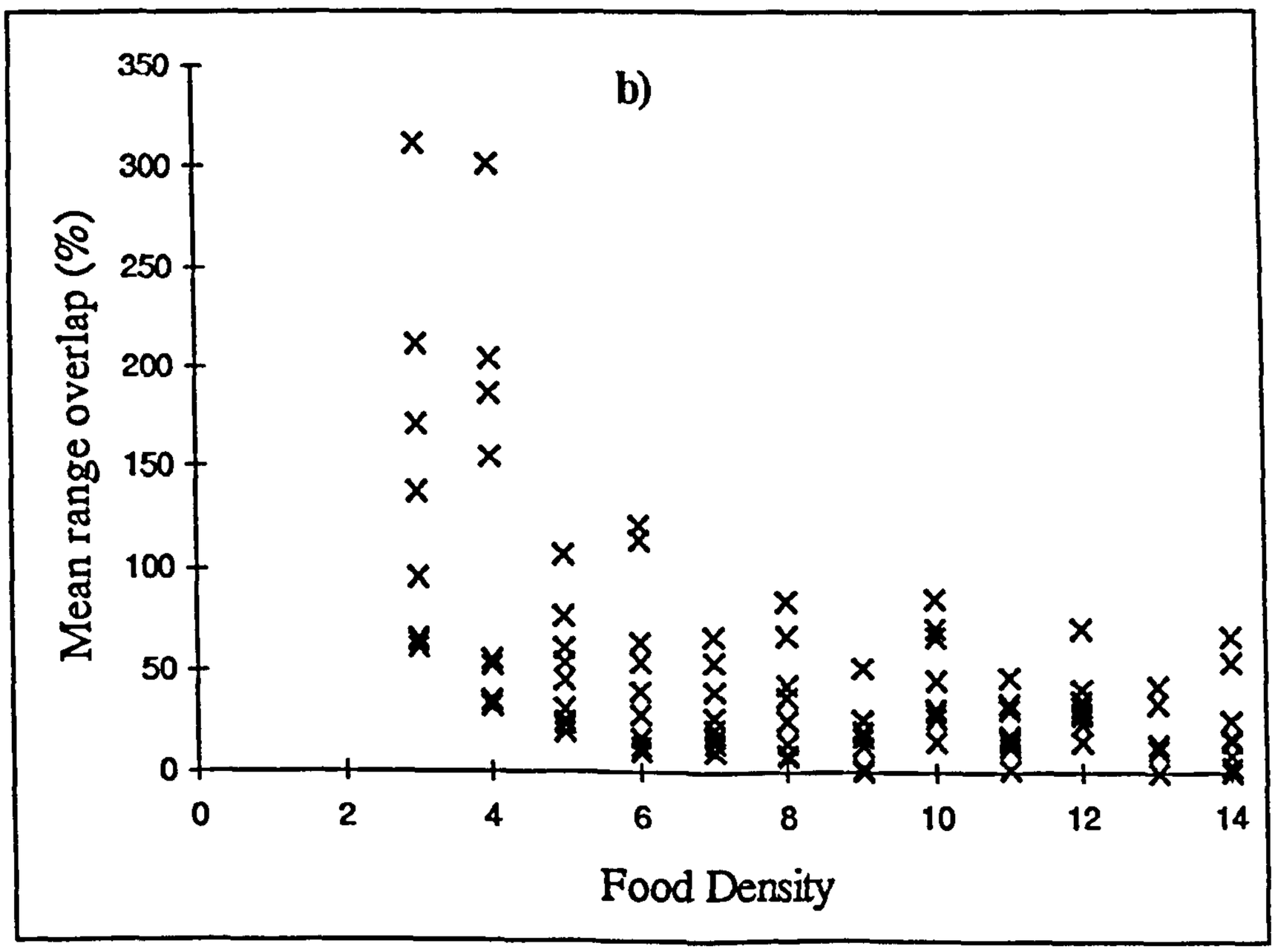


Figure 3.5 : Relationship between mean range overlap generated by each model run and food density for the depletion scenario. (a) Series 1, food density alone varied. (Spearman rank correlation, $r_s = -0.668$, $p < 0.001$) (b) Series 2, uncertainty analysis, all parameters in Table 1 varied(Spearman rank correlation, $r_s = -0.514$, $p < 0.001$).

3.3.2 Interaction between Mean Range Area and Overlap

Figure 3.6 shows the relationship between mean range area and mean range overlap according to food density for the series 1 runs (a similar pattern was generated for the series 2 runs). Neither range area or overlap is an independent variable as they are both attributes of the same model output. The general pattern of decreasing range area and overlap with increasing food density, previously shown in Figures 3.4 and 3.5, is apparent. As outlined previously this is a logical direct response whereby lower food densities lead to increased range area which in turn leads to increased range overlap. In addition, it can be seen that within each food density value there was a positive relationship between range area and range overlap. When food density is held constant range areas would be expected to stay constant. Thus the difference in range area within each food density value must be a result of depletion competition (i.e. a response of area to overlap rather than a direct response of overlap to initial food density).

Figure 3.6 also shows that the slope of the relationship between overlap and area within each food density category increases with increasing food density. This is likely to be an incidental result of expressing overlap as a percentage of range area. When range areas are large (in response to low food densities) the size of the overlapped portions of those ranges will be larger. Therefore at higher food densities a defined change in mean percentage range overlap will lead to a greater change in the absolute size of the area overlapped. This will lead to a greater change in overall range area to compensate for the depletion competition experienced and thus have caused the greater slope.

The strength of the correlations between mean range area and food density (Fig. 3.4) were much greater than those between mean range overlap and food density (Fig. 3.5). This is not surprising as food density has a direct influence on range area through an animals requirement for food whereas the link between range overlap and food density is indirect. Food density influenced range overlap through its effect on forager movements. This indirect effect will have been influenced by the movements of foragers relative to each other, which in this model was influenced by the random positioning of nests, and the random positioning of foragers in nests, at the start of the season.

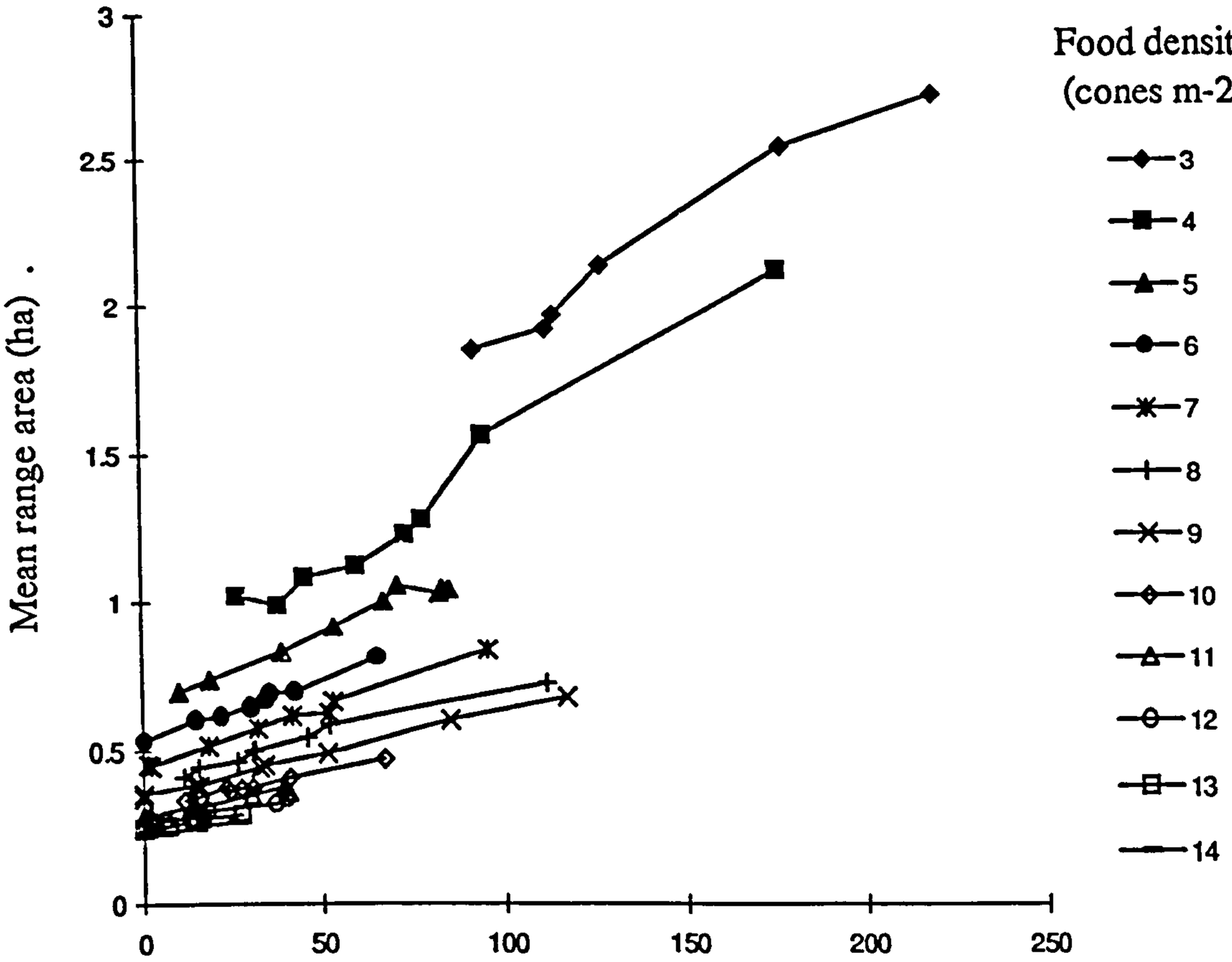


Figure 3.6 : Relationship between mean range overlap and mean range area according to food density, for Series 1. (overlap and range area are both outputs of model runs for which food density is the independent variable, the fact that overlap is plotted on the x-axis does not imply that it is the independent variable).

3.3.3 Uncertainty analysis

The partial rank correlation analysis applied to the series 2 runs showed food density to have the greatest effect on both outputs (Table 3.2). For mean range area the next strongest correlations were with the energetic content of a cone, the energetic cost of staying in the nest and the energetic cost of activity, while for mean range overlap the next most important were the length of a time step, the time to assess the food value of a previously unvisited cell and the number of nests. The parameters other than food density that were shown to be significantly related to outputs in the uncertainty analysis can mostly be explained in mechanistic terms. The energetic content of a cone effects range area by the same mechanism as food density, the energetic costs of activity and staying in the nest act

in the opposite direction by increasing energy requirements. The mechanism leading to the positive relationship between the length of a time step and range overlap is however not clear. Higher values of time step length decrease available foraging time and could lead to smaller ranges (consistent with the PRCC) and less overlap (inconsistent with the PRCC), but this seems unlikely in these simulations as very seldom do foragers spend all of available time active. Similarly the effects of some of the other less significant parameters are consistent with plausible mechanisms (e.g. increasing the number of nests means that nests are more likely to be closer together and range overlap greater) and some are not (e.g. the negative effect of the time to assess the food value of an unvisited cell on range overlap).

	Mean Range area	Mean Range overlap
Parameter	PRCC	PRCC
food_density	- 0.947 ***	- 0.524 ***
nest_cost	0.313 ***	- 0.018
active_cost	0.166 **	0.134 *
move_cost	0.082	- 0.072
cone_energy	- 0.642 ***	- 0.086
max_speed	- 0.096	- 0.134 *
day_satiation	- 0.027	0.116 *
min_weight	- 0.025	0.049
max_weight	0.104	0.138 *
assess_time	- 0.114 *	- 0.144 *
num_nests	0.116 *	0.143 *
tstep_length	- 0.136 *	0.202 **

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

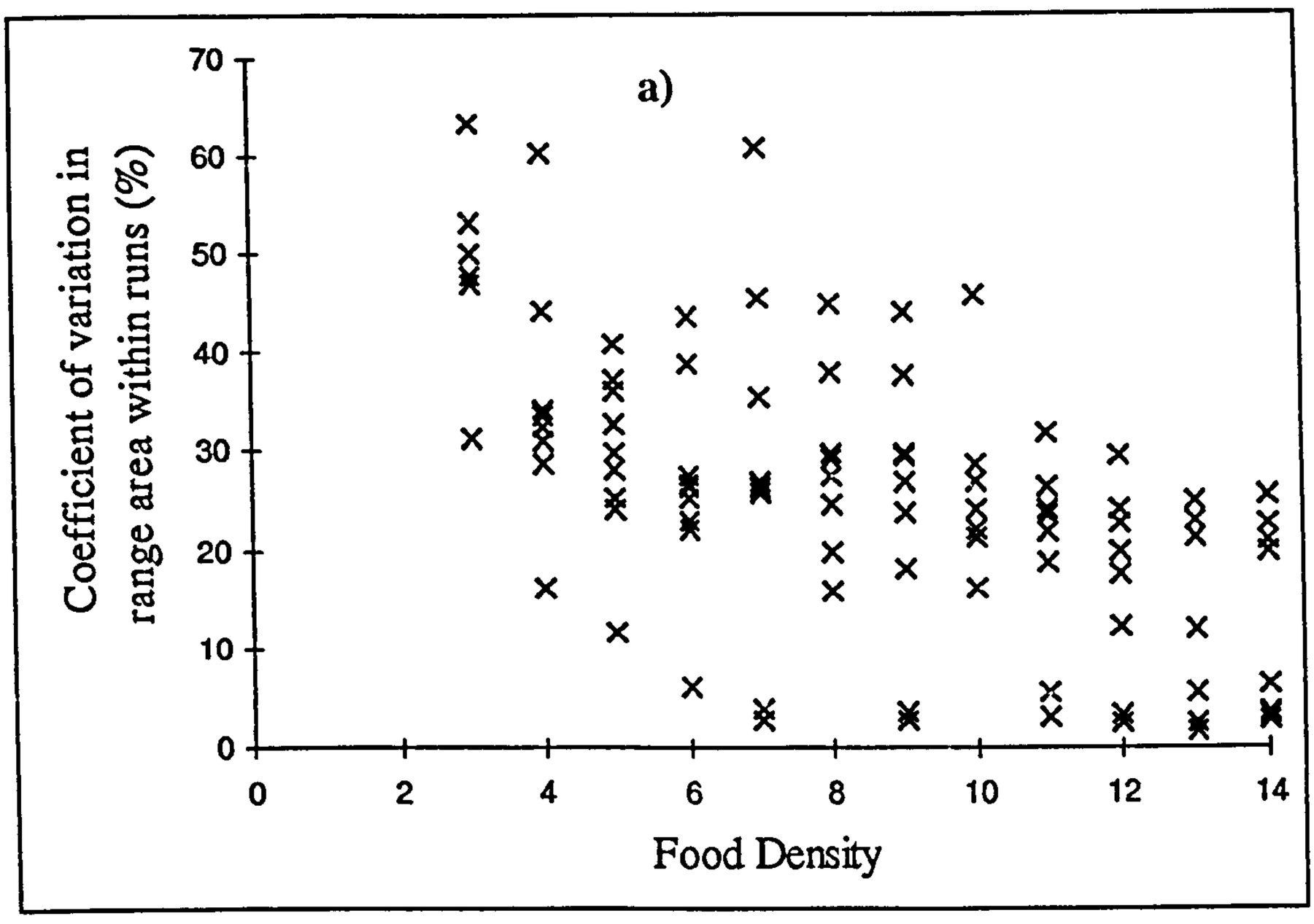
Table 3.2. Partial rank correlation coefficients between input parameter values and the outputs, mean range area and mean overlap, for the series 2 (uncertainty analysis) runs (n=100).

3.3.4 Variability in range area and overlap within each simulation

The patterns of variability in range area and overlap within each simulation run were similar for the series 1 and series 2 runs, for brevity only the results of the series 1 runs are presented here. Coefficients of variation (standard deviation/mean) of range areas within each run were higher at lower food densities (Fig. 3.7a). This indicates that range areas were more variable at lower food densities and that this increased variability was not just a result of the range areas being larger. At the lowest food density the ratios of the area of the largest range in a run divided by the area of the smallest were between 4.7 and 2.6, while at the highest food density they were between 1.8 and 1.05. This confirms the pattern suggested in Figure 3.3 that range areas were more variable at lower food densities. As range overlap is expressed as a percentage, it is already dimensionless, and it is not informative to calculate the coefficient of variation. The standard deviation in range overlap increases with decreasing food density (Fig. 3.7b).

Following the logic that ranges that are overlapped should be larger to compensate for depletion competition, a greater difference in range overlap should lead to a greater difference in the amount of depletion competition and thus a greater difference in range area. Thus the greater variability of range areas within each run at lower food densities is likely to have arisen as a result of the higher variances in range overlap. This effect will have been compounded by the fact that at lower food densities range areas were larger and thus a defined difference in percentage overlap represents a larger difference in the size of area overlapped.

This leaves the question of the mechanism causing the higher variance in range overlap at lower food densities. At low food densities the largest range overlap within a run was greater than at high food densities, but there was still always at least one range that was not overlapped at all (see Fig. 3.3). This pattern is at least partly a result of the random spacing of nests, if nests were uniformly spaced the magnitude of the variance in range overlap would be much less.



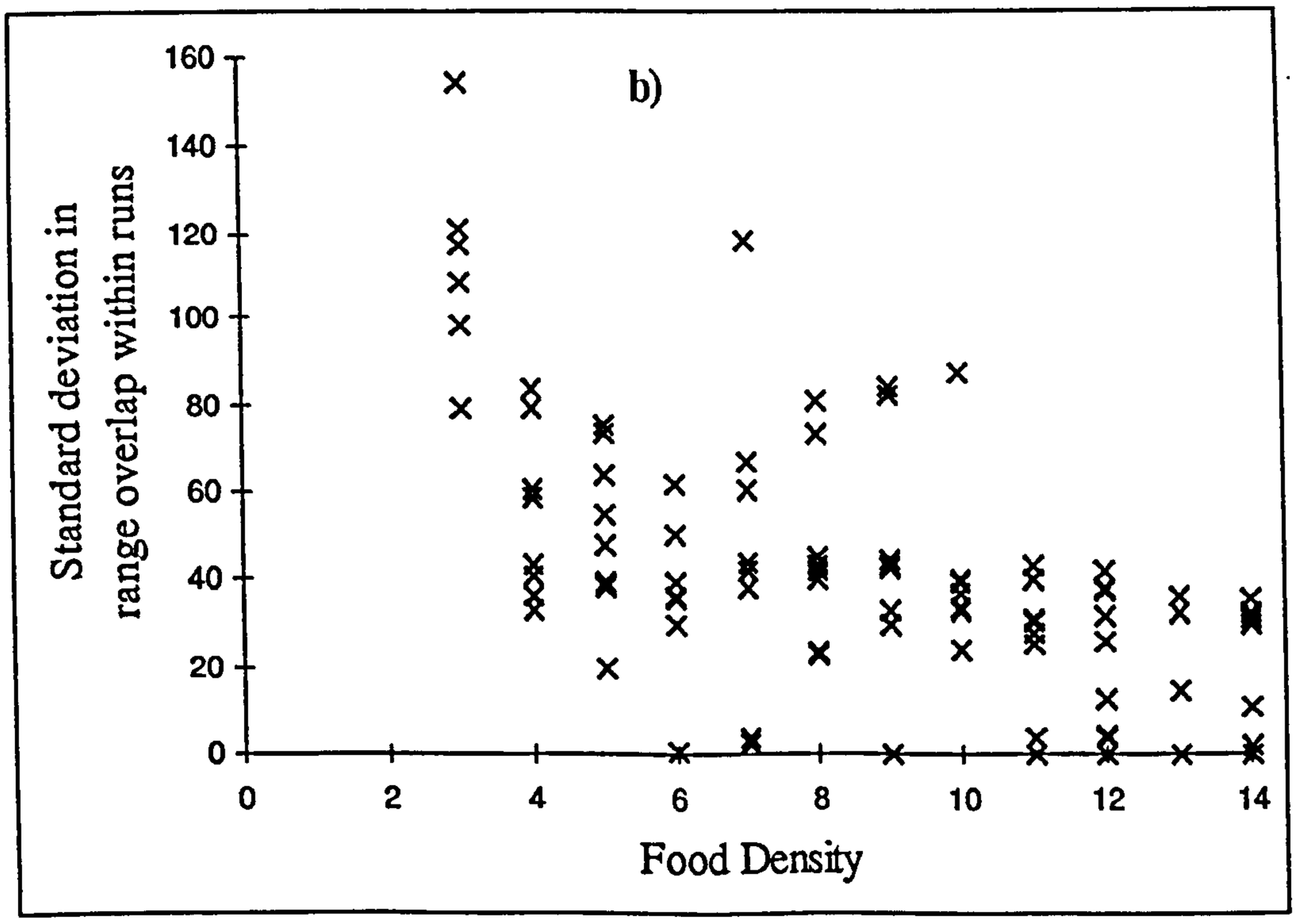


Figure 3.7 : (a) Relationship between food density and the coefficient of variation in range area under the depletion scenario. **(b)** Relationship between food density and the standard deviation in range overlap within simulation runs. (Both graphs are for Series 1 runs).

3.3.5 Comparison with the interference scenario

Figures 3.8 and 3.9 compare the patterns of range area and overlap generated by the series 1 depletion model runs to the alternative scenario based upon a simple form of interference. The responses of range area and overlap to changing food density were very similar between the two scenarios.

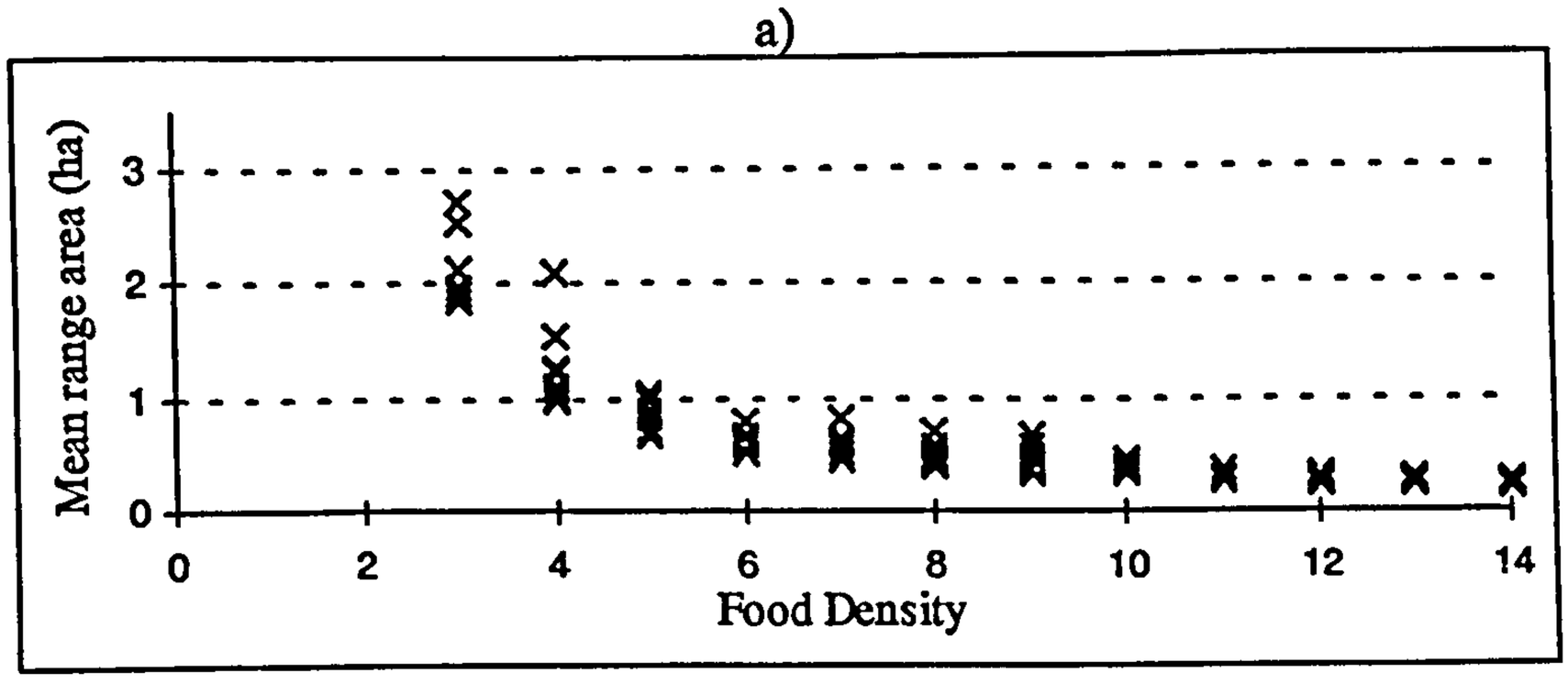
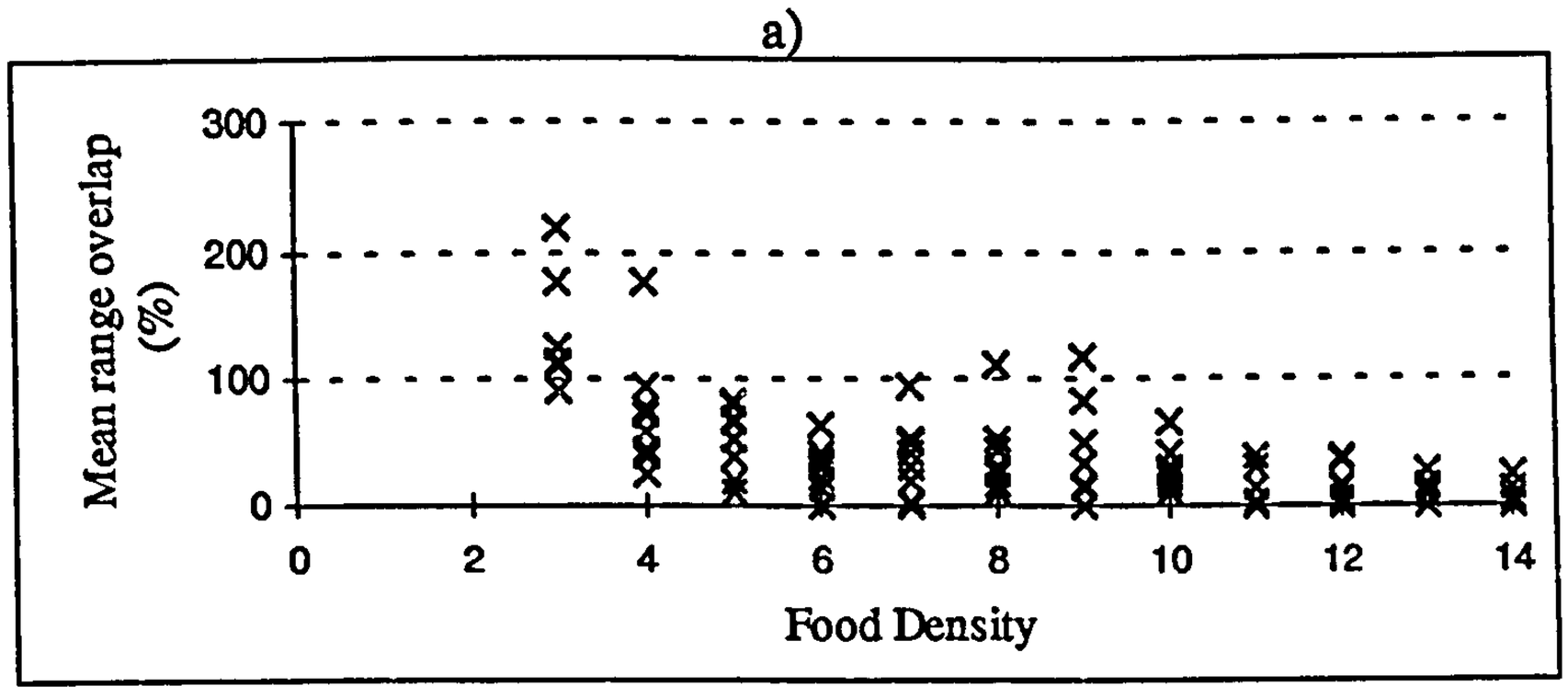
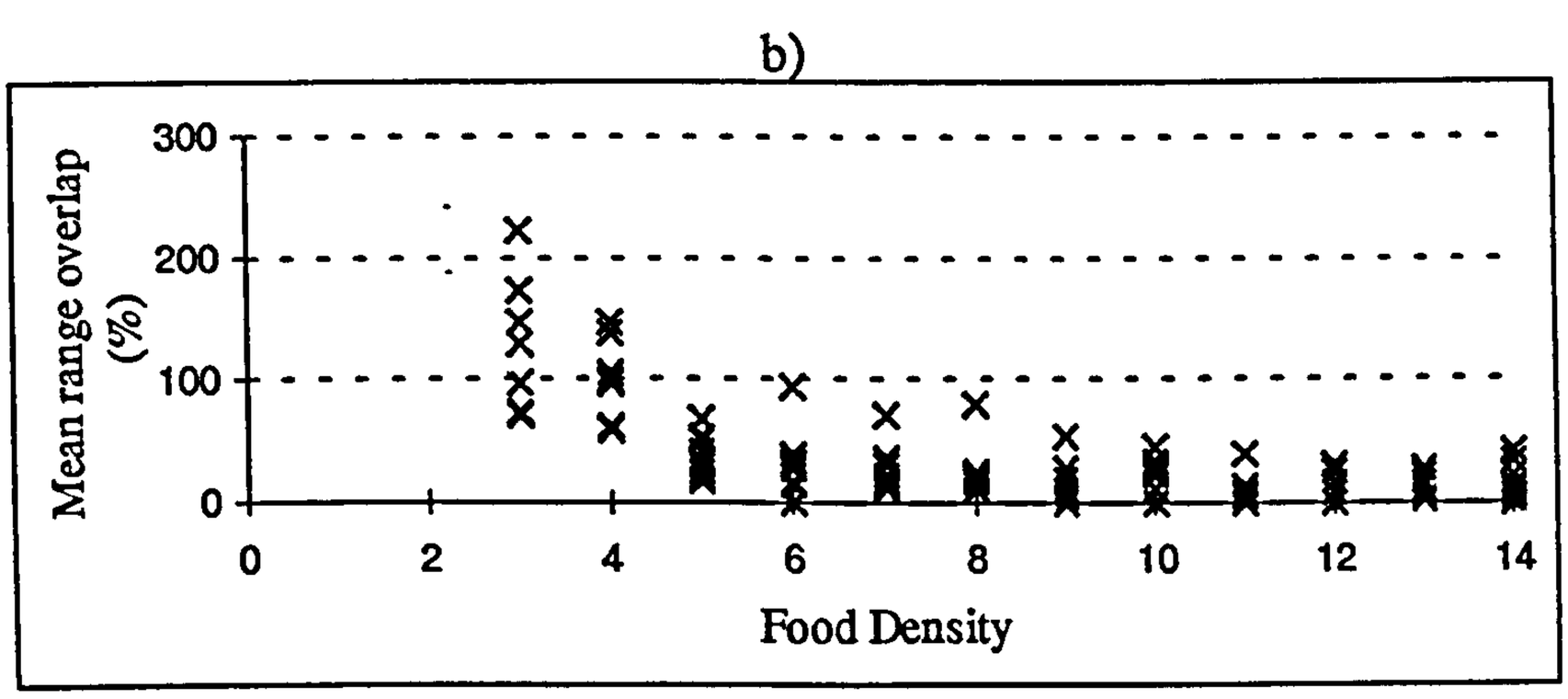
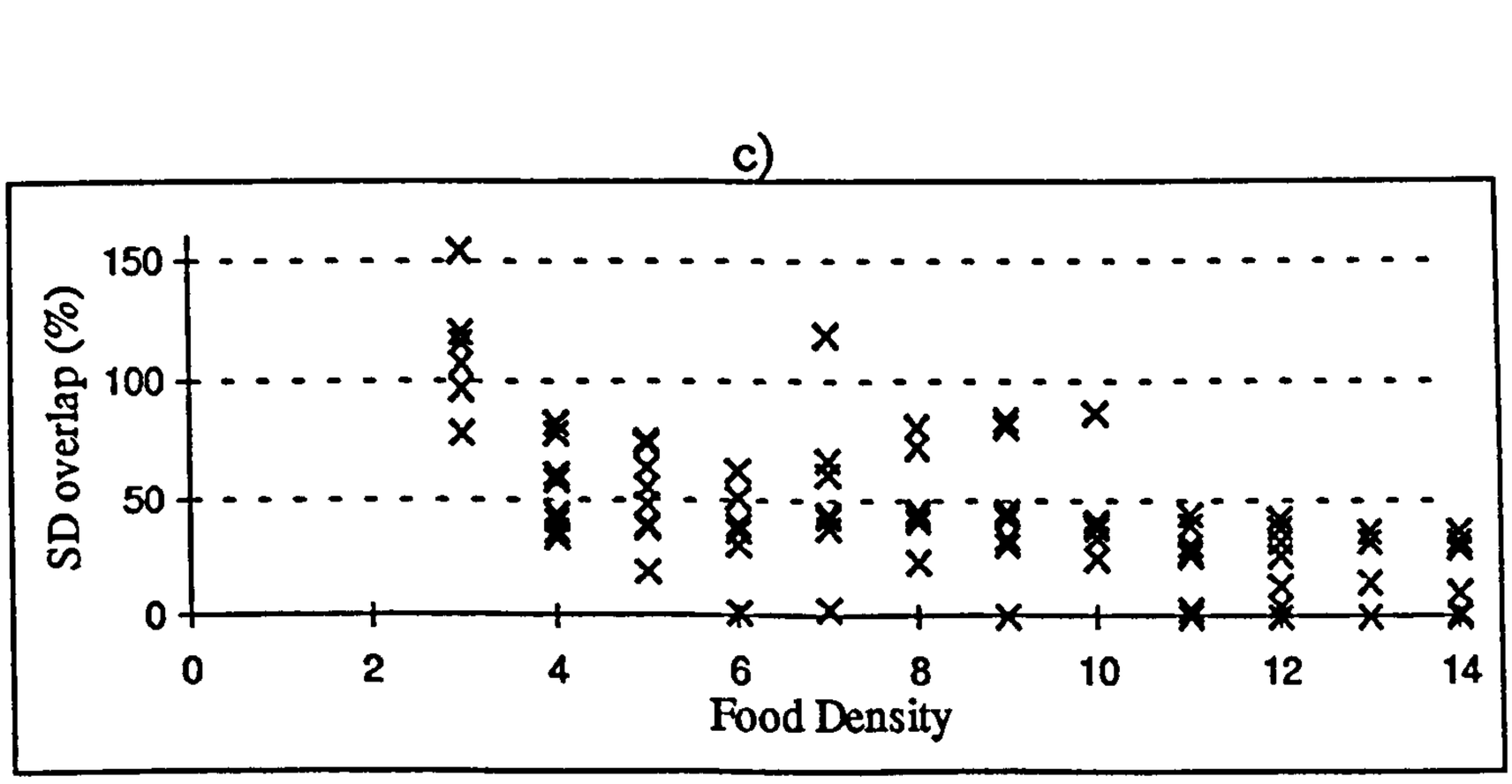


Figure 3.8 : Comparison of range area patterns generated by the depletion model (a & c), and the interference/avoidance mechanism (b & d).







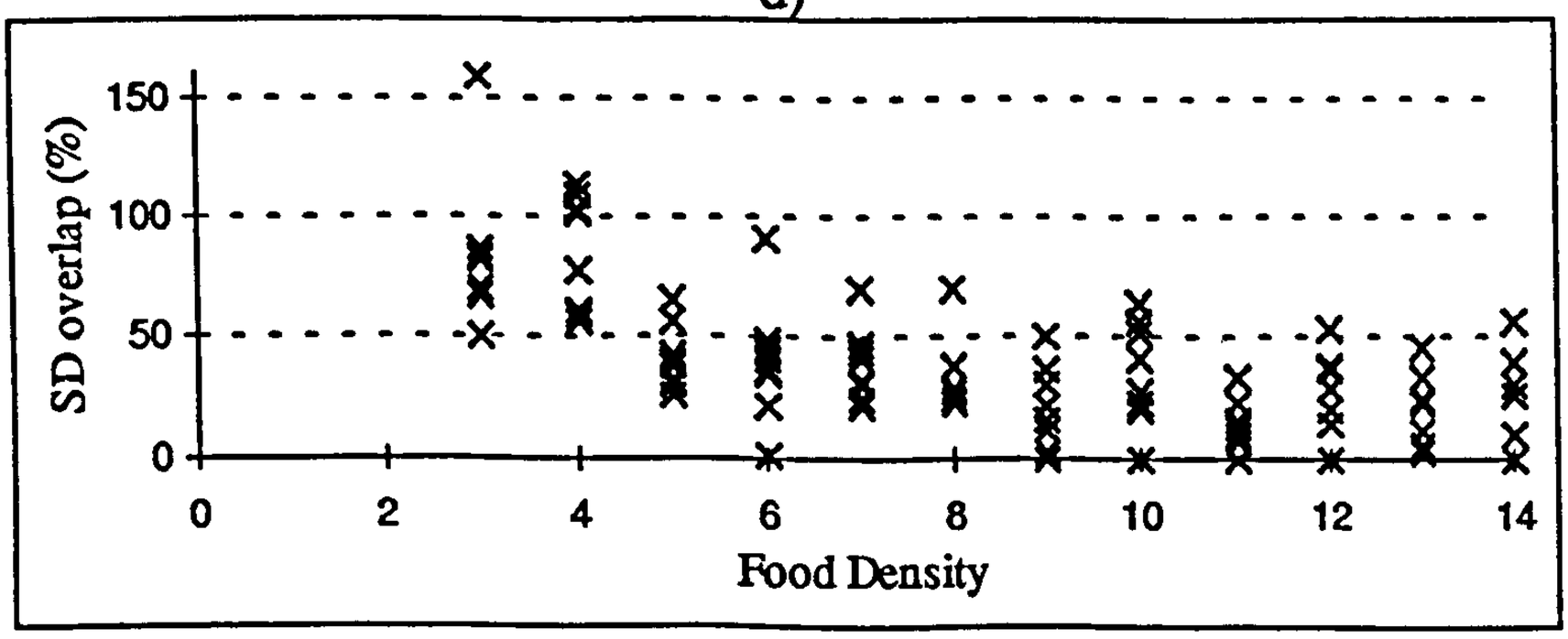


Figure 3.9 : Comparison of range overlap patterns generated by the depletion scenario (a & c), and the interference scenario (b & d).

3.3.6 Preliminary comparison of model results to field data

Table 3.3 shows that the mean female yearly range areas estimated in Lurz (1995) and Wauters and Dhondt (1992) were both larger than the mean range areas generated by the model runs that were closest to the respective field conditions. The coefficients of variability in range area from the field studies were within the limits generated by the model.

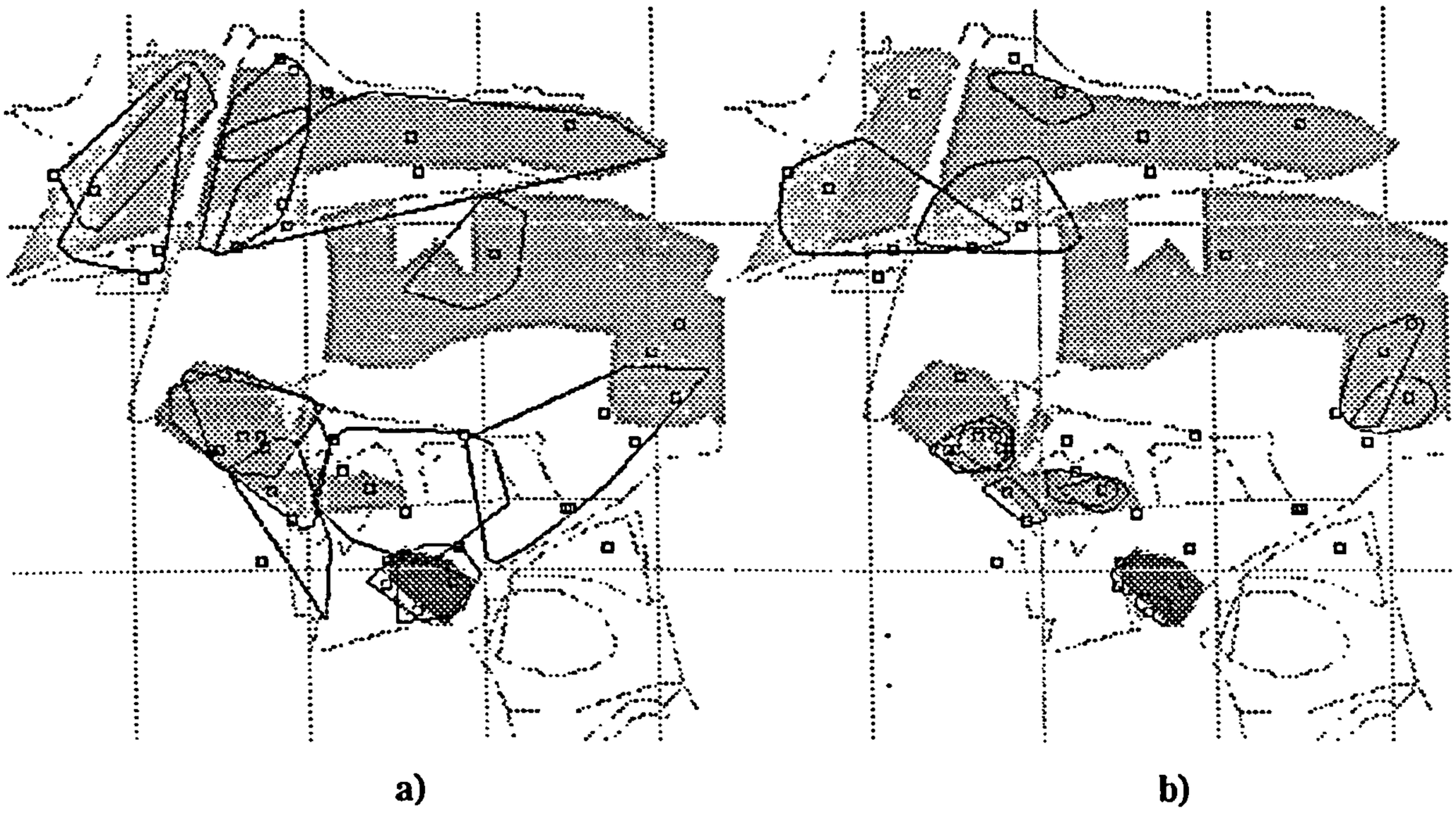
	Independent variables in the model runs		Dependent variables in the model runs	
	Squirrel Density (ha^{-1})	Cone Density (m^{-2})	Mean Range Area (ha)	CV in Range Area (%)
Model, depletion scenario				
Simulated low food	0.4	3	1.5 - 4.0	30 - 62
Simulated high food	0.4	14	0.2 - 0.5	2 - 25
Model, interference scenario				
Simulated low food	0.4	3	1.5 - 3.0	26 - 54
Simulated high food	0.4	14	0.2 - 0.3	4 - 33
Field data (females)				
Lurz (1995)	0.33	1	8.7	44
Wauters and Dhondt (1992)	0.84	10 - 20	2.8	5

Table 3.3. Comparison between simulated range areas and field data. For the two field studies the range areas are the 100% minimum convex polygon estimates.

3.3.7 Application of the model to detailed food availability data

Initial running of the model under the same depletion scenario as described previously resulted in many individuals dying within a few days as they were unable to locate sufficient food. An alternative scenario was modelled in which individuals were assumed to have perfect knowledge of food availability at the start of the season. Figure 3.10 shows the distribution of food represented, the home ranges estimated in the field and those generated by one model run.

In figure 3.11, mean range areas and overlaps are compared to those from 10 model runs. Although mean range overlap measured in the field was within the spread of predictions, mean range area in the field was approximately twice that of the predictions.



a) b)

Figure 3.10 : Maps of estimated food availability for a 4km^2 area of conifer plantation, darker colours represent higher estimated food densities. Polygons are 100% minimum convex polygon home range estimates derived from **a)** field data for 13 females for July, **b)** one model run. The small squares represent drey positions, and the grid resolution is 500m.

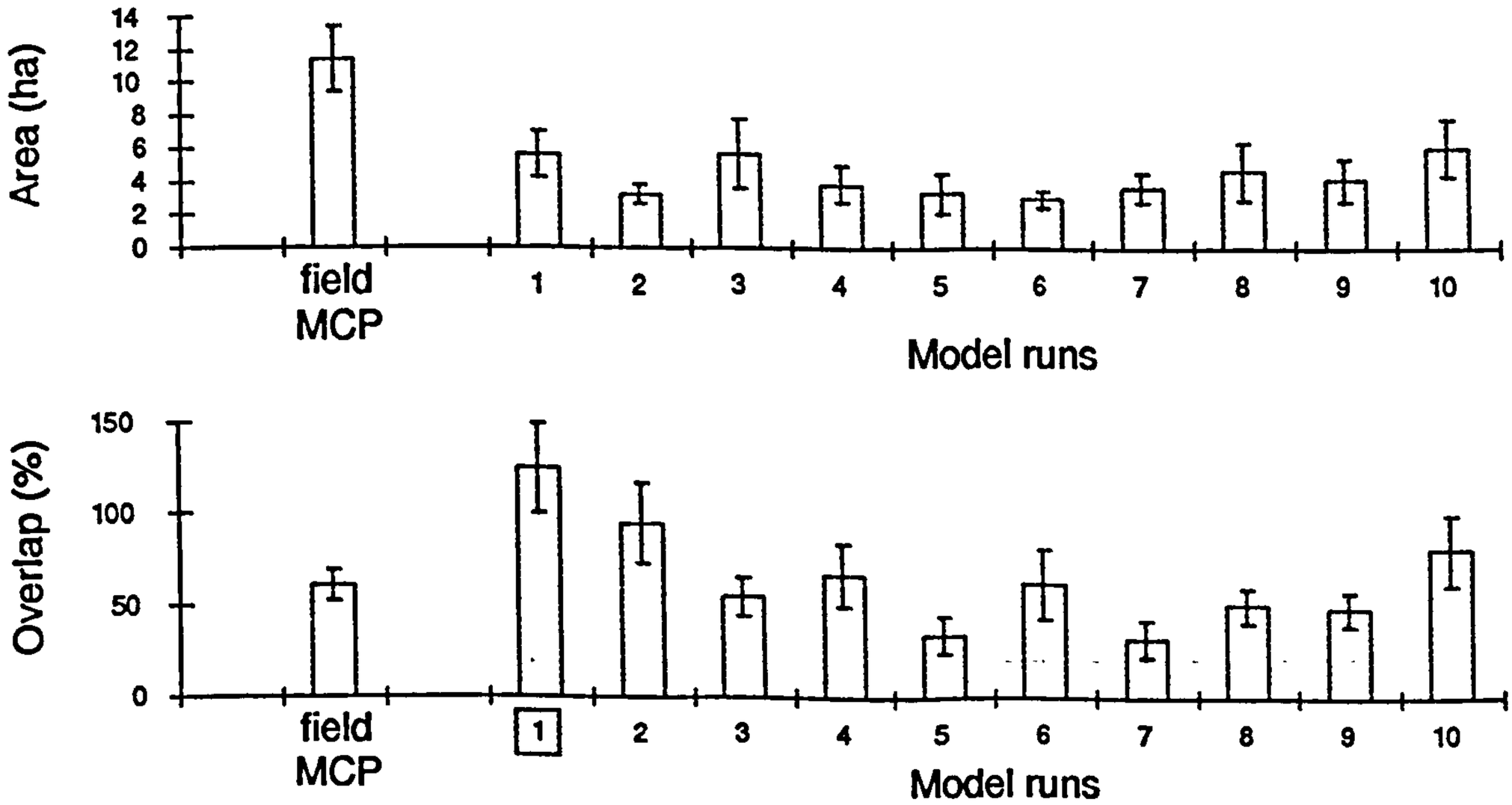


Figure 3.11 : Comparison of range area and overlap generated by ten runs of the foraging model and those measured in the field by Lurz (1995). Error bars indicate +/- 1 standard error.

3.4 Discussion

In common with many recent simulations of animal movement (e.g. Armstrong et al. 1987; Saarenmaa et al. 1988; Turner et al. 1993; Turner et al. 1994; Moen et al. 1997) this model used behaviour rules which owe more to a 'standard of plausibility' (Lima and Zollner 1996) than to empirical data. The need to spend the night in a nest, the need to move between spatially separated food supplies and the approximate movement speed were derived from field observations. The foraging and exploring movement algorithms were based on the plausible rule that a forager minimises the distance it has to move and secondarily minimises the distance it moves away from a nest. The incorporation of exploring behaviour and spatial memory was based on the view that these are important components of foraging and home ranging behaviour (e.g. Armstrong et al. 1987; Benhamou and Poucet 1996). The limitation of exploration behaviour by a food knowledge threshold was based on the empirical observation that red squirrels are seldom active for all hours of available daylight (Reynolds 1985; Lurz 1995) and the plausible logic that foragers are likely to balance the benefits of knowledge against the costs and risks of activity. Setting this food knowledge threshold to the amount of food necessary to sustain the forager until the end of the season was a further extension of this cost/benefit logic, based on no empirical information. In addition to relying on a standard of plausibility the model included no attempt to determine the relative fitness consequences of different movement rules. In the light of the resultant uncertainty in the structure of the model the predictions presented should be considered with caution.

The reliance of model rules on a standard of plausibility was a result of an effort not to use artificially imposed constraints. No artificial constraints were imposed upon range size and overlap or the distance and location of movements. In addition the model does not assume that foragers have perfect knowledge of food availability across the landscape, but instead considers explicitly the acquisition of local knowledge and movements based upon this. It has greater general applicability and mechanistic appeal than models in which movements are based upon empirically derived distributions of path lengths and turning angles (e.g. Siniff and Jensen 1969) or movement rates in different habitats (With and Crist 1996). Additionally it addresses the fact that mammal foraging at these scales is not merely a random process (e.g. Gross et al. 1995;

Benhamou and Poucet 1996). This approach addresses space use at larger spatial and temporal scales than that conventionally considered by approaches based upon optimal foraging theory and the ideal free distribution (e.g. Stephens and Krebs 1986; Newman 1991). The framework of the approach is based on relatively few assumptions and their is the opportunity to incorporate scenarios based on different assumptions to those used here.

Within the high food density simulations, foragers following much simpler behavioural rules, with no memory or exploring, would still have survived the season. It has been shown elsewhere that foraging rules differing in complexity can perform almost equally at high food densities but cause large energetic differences at low food densities (Turner et al. 1993). The object here was to predict the response of spacing pattern under one set of plausible movement rules, not to assess the relative fitness benefits of alternative rules. Even at the lower food densities certain of the behavioural rules used in the model may seem strange, foragers were programmed to explore food availability at the start of the season and yet food availability was uniform. The rules developed were designed to be generally applicable, irrespective of the pattern of food availability. A uniform landscape was used to keep the system as simple as possible to begin with and because of a lack of fine scale data on which to base any other pattern of food availability.

3.4.1 Depletion scenario

The uniform nature of the landscape and the relatively straightforward behaviour of the foragers are reflected in the simple general trends in the model outputs. The negative relationship generated between range area and food density is intuitively obvious considering the model rules. It is broadly consistent with field data (e.g. Kenward 1985; Tufto et al. 1996; Powell et al. 1997) but does not preclude other mechanisms (such as intruder pressure) from being responsible for the same relationship observed in the field (Kenward 1985). The negative relationship generated between range overlap and food density is also a relatively straightforward result of the structure of the model. As the number of foragers was kept constant it is not surprising that at lower food densities foragers covered a larger area and thus tended to overlap more. This is effectively a result of the changing ratio of population density to carrying capacity; at low food densities the landscape was close to saturation, at the higher food densities many more

foragers could potentially have survived the season on the available food. Therefore the predicted response of range overlap to food density is likely to be different in a system where the habitat is maintained close to saturation by recruitment. The increased variability in range areas and overlaps at lower food densities appears to have been at least partly a result of the random distribution of nests. This suggests that the spatial distribution of nests may have an important influence on patterns of home range area and overlap in ranging mammals. Even in a landscape of uniform food availability a non uniform positioning of nests could lead to variation in range overlap and from that variation in range area. In this model nest positions were a pre-defined random input, their importance to the output warrants a more thorough investigation of the processes that determine their positioning in the field.

3.4.2 Interference scenario

The interference scenario generated very similar patterns of range area and overlap to the depletion scenario. It might have been expected that the interference scenario would generate less range overlap. However, as there is nothing to stop foragers from moving through areas marked by others, foragers starting at dreys close to each other can utilise a checkerboard type pattern of cells. Thus, although at a fine scale they are prevented from feeding within the same cells, at a larger scale foragers can use the same areas of space.

This could explain the similar patterns of space use between the two scenarios. In the depletion scenario at lower food densities, ranges are larger, increased overlap leads to increased depletion competition and a positive feedback on range area. In the interference scenario, as modelled here, the mechanism could be very similar. At lower food densities in the interference scenario ranges are likely to contain more cells that have been depleted by others, in the depletion scenario ranges are likely to contain more cells that have been monopolised by others.

The similarity between the results of the depletion and interference scenarios, may just be a result of the details of the representations of the behaviours. An interference scenario including complete avoidance of cells marked by others, or a decreased intake rate when two or more foragers are close to each other, may produce different patterns. Alternatively the similar results could represent the inability of the relatively coarse

measures of range area and overlap used here to differentiate between alternative spacing behaviours.

3.4.3 Preliminary comparison to field data

Range areas generated by both scenarios, at low and high food densities were smaller than field data collected under similaer conditions (see Table 3.3). In both cases, the field ranges were estimated from fixes taken throughout the year, whereas the model simulated space use for just 10 months, so this could be one source of the difference. The larger ranges in Lurz (1995) could be also explained by the lower food density. Extrapolating from the predicted trend in range area to food densities of 1 cone m^{-2} (equivalent to those estimated by Lurz 1995) gives predictions of a similar magnitude to the 8.7 ha measured in the field (see Fig. 3.4). Lower food densities were not included in these simulations as at food densities of 1 and 2 cones m^{-2} forager mortality was common (South et al. 1997), thus changing the population density and introducing an additional source of variation into the analysis. This mortality of foragers at lower food densities is not inconsistent with field data as in the field a high turnover of squirrels was observed (Lurz 1995). The difference between the range areas predicted by the model and those estimated by Wauters and Dhondt (1992) could also be partly a result of a mismatch between model input parameters and the field conditions. The larger range sizes recorded by Wauters and Dhondt (1992) are consistent with the higher squirrel densities having lead to greater overlap, more depletion competition and increased range size to compensate for this.

The correspondence between the coefficients of variability in range areas from the field studies and those generated by the model is somewhat surprising as the model does not include any of the spatial variation in food density that is likely to occur in the natural systems. This suggests that the competition mechanisms simulated here could be an important component of the variability in red squirrel range areas in the field.

The brief comparison of model outputs to field data does not represent a comprehensive test of whether the mechanisms simulated in the model are important in shaping space use patterns seen in the field. In order to assess this rigorously, input parameters need to be more closely fitted to field data and alternative behavioural mechanisms need to be simulated. Alternative mechanisms could be developed to represent other theories for

the determinants of spacing behaviour in mammals. Territoriality could be represented by giving foragers exclusive use of areas and the effect of intruder pressure could be modelled by changing forager movements according to their rate of encounter with other foragers. Forager movements could also be modified according to their energetic status, such that animals with a higher food intake could be made to explore more or less and the exploration mechanism could be changed to get foragers to re-explore previously visited areas. Uncertainties regarding foraging, exploring and conspecific interaction mechanisms can be confronted by the development of these new models. This approach provides a means of translating verbal or conceptual models to quantitative testable predictions.

3.4.4 Application of model to detailed food availability data

When the model was applied to detailed food availability data range areas generated were smaller than those measured in the field (see Fig. 3.11). Potential reasons for the difference between predictions and observations, maybe inaccuracies in the movement rules, social interactions or other species depleting the food resource, need to be explored.

3.4.5 Future prospects

The modelling approach described here needs to be conducted in tandem with fieldwork and could be used to clarify what data are necessary to test alternative hypotheses. The linkage of this model to software designed to analyse space use data collected in the field (Kenward and Hodder 1996) offers the opportunity to analyse model outputs in the same way that field data are analysed. Minimum convex polygons were used to represent space use in this analysis for their simplicity and as they are commonly used in studies of mammal ranging behaviour (Kenward 1987). Home range descriptors that include the temporal dimension of space use (such as cluster or kernel analysis) would have greater power to test model outputs against field data.

One danger with such modelling approaches is their complexity. This can make it difficult to establish the mechanisms by which results are generated. Attempts should be made to keep models of animal movement simple enough that, as in this analysis, the mechanisms by which patterns are generated can be determined.

3.4.6 Conclusion

This is the first attempt to extrapolate from individual movements over short time scales to the spacing pattern of a ranging mammal. It builds upon models of the movement of nomadic mammals (Saarenmaa et al. 1988; Turner et al. 1993; Turner et al. 1994; Moen et al. 1997), models of home ranging movement (Siniff and Jensen 1969; Benhamou 1989) and models where the distribution of animals over relatively short time scales is generated from their movements (Turchin 1991; With and Crist 1996). The model predicts increasing range areas, overlaps and variation in both of these in response to decreasing food densities. These predictions may be dependant on the changing habitat saturation and the random positioning of nests, factors that should be considered in future analyses.

The analysis presented here does not resolve the behavioural mechanisms behind spacing behaviour in red squirrels or mammals in general but it does generate testable predictions from two sets of relatively simple behavioural rules and it does provide a methodology for generating alternative predictions based on other potential mechanisms. The challenge is to extend this approach, in tandem with fieldwork, to determine the relevance of animal behaviour at small spatial and temporal scales to the distribution of animals within landscapes (Lima and Zollner 1996).

4. Chapter 4 : Predicting the distribution of the badger, comparing an associative model and a process based, sett site suitability model

4.1 Introduction

The badger is an adaptable species inhabiting deciduous woodland, agricultural, suburban and moorland landscapes in Britain and a range of other landscapes from mountains to Mediterranean coasts in other countries (Kruuk 1989; Neal and Cheeseman 1996). Habitat suitability is determined by the availability of suitable sett sites and foraging areas. Setts are preferably located in woodlands with well drained, diggable soils; permanent pasture and deciduous woodland provide the highest density of the badgers principle food, worms (Neal and Cheeseman 1996). Thus maximum badger densities exist in landscapes consisting of a mosaic of deciduous woodland and pasture (Cheeseman et al. 1981). Home range size and spacing strategy vary considerably according to habitat. In deciduous woodland and productive pastoral landscapes groups of around 5-10 individuals share a single main sett, ranges are in the order of 20-40 hectares and an area around the sett, commonly referred to as a territory, is marked with latrines and may be actively defended (e.g. Cheeseman et al. 1981). In other, less productive or predictable regions (e.g. suburban Bristol and the New Forest) group sizes tend to be smaller, their is less evidence of territorial defence (Cresswell and Harris 1988, Packham 1983), and ranges are larger, in the region of 150 to 300 hectares in parts of Scotland (Kruuk and Parish 1982). There is some disagreement as to whether territorial defence is principally motivated by food, sex or sett sites (e.g. da Silva et al. 1993; Roper et al. 1986) and whether density is principally limited by food or sett site availability (e.g. da Silva et al. 1993; Roper 1993). The most recent review (Neal and Cheeseman 1996) concludes that the case for food limitation is most convincing but this is likely to vary between regions.

The plasticity in badgers habitat requirements and range sizes means that development of methodologies for extrapolating distributions of this species is not easy. Previous

approaches that have been applied to predicting the distribution and abundance of badgers are reviewed in chapter 2.

I developed an approach for predicting the density of badger main setts based on the suitability of sites for main sett construction. I applied the model to two areas, Wytham woods in Oxfordshire (approx 2km x 3km) and an area of Northumberland (15km x 14km). The results were compared to surveyed sett density for Wytham (Chris Newman pers. comm.) and sett records for Northumberland held by the Northumberland Wildlife Trust.

4.2 Methods

The model developed, considered the suitability of sites for the location of badger main setts at three scales. In order of increasing spatial scale these were, 1) suitability of the site itself, 2) suitability of the location in relation to the distribution of nearby foraging habitats, 3) suitability of the location in relation to the positioning of neighbouring setts. Application of rules at each of these three scales was used to progressively narrow down sites potentially suitable for main sett location. The landcover map of the Institute of Terrestrial Ecology (Fuller et al. 1994) was used as the source of habitat data. This classifies all 25m x25m squares into one of 25 landcover types based on Landsat satellite imagery.

4.2.1 Scale 1: Defining suitability of sites for sett construction

Badger main setts are most often located in deciduous or coniferous woodland, and close to the edge if in the latter (Neal and Cheeseman 1996). In the model suitable sites for sett location were defined as 25m cells classified as deciduous woodland or as coniferous woodland within 100m of an edge.

4.2.2 Scale2 : Defining suitability of sites in terms of proximity to foraging habitats

Proximity to foraging areas is held to be an important factor in sett location (Neal and Cheeseman 1996). Earthworms are the primary food, often making up more than half of the diet, and these are most abundant in pasture and deciduous woodland (Kruuk 1987).

Kruuk and Parish (1982) gave evidence that 5 food patches were required by badger social groups, but these patches were not defined explicitly in terms of area, being between a half and several hectares. There is little quantitative evidence regarding a necessary minimum amount of foraging habitat and its proximity to sett sites. In the model 25 m cells were defined as suitable in terms of their proximity to foraging habitat if the surrounding 600 m x 600 m area contained at least 1.5 ha of pasture or deciduous woodland. This estimate is fairly arbitrary and probably overestimates suitable habitat, but acts to exclude those areas that are isolated from potential foraging sites. Model development in another study area 10 km further south in Northumberland, showed that more conservative classifications tended to exclude sites that were occupied by main setts.

4.2.3 Scale3 : Defining suitability of sites in terms of proximity to other setts

A minimum inter-sett distance of 300 m has been observed in productive areas (Kruuk and Parish 1982, Thornton 1988) and there is evidence that this distance is greater in less suitable regions (Kruuk and Parish 1982). The spacing of animals or their dens can be modelled in a simple way using hard-core models which assume that individuals or groups pre-empt a certain amount of space to the exclusion of others (see chapter 2). In this model a random sequential hard core process (Upton and Fingleton 1986) was used to place "setts" into the areas defined as suitable in the earlier components of the model. This simulates badgers arriving in a previously unoccupied area and locating a sett at random within the areas suitable for sett construction and foraging. Subsequent arrivals do likewise, but avoiding sites at less than the minimum inter-sett distance around existing setts. In practice this was achieved by randomly selecting a 25 m pixel from the areas defined as suitable at the two previous scales, further pixels were selected randomly and only retained if they were further than 300 m from previously retained pixels. Pixels continued to be selected until 500 consecutive selections failed to be retained as they were too close to an existing point (i.e the landscape was effectively saturated). The process was repeated 20 times to obtain an estimate of the number of setts that an area could be expected to support.

The hard-core model was applied to Wytham using a minimum inter-sett distance of 300 m (Kruuk and Parish 1982) and to the Northumberland study area using a minimum inter-sett

distance of 900 m based on the surveyed location of 15 setts in a study area 10 km to the south.

Initial application of the model to the Northumberland study area resulted in a large over prediction of sett numbers relative to the survey data. To see if this was a result of the liberal classification of suitability in terms of proximity to foraging habitat, I repeated the model runs with increased requirements for foraging habitat. The new requirements used were 2.5 ha and 5 ha of pasture or deciduous woodland within the 600 m x 600 m square centred on each cell.

4.3 Results

Table 4.1 shows the results of the first two scales of the model. For the Northumberland study area 11 % was classified as suitable for sett construction (see figure 4.1). Adding on the low foraging areas requirement decreased the area classed as suitable area to 3.2 % (figure 4.2), and the higher requirement decreased it further to 2.2 %. Six of the recorded sett positions fell outside areas classed as suitable at scale 1, and this increased to eight when the high foraging areas requirement was included. For Wytham, 73% of the study area was classed as suitable at scale 1 and adding even the higher foraging areas requirement did not decrease the area classed as suitable (Table 4.1). Two of the recorded sett positions fell outside areas classed as suitable at scale 1, and this was not increased by the incorporation of the foraging areas component.

	Wytham (~ 2 x 3 km)		Northumberland (15 x 14 km)	
habitat classification	% suitable	no. setts excluded	% suitable	no. setts excluded
suitability for sett construction	73	2	11.3	6
proximity to 1.5 ha of foraging habitat	100 (73)	0 (2)	48 (3.2)	0 (6)
proximity to 2.5 ha of foraging habitat	100 (73)	0 (2)	42 (2.8)	2 (6)
proximity to 5 ha of foraging habitat	99 (73)	0 (2)	31 (2.2)	4 (8)

Table 4.1 Effect of the different habitat classifications on the percentage of the landscape classed as suitable and the number of surveyed setts that fall in areas classed as unsuitable. The numbers outside of parentheses are the result of that classification in isolation, the numbers within parentheses show the cumulative results of the foraging habitat classification when added to the suitability for sett construction component.

The 'sett' positions generated by one run of the space pre-emption component of the model applied to Northumberland are shown in figures 4.2 and 4.3 (for the low and high foraging area requirements respectively). Predicted numbers of setts under both scenarios were much greater than the number recorded from the field (figure 4.4). For Wytham the different foraging area requirements made no difference to the area of habitat classed as suitable so the space pre-emption component was run under one set of conditions. The 'sett' positions generated by one run are shown in figure 4.5 and the numbers can be seen to be similar to the distribution of setts recorded in the field (figure 4.6).

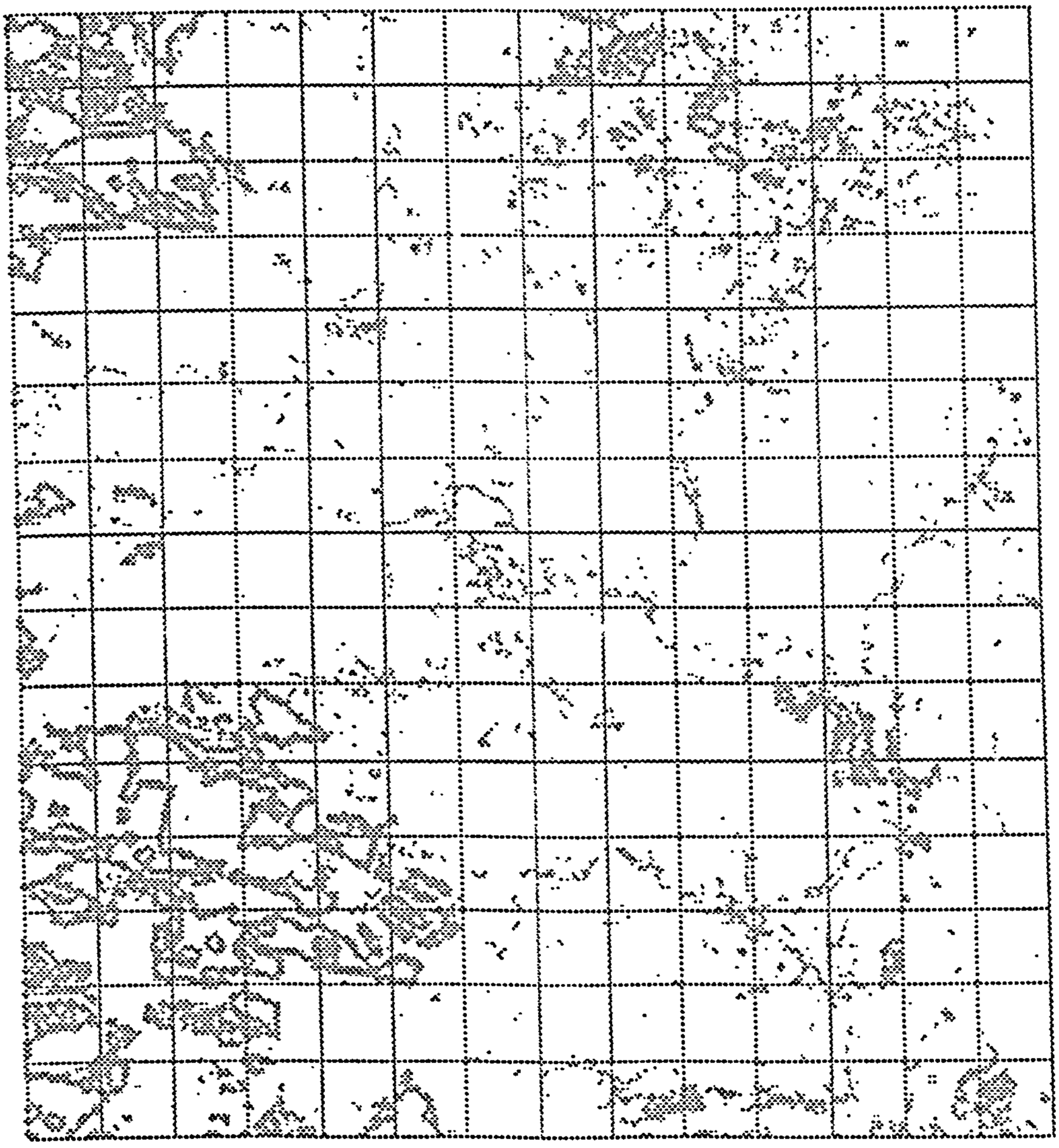


Figure 4.1 Areas in the Northumberland study area classified as suitable for sett construction at a local scale by the space pre-emption model. 1km grid.

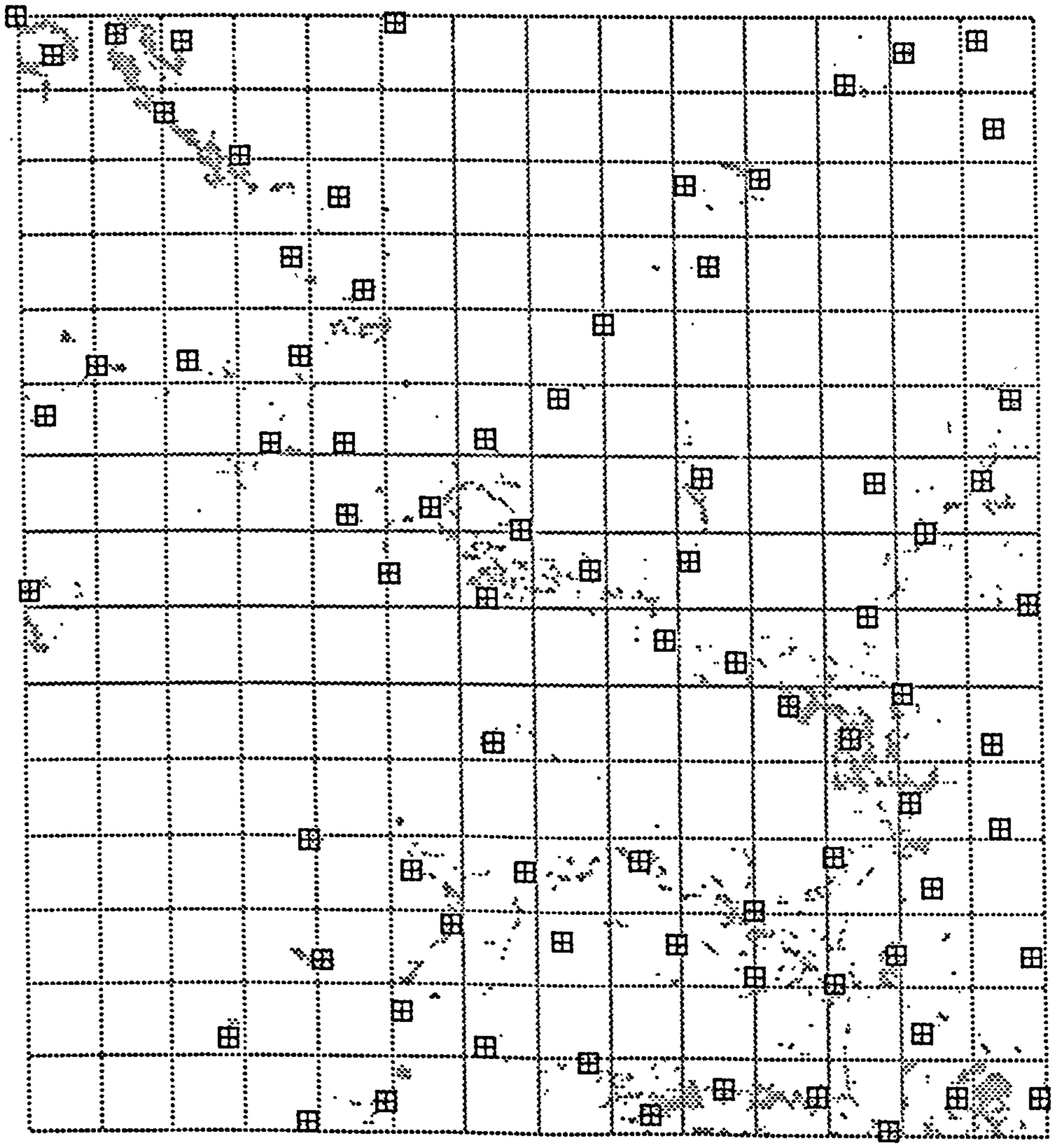


Figure 4.2 Areas in the Northumberland study area classified as suitable for sett construction and relative to the distribution of foraging habitat by the sett site suitability model (using the low foraging habitat requirement of 0.5ha within the 36ha square centred on the sett location). Boxes with crosses in show the positions of 'setts' generated by one run of the space pre-emption component of the model. 1km grid.

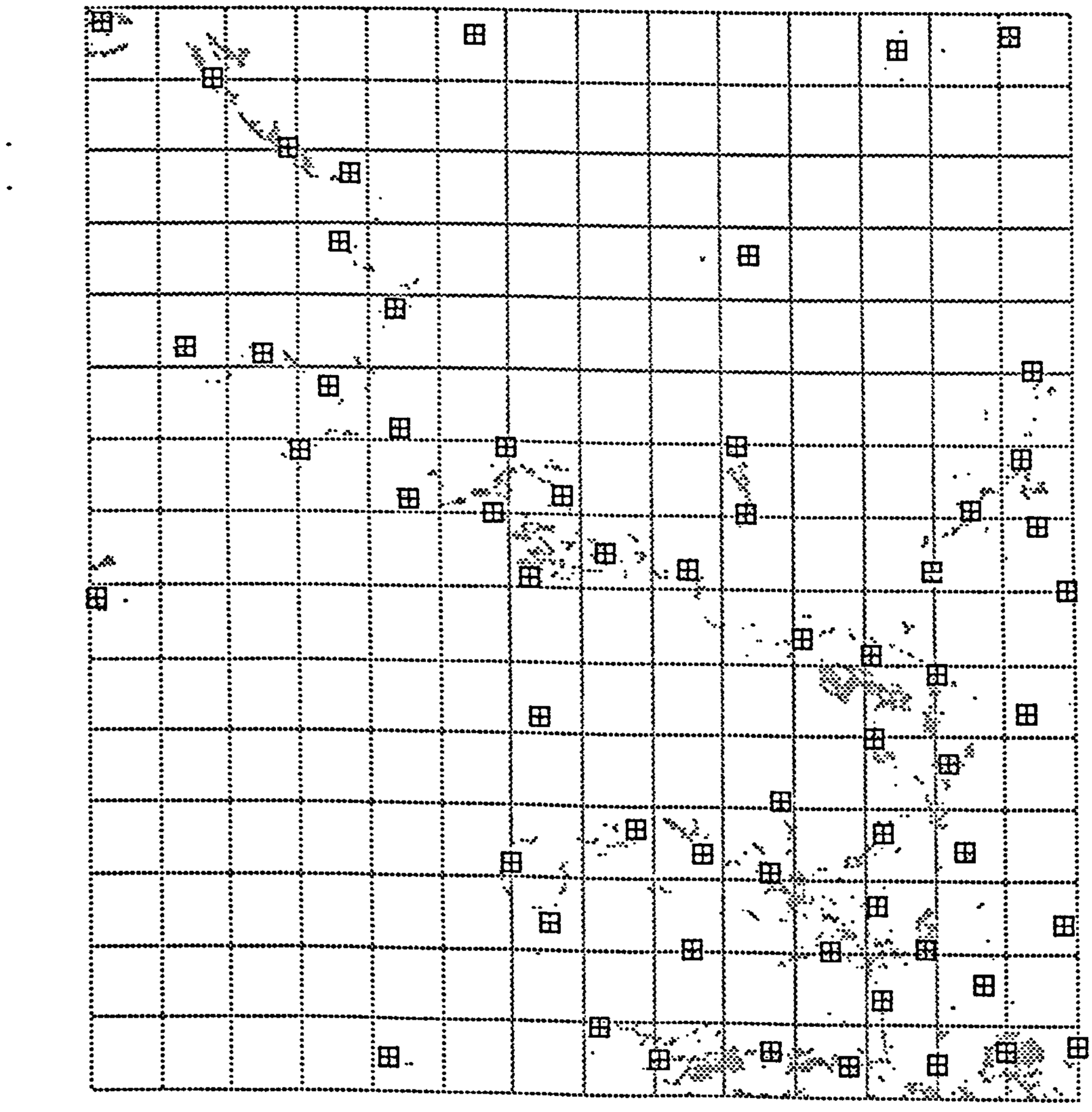


Figure 4.3 Areas in the Northumberland study area classified as suitable for sett construction and relative to the distribution of foraging habitat by the sett site suitability model (using the high foraging habitat requirement of 2ha within the 36ha square centred on the sett location). Boxes with crosses in show the positions of 'setts' generated by one run of the space pre-emption component of the model. 1km grid.

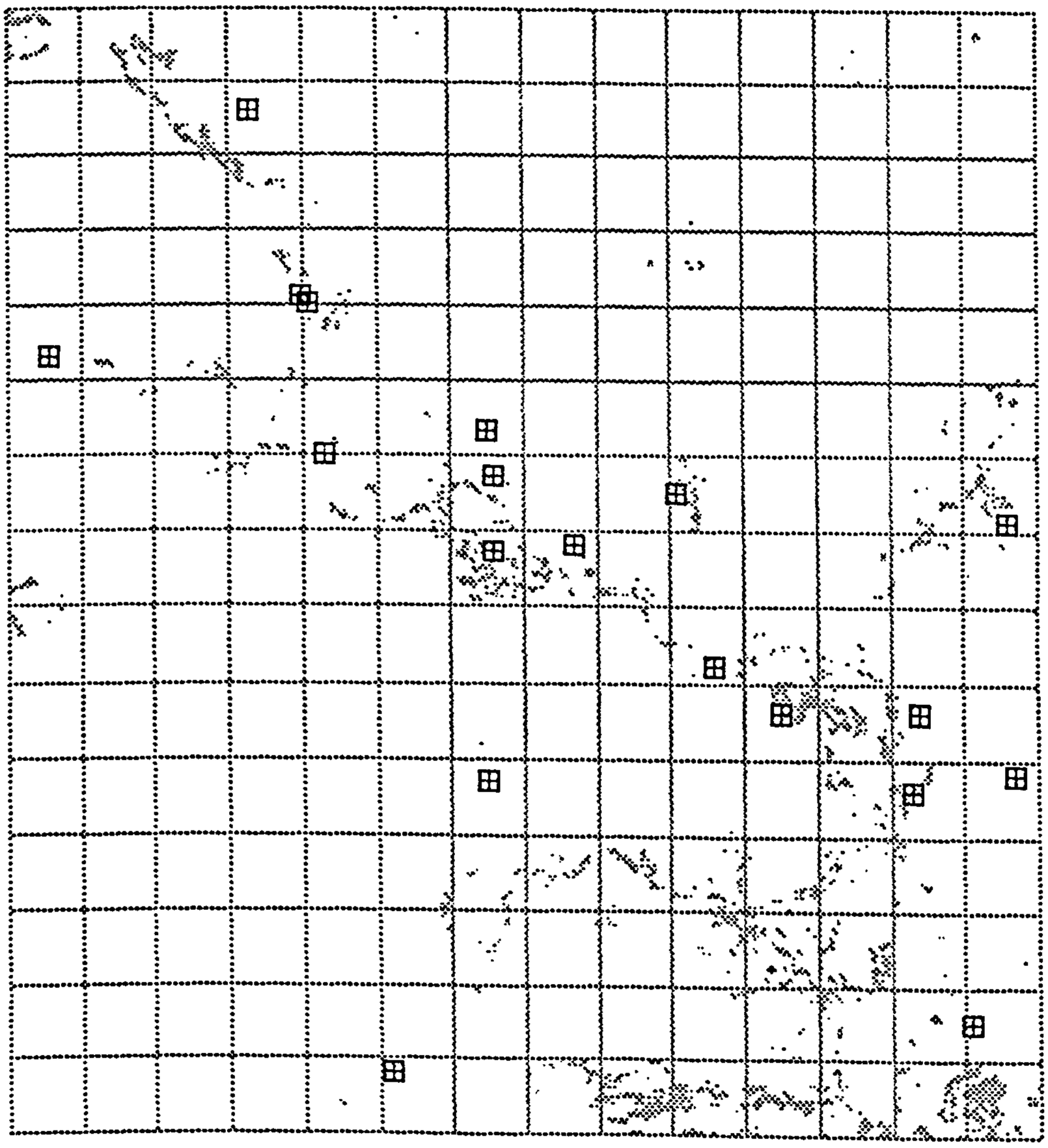


Figure 4.4 Areas in the Northumberland study area classified as suitable for sett construction and relative to the distribution of foraging habitat by the sett site suitability model (using the high foraging habitat requirement of 2ha within the 36ha square centred on the sett location). Boxes with crosses in show the positions of setts as indicated by records held by the Northumberland Wildlife Trust. 1km grid.

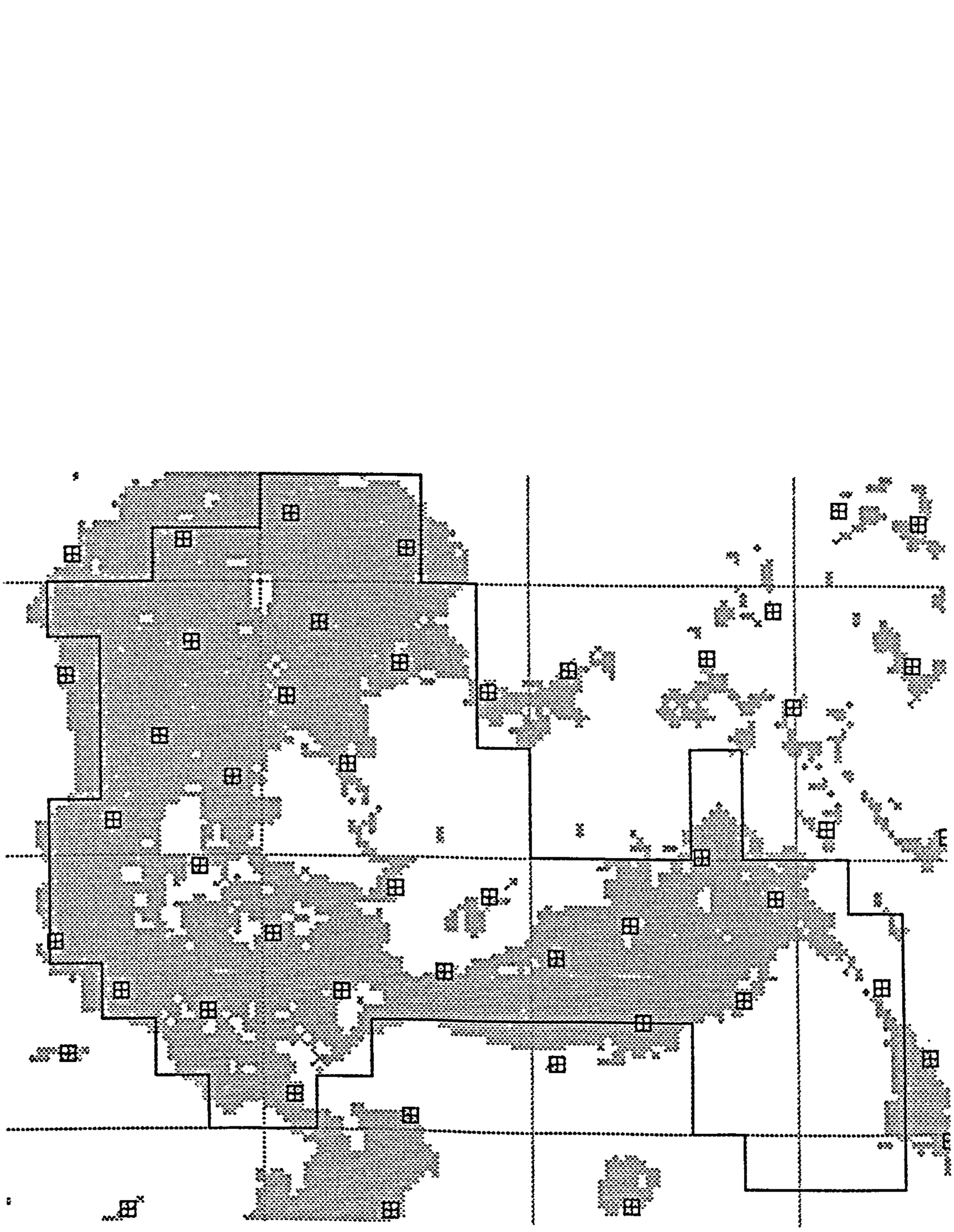


Figure 4.5 Areas in the Wytham study area classified as suitable for sett construction and relative to the distribution of foraging habitat by the sett site suitability model. Boxes with crosses in show the positions of 'setts' generated by one run of the space pre-emption component of the model. The black line represents the approximate boundary of the area surveyed for the presence of main setts. 1km grid.

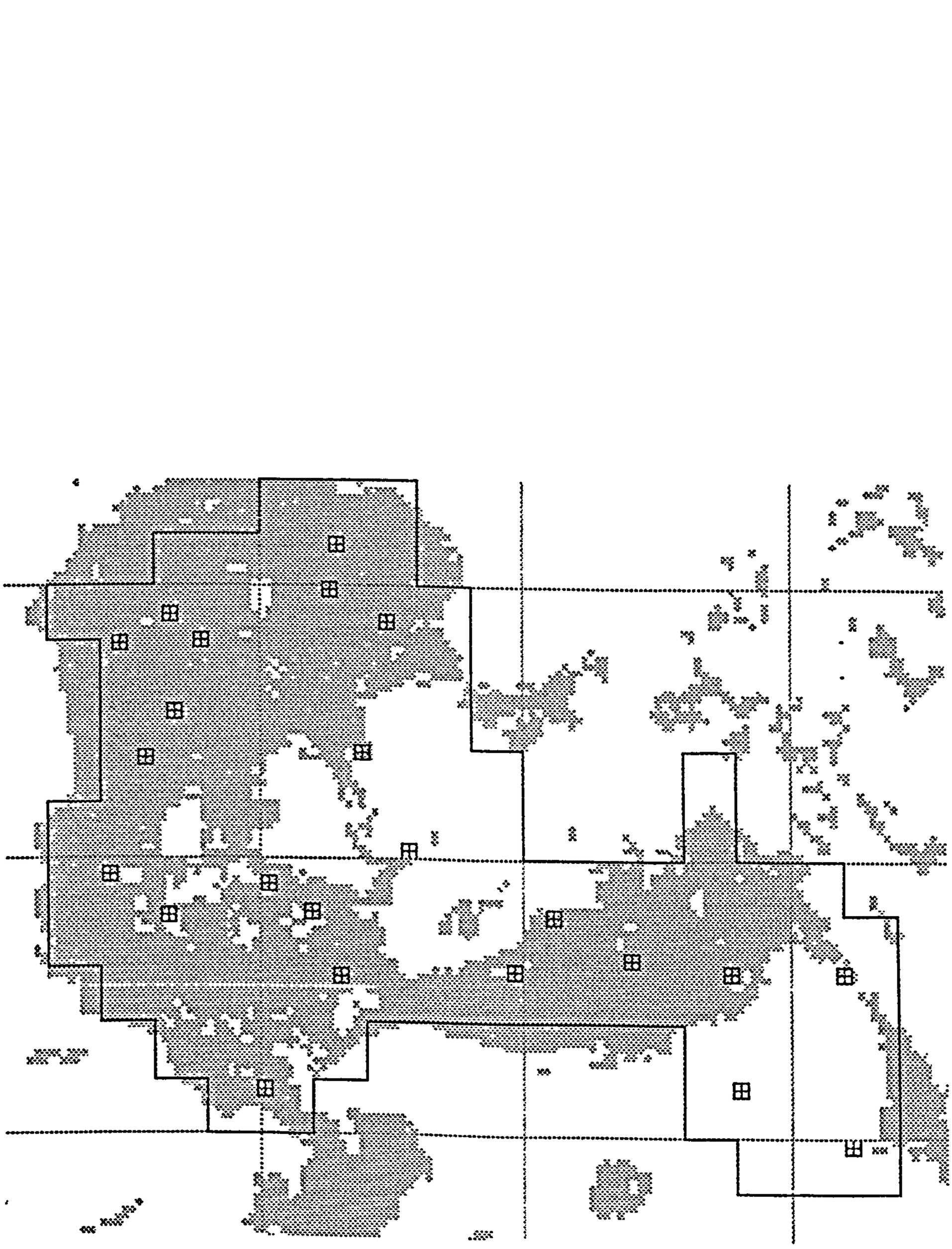


Figure 4.6 Areas in the Wytham study area classified as suitable for sett construction and relative to the distribution of foraging habitat by the sett site suitability model. Boxes with crosses in show the positions of setts as determined by field survey. The black line represents the approximate boundary of the area surveyed. 1km grid.

Table 4.2 summarises the predicted number of setts versus the number recorded from the field. For the Northumberland study area the model predicted between 4.6 and 3.3 times as many setts as were recorded under the low and high foraging area requirements respectively. The model applied to Wytham performed well, the observed number of setts falling within the range predicted.

Number of main setts, for model results the mean and range from 20 replicates is presented.	Wytham (~ 2 x 3 km)	Northumberland (15 x 14 km)
model result, low foraging area requirement (1.5 ha)	**24.3** (19-30)	**79** (74-85)
model result, medium foraging area requirement (2.5 ha)	"	**69** (63-74)
model result, high foraging area requirement (5 ha)	"	**56** (49-65)
Survey data	**23**	**17**

Table 4.2 Comparison of number of main setts predicted by the model and survey data (systematic survey for Wytham, records held by the local wildlife trust for Northumberland). The foraging area requirement made no difference to the area of habitat classed as suitable for Wytham.

4.4 Discussion

Here I developed a method for predicting the distribution of badger main setts based upon the distribution of sites for the location of main setts. Wytham woods are good badger habitat (Kruuk 1987) and this was reflected in the model classifying 73 % of the area as suitable for sett construction based on local factors and access to potential foraging areas. The abundance of potential foraging areas was reflected in the fact that incorporation of the proximity to foraging areas component did not decrease the area of habitat classified as suitable. The good performance of the sett site suitability model in Wytham gives some support to the representation of main sett spacing as a relatively simple hard core process. However the spacing of 'setts' generated by the model is more regular than that observed in the field (compare figures 4.5 and 4.6), suggesting that other factors may be operating in the field. Kruuk (1987) relates the distribution of main setts in Wytham to the distribution of favourable soils. Also two of the real setts are located in areas classified as unsuitable by the model (see figure 4.5).

Application of the sett site suitability model classified only 11.3 % of the Northumberland area as suitable at a local scale and this declined to between 3.2 % and 2.2 % when access to potential foraging areas was considered. The number of setts predicted by the space pre-emption component of the model was 4.6 times greater than the field data, when the lower foraging area requirement was used, and 3.3 times greater when the higher requirement was used. Although increasing the foraging habitat requirement made the predictions slightly closer to the survey data, it also resulted in an increased number of recorded setts falling in areas classed as unsuitable by the model (table 4.1). Thus, although simply increasing the foraging area requirement will improve the fit between predicted and observed numbers of setts this is unlikely to be a good representation of the mechanisms determining spatial positioning in the field.

The Wildlife Trust records used to assess model performance in the Northumberland study site were based on reports from the public rather than a systematic survey strategy and it

seems unlikely that they include all setts. Therefore, although the results suggest that the model overpredicted this should be treated with some caution.

At a finer scale, other aspects of the predictions of the sett site suitability model are not consistent with the field data. As mentioned above, six to eight of the recorded sett positions fall within areas classified as unsuitable by the model (see table 4.1). This could be a result of errors in positioning of the wildlife trust records, errors in the classification of the satellite data or of badgers being more adaptable in their positioning of setts than the rules used in the model. In addition two of the recorded sett positions were within 250m of each other, closer than the 900m used in the model. This could represent a missclassification of a subsidiary sett as a main sett in the records or could put into question the hard core mechanism used in the space pre-emption component of the model. These finer scale inconsistencies, setts in areas classed as unsuitable and closer together than allowed in the model, would be expected to lead the model to underpredict the number of setts. However, as outlined above, the model overpredicted the number of setts in the Northumberland area, thus suggesting inaccuracies in the representation of spacing mechanisms in the model.

A number of reasons could be put forward for the apparent overprediction of the sett site suitability model as applied to the Northumberland study area. These include: poor representation of local scale suitability for sett construction, poor representation of food availability and necessary access to foraging areas, poor representation of the space pre-emption process. Alternatively, the model may be a good representation of sett distribution at saturation, but the badger population in Northumberland may still be below saturation due to past persecution. The results of the most recent national badger survey (Wilson & Harris 1997), suggest a national increase in the badger population over the past 10 years which is thought to be a continued response to recent increases in protection from persecution. A sensitivity analysis of the model presented here could be conducted, but until more reliable survey data is available to develop and test models this is unlikely to produce precise predictions of applied use or generalisable results of theoretical interest.

4.4.1 Applying an associative model based upon ITE land classes

The land classification system of the Institute of Terrestrial Ecology (Bunce et al. 1983) is a system whereby 1km squares within the British Isles are classified as one of 32 land classes based on a multitude of factors including topography, climate, soils, land-use and native plant species. Cresswell et al. (1990) produced an estimate of the mean number of main setts per km^2 for each land class, based on the National badger survey of 2455 1km squares (around 40 per land class), completed in 1988. They used these figures to generate population density estimates at a national and regional level. As these estimates were obtained from samples taken across the whole country and thus represent the variability experienced within each land class, Cresswell et al. (1990) recommend that they shouldn't be applied at anything smaller than a regional scale. Applying them to smaller areas creates the risk that the areas may not represent the mean conditions for the relevant land classes and thus estimates will be biased. Despite this, these land class relationships are the only presently available method of predicting main sett densities across Britain (see chapter 2). Here I test the use of the relationships by applying them to the two relatively small study areas. Cresswell et al. (1990) also give the standard errors of the mean density estimates. These can be used to provide a measure of confidence in generated predictions.

The Northumberland study area was made up of land classes 22, 25, 27 and 28, for which the mean main sett densities per km^2, reported by Cresswell et al. (1990), were 0.009, 0.069, 0.098 and 0.087 respectively. These added up to an estimate of 13 main setts (+/- SE = 7 -19) for the 210 km^2 area. The Wytham study area was made up of land classes 1 and 2, for which the mean main sett density estimates were 0.482 and 0.460 per km^2. For the 4.8 km^2 area of Wytham, an estimate of 2.3 main setts (+/- SE = 2.1 - 2.6) was generated.

The land class model under predicted by a large margin when applied to Wytham and this highlights the danger of using this approach at such a fine scale. There is a large amount variation in habitat composition within each land class, the small sample of squares used in this analysis do not fully represent this variation. The 1km squares that make up Wytham must be of above average quality for badgers when compared to an 'average' square within land classes 1 and 2. In contrast application of the land class model to the Northumberland

study area generated predictions that were consistent with the number of setts recorded in the wildlife trust records. As the Northumberland study area was much larger than the Wytham one, the risk of bias in applying the land class model will have been reduced.

4.4.2 Prospects for models to predict the spatial distribution of badgers

The development of models to predict the spatial distribution of badgers is confounded by a number of factors. Badgers are highly adaptable, able to travel large distances and can incorporate large areas of apparently 'unsuitable' habitat within their ranges, as such it is hard to classify whether an area is likely to be occupied or not.

Problems are also created by the combination of the use of main setts as an index of badger density and the use of small sample areas (1km squares for the National badger surveys). Badgers do not merely use the sett site itself but have home ranges that can be between 20 and 300 hectares (Cheeseman et al. 1981, Kruuk and Parish 1982). This means that when sample areas are small, the abundance of setts within the sample area are likely to be highly dependant upon the nature of the landscape outside the sample area, and also upon the distribution of setts outside of the sample area. Collecting sett distribution and habitat data for small sample areas thus ignores this source of variation. This limits the utility of such data for developing and testing models of the spatial distribution of badgers. It may not be a coincidence that the study that demonstrates the greatest success at predicting badger distributions (Thornton 1988) used tetrads (2km x 2km) rather than 1km squares.

The associative models that have been developed to predict badger densities have generally performed poorly, even when large amounts of habitat data have been collected (see chapter 2). Despite the large amount of research that has been conducted on the badger, the understanding of processes determining densities at the landscape scale is patchy at best. This limits the development of process based models and those that have been developed to date are unable to predict population densities in real landscapes (see chapter 2).

The sett site suitability model described here is based largely on habitat requirements and behavioural rules derived from the literature (summarised in Kruuk 1987 and Neal and

Cheeseman 1996). It can be dangerously attractive to use habitat preferences exhibited in the field, as rules for habitat requirements in models such as this. For example, although the conventional wisdom is that main setts are preferentially located on well drained, sloping ground in deciduous woodland in proximity to pasture, in Northumberland I found a main sett in the middle of a conifer plantation, on flat ground next to a stream. The ability to apply such rules easily within a GIS increases this attractiveness, but does not necessarily increase the likelihood of generating useful outputs.

With the current state of knowledge of badger biology at the landscape scale, GIS and modelling approaches such as those described here could perhaps be more usefully directed at investigating the mechanisms determining badger spacing patterns in different areas. For these issues to be confronted there is a need for badger distribution and habitat data to be collected across relatively large contiguous areas rather than the 1km squares that tend to be used at present.

5. Chapter 5 : Predicting the outcome of a proposed reintroduction of the European beaver (*Castor fiber*) to Scotland : a comparison of two modelling approaches

5.1 Introduction

The European beaver (*Castor fiber*) became extinct in Scotland in the 16th Century (Kitchener and Conroy 1996). The principle cause of this extinction is thought to have been over hunting (Macdonald et al. 1995; Nolet and Rosell 1998). The decline was mirrored throughout Europe to the extent that at the beginning of this century there were only a few scattered populations. In seven European countries where the beaver was extinct, reintroductions have lead to the formation of large, apparently viable populations. In four others reintroductions have lead to large expansions in range. In Switzerland reintroduced populations had increased to around 350 animals by 1993 despite initially appearing not to expand (Macdonald et al. 1995). In the Netherlands a reintroduction program was started in 1988 and the population presently numbers around 70 animals (Nolet and Rossell 1998). Latterly there has been considerable interest in re-establishing the species in Scotland (Macdonald et al. 1995; SNH 1998).

Beaver live in small family colonies which usually contain a pair of breeding adults and related young of different age classes. They are long-lived for rodents, generally reaching 7 - 8 years (Macdonald et al. 1995) and have few predators in Europe. They have considerable reproductive potential and are capable of irruptive growth (Hartman, 1994) with introduced populations capable of expanding at up to 30% per year. Whilst there is evidence of success in the past reintroduction schemes in Europe, it is by no means certain that a release scheme for Scotland would be successful, where suitable beaver habitat is highly fragmented (Macdonald et al. 1997).

Current IUCN guidelines for reintroductions (IUCN, 1995) state that modelling should be used to assist in the assessment of project feasibility. Modelling approaches are being

increasingly applied to reintroductions both prior to the translocation of animals (e.g. de Jong et al. 1997; Howells and Edwards-Jones 1997; van Ewijk et al. 1997) and afterwards (e.g. Southgate and Possingham 1995; Bustamente 1996; Nolet and Baveco 1996; Novellie et al. 1996; Brook et al. 1997). With the exception of Nolet and Baveco (1996) all of these cited references have been based on the application of generic packages for population viability analysis (PVA).

There have been several attempts to investigate the potential viability of reintroduced beaver populations. Nolet and Baveco (1996) developed a simulation model to analyse the viability of a beaver population that has been established in the Netherlands by translocating animals from Germany. Their analysis concentrated on a single area of contiguous suitable habitat that they estimated could support a population of 190 beaver. They used data on survival and reproduction derived from the established source population in Germany and the translocated population in the Netherlands. The principal difference between the two populations was the lower natality rates in the translocated population. The model predicted a low probability of persistence when it was assumed that the low natality rates were a permanent result of poor habitat, and a high probability of persistence when it was assumed that natality rates would return to high levels for the offspring of the original founders. They also simulated the effect of establishing additional populations to create a 2 or 3 deme metapopulation, and showed how this could increase population viability. Macdonald et al. (1995) demonstrated how a generic PVA package could be applied to the beaver in Scotland. They simulated a single, randomly mixing population with a mean carrying capacity of 200 - 400 animals, with reintroductions of 10 - 100 animals, with and without supplementary releases. Macdonald et al. (1997) outlined how a more realistic, custom-built model linking beaver life history processes to habitat data could be used to predict the result of reintroductions to three selected sites in Scotland. This initial analysis (under a limited range of parameters) predicted that populations would persist, but that spread to new areas would be low.

The aim of this paper is to assess the outcome of a beaver reintroduction to Scotland based on currently available information. We include no consideration of the effect of inbreeding or the loss of heterozygosity. Ellegren et al. (1993) document very low

levels of genetic variability in the Swedish beaver population but no inbreeding effects have been observed (Nolet and Baveco 1996) and many of the beaver reintroductions to Europe have resulted in large populations despite initially small propagule sizes (Macdonald et al. 1995; Nolet and Rossell 1998). Nolet and Rossell (1998) suggest that the minimum viable population size that will allow the beaver to retain sufficient genetic variability to respond to future environmental change is c. 1880 individuals. This is based on a calculation of the actual population size that is equivalent to the effective population size of 500 suggested by Franklin (1980), a number originally estimated as the effective population size necessary to retain the amount of genetic variability measured for *Drosophila* bristle counts (Lande and Barrowclough 1987). The use of such 'magic numbers' has been questioned and 'no instance of extinction by genetic malfunction has been reported' (Caughley 1994). This and the success of small beaver reintroductions elsewhere in Europe suggests that genetic considerations will be secondary to demographic ones in their effect on initial population spread and establishment of a persistent population in Scotland.

We describe the development of a custom-built, stochastic simulation model for investigating the spread of beaver from potential release sites across mainland Scotland. Using a custom-built model allowed us to represent beaver family structure and to model dispersal explicitly, both of which would have been more difficult using a generic package. We use the model to predict the responses of beaver populations to different release protocols over a range of life history parameters. The results are compared with those derived from the application of a generic software package for analysing population viability (Vortex, Lacy 1993). The implications for schemes aimed at reintroducing beaver populations to Scotland are discussed.

5.2 Methods

Two modelling approaches were used to investigate the viability of introduced populations of beaver in Scotland. The first approach was based on a custom-built model that linked population dynamics and dispersal to a geographic information system (GIS) holding data on the spatial distribution of habitat suitable for occupation by beaver. The second approach was based on the application of Vortex (Lacy 1993), a generic software package for population viability analysis. The Vortex analyses were designed to complement the custom-built model and to highlight the dependence of

predictions on model structure. Both approaches were applied to a 40,000km^2 square study area delimited by National Grid coordinates 200000, 700000 to the SW and 400000, 900000 to the NE.

5.2.1 The custom-built GIS-population dynamics model

5.2.1.1 Model outline

The model had two main components. First, a GIS (GRASS, Westervelt et al. 1990) which stores environmental, habitat and animal population information. Second, an individual-based population dynamics module which simulates the life histories of individual beavers and their dispersal within the GIS-held landscape. The population dynamics module was written in the programming language C and integrated with the GIS component through a UNIX-shell environment. A flow diagram illustrating the links between the GIS and population dynamics modules is shown in Figure 5.1.

5.2.1.2 Creating the habitat template for the model

The land surface was partitioned into three; firstly, blocks of habitat which could be used by the beaver as home-ranges for foraging and breeding; secondly areas through which animals could move when dispersing, but which they could not exploit for home ranges, and finally areas which beaver were assumed not to enter. These classifications were based on The Land cover of Scotland 1988, a land cover map based on the interpretation of aerial photographs (MLURI 1993) and a river network derived from the 1:250000 Bartholomew Digital map for the UK.

The minimum territory size of a beaver family is approximately 3km of wooded river banks (Nolet and Baveco 1996). The land cover map was generalised to 200m resolution. Patches of habitat capable of supporting beaver were identified as those consisting of 15 or more contiguous woodland cells also containing a watercourse (15 * 200m = 3km). A total of 94 sites were identified as providing suitable breeding habitat for beaver by these criteria. The mean carrying capacity of each of these habitat patches (in numbers of beaver families) was estimated simply by dividing the number of cells in the patch by the estimated habitat requirement of a single family. To address the uncertainty in these estimates, in the model runs and sensitivity analysis the habitat requirement was varied about a mean of 3km of wooded banks (see below). These 94

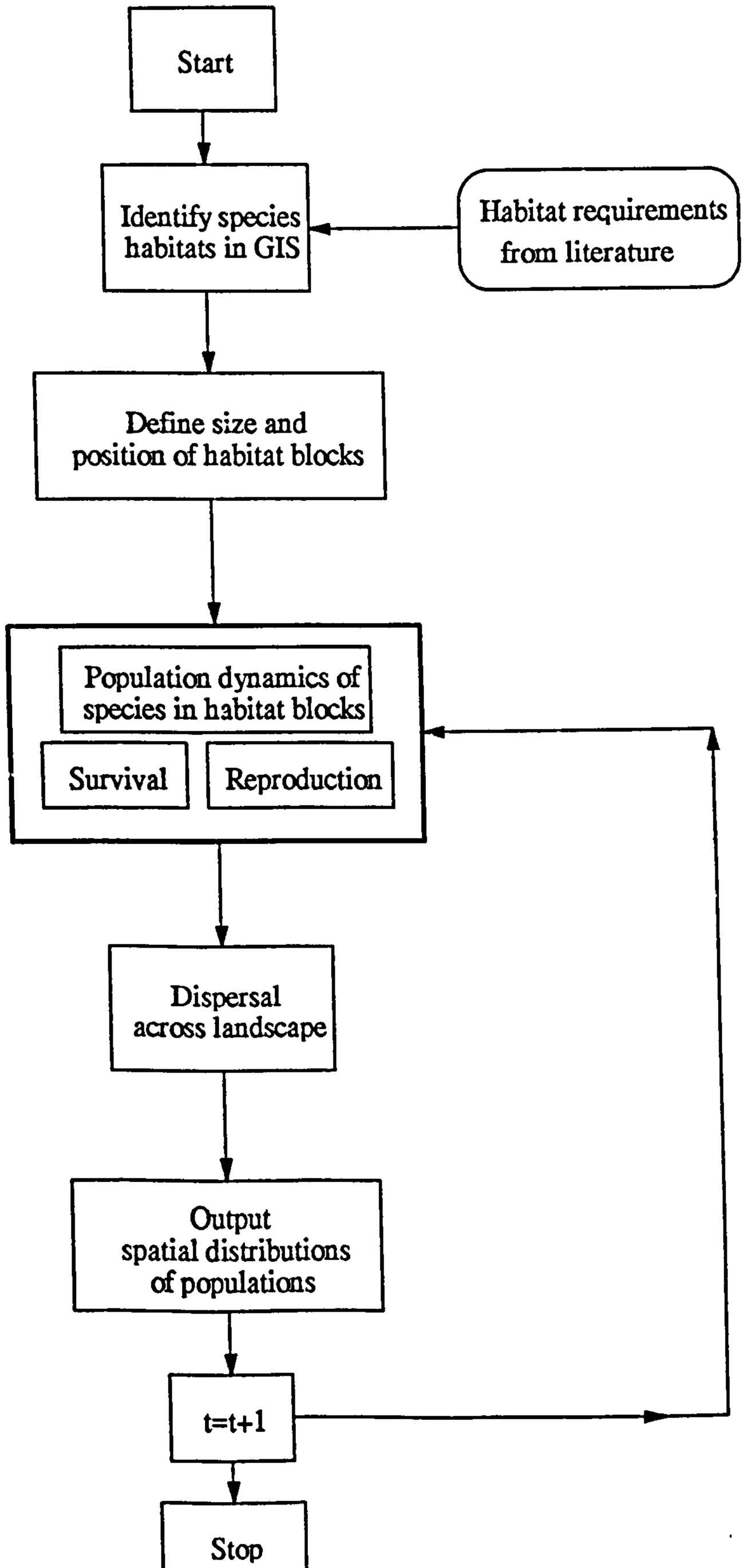


Figure 5.1. Outline of the custom-built model for beaver populations.

sites were used as potential release sites in the extended population viability model. The distribution of the 94 sites is shown in Figure 5.2a. A histogram showing the size distribution of habitat parcels in terms of the estimated numbers of beaver families they could support (under the mean habitat requirement) is shown in Figure 5.3a. Under these criteria more than 70% of the habitat blocks were predicted as able to support just one beaver family and fewer than 4 blocks were predicted as able to support more than 3 families.

Suitable dispersal habitat was classified at a 2km resolution. A 2km grid was overlayed onto the river network and all cells containing a watercourse were classed as suitable for dispersal. This is based on evidence that beaver disperse principally along rivers and that movement across watersheds is restricted (Hartman 1994; 1995).

5.2.1.3 Population dynamics and dispersal of beaver in the custom-built model

The model simulated separate blocks of habitat each of which could contain a number of beaver family groups. Family groups were divided into four classes : new young, juveniles (less than one year of age), sub-adults (less than 2 years of age) and adults (greater than 2 years of age). For each block of habitat, in each year, change in size of the population was modelled in terms of gains due to births and immigration, and losses due to deaths and emigration. Reproduction in the beaver was assumed to occur in one adult female in each family group. The number of pups produced in each litter in each family group was calculated by drawing deviates from a Poisson distribution with a mean number of animals per litter (Burgman et al. 1993). Mortality in adult beaver was assumed to occur after breeding. The likelihood of death for each individual was determined by sampling deviates from a uniform distribution in the range 0 to 1, with mortality occurring if the deviate was in the range of the average mortality for the relevant life stage.

The dispersal process was modelled explicitly. In each patch in each year, sub-adults exceeding carrying capacity following the imposition of mortality were put into a dispersal pool. Dispersal mortality was imposed probabilistically in the same way as the annual mortalities. Each individual that survived the imposition of dispersal mortality was then simulated as moving through suitable dispersal habitats. Individuals were

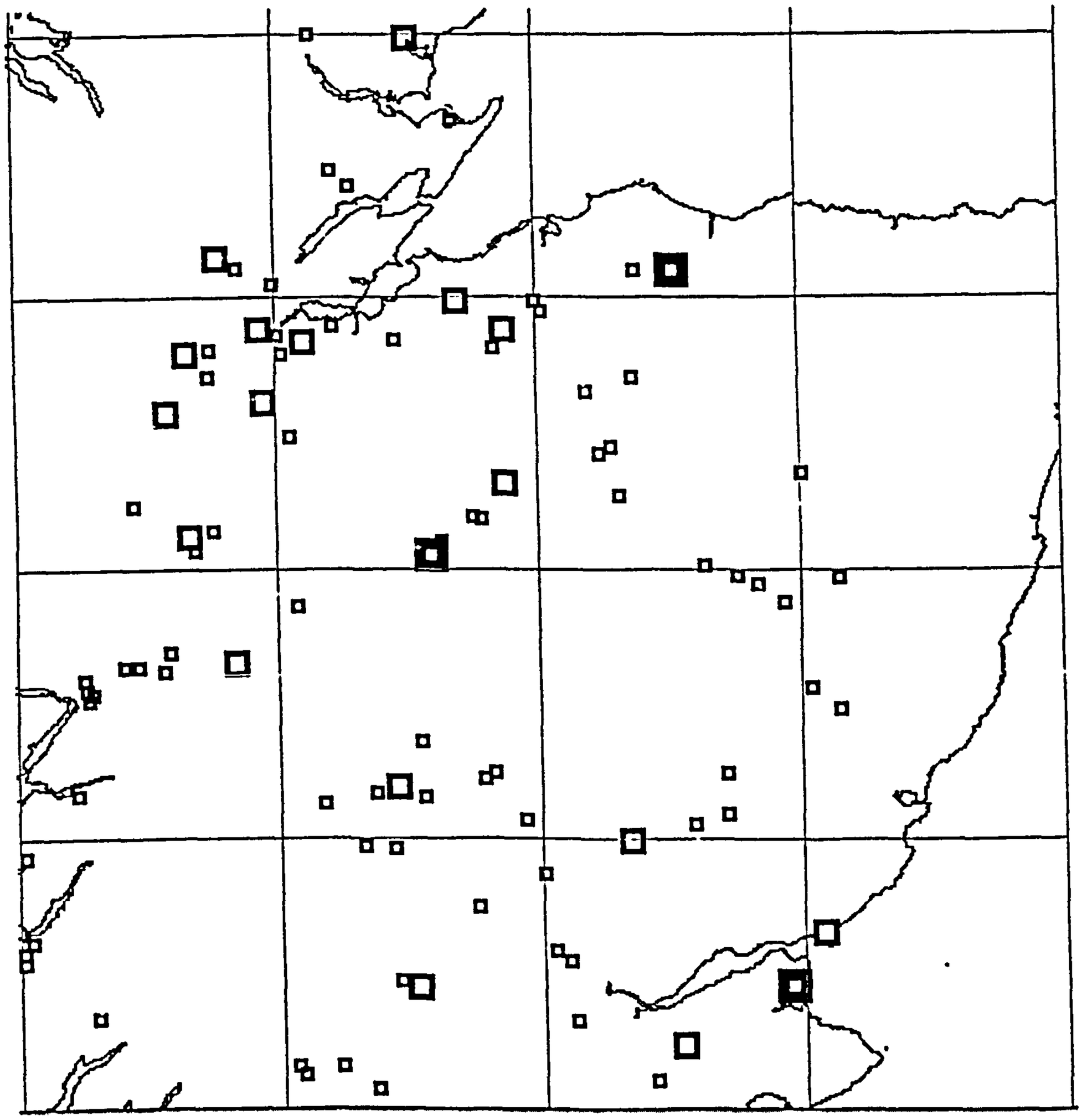


Figure 5.2a. Distribution of the 94 habitat patches predicted as being able to support at least one beaver family in the 40,000km^2 study area in Scotland. Small squares = 1 family, medium squares = 2-3 families, large squares = 7-10 families. Grid squares = 50km. National Grid boundaries : N = 700,000 , S = 200,000, E = 400,000, W = 200,000.

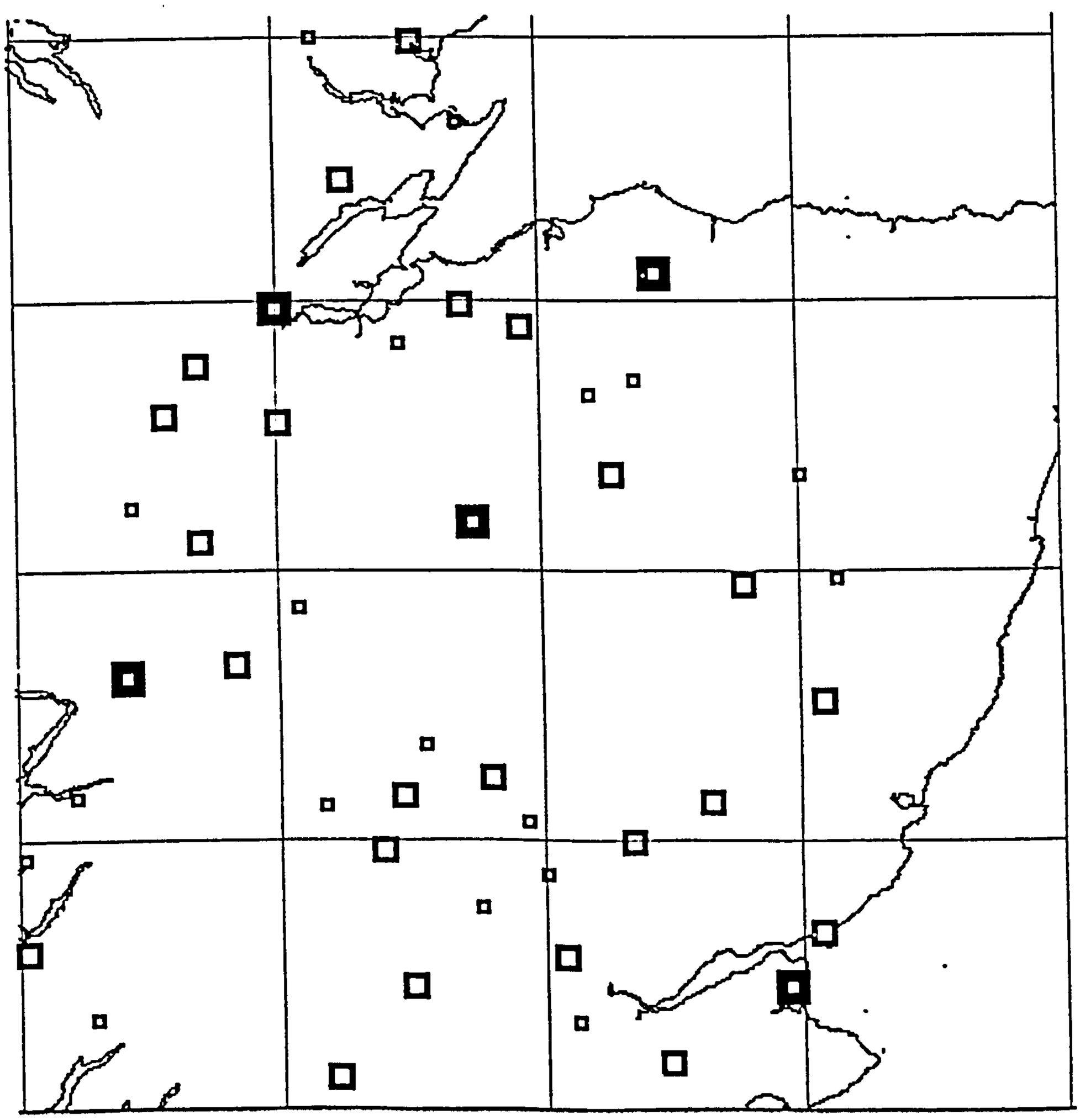
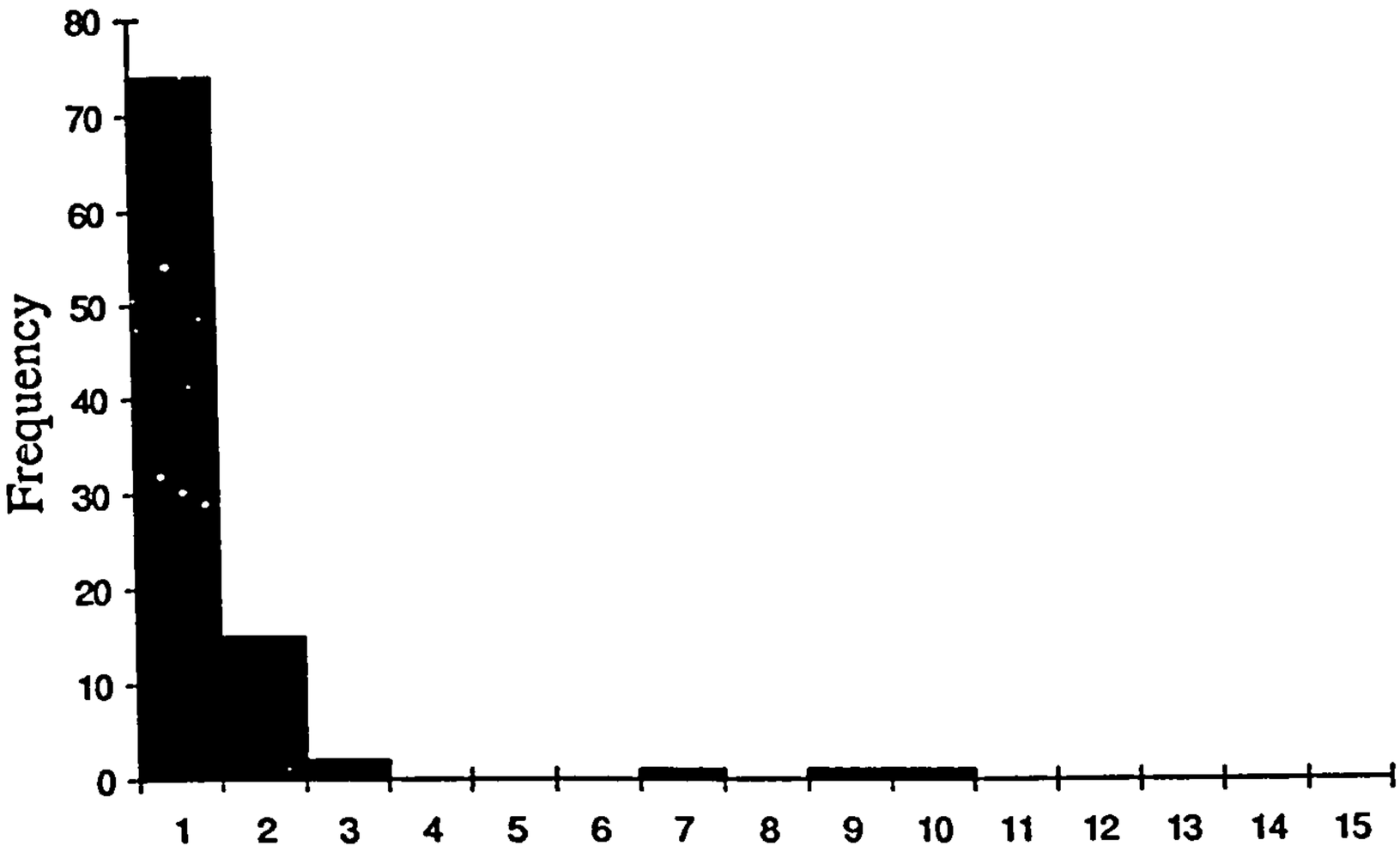


Figure 5.2b. Distribution of the centroids of the 46 amalgamated habitat patches used in the Vortex analyses for the 40,000km^2 study area in Scotland..(Habitat patches within 9km amalgamated and their predicted carrying capacities summed). Small squares = 1 family, medium squares = 2-5 families, large squares = 7-15 families. Grid squares = 50km. National Grid boundaries : N = 700,000 , S = 200,000, E = 400,000, W = 200,000.

a)



b)

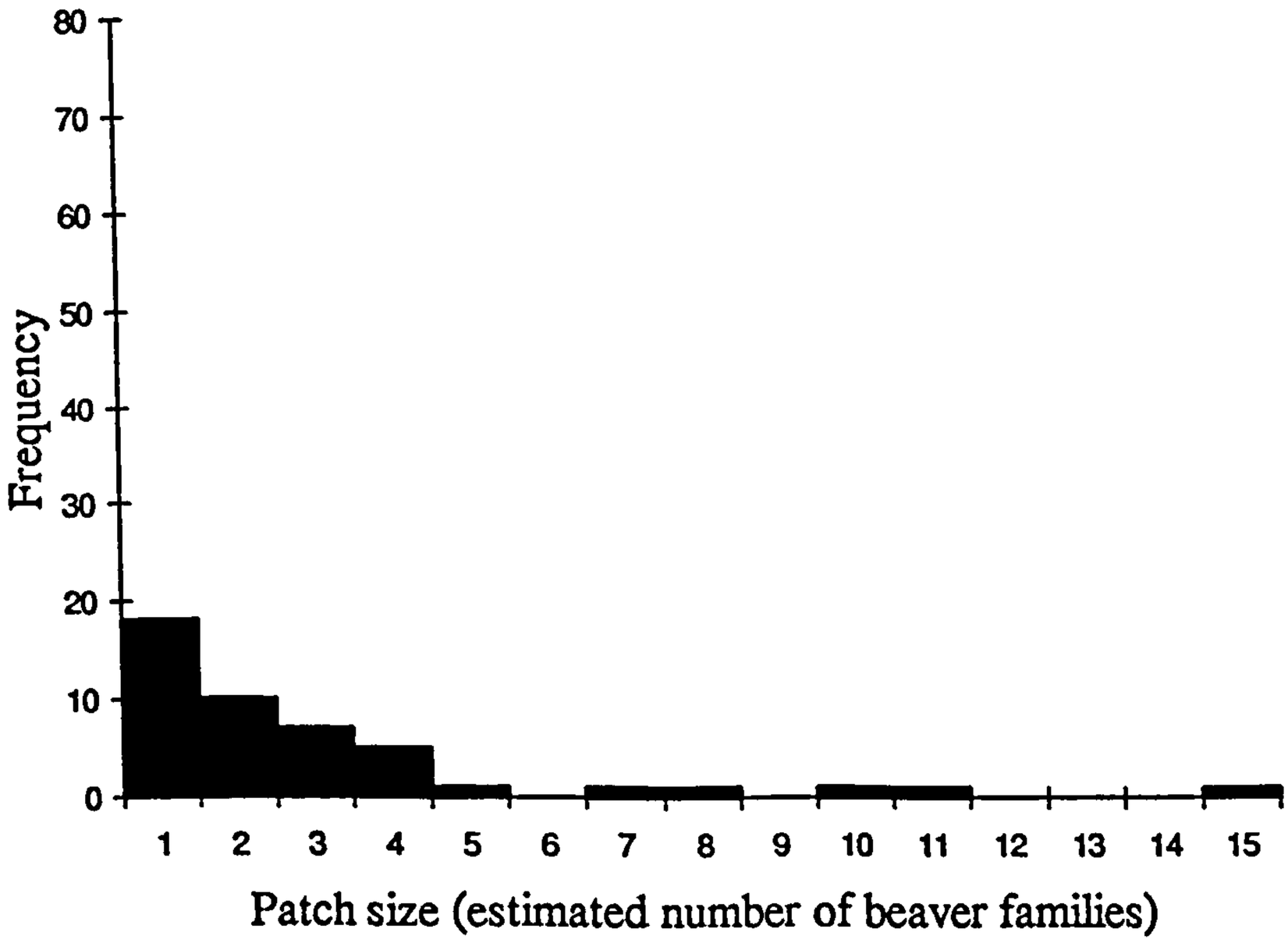


Figure 5.3 Size distribution of habitat patches used in a) the custom-built model and b) the Vortex subdivided population runs (the latter resulting from amalgamation of patches closer than 9km apart).

simulated as moving one grid cell at a time through the 2km dispersal grid created from the habitat map. Where there was a choice of more than one suitable neighbouring cell, the cell that was furthest from the previously occupied cell was chosen. Where there was more than one cell equidistant from the previously occupied cell, the choice was made randomly. These simple rules stopped an individual from backtracking on itself and created dispersal paths with a stronger directional component than a simple random walk. Dispersal movement was stopped if an individual reached a grid cell containing suitable breeding habitat below carrying capacity or if a dispersal distance threshold was exceeded. In the former case the individual was added to the population of the patch in the latter case the individual was assumed to die and was removed from the simulation. All simulations were run for 30 years.

5.2.1.4 Range of model parameters

A Latin Hypercube Sampling (LHS) strategy following the methods of Vose (1996) was used to select input parameters for the model from estimated ranges. In this methodology, sample values of the input parameters are selected using a randomisation procedure subject to constraints on the extent of correlation of input variables that are imposed by the modeller. Nine parameters were considered, these are shown in Table 5.1. In all cases there were insufficient data available to model the actual statistical distribution of each parameter. Furthermore there were no data available to assess the extent to which each of the life history parameters were correlated with the others. A uniform distribution was assumed for each variable with upper and lower limits around the average derived from the literature. Constraints on the extent of correlation allowed between each variable were set at a low level of 0.5. The LHS methodology was used to create 50 different parameter combinations. For each release scenario, described in the following section, the model was run 50 times, once for each parameter combination.

The variation in family habitat requirement (2 - 3.6 km) effectively altered the distribution of patch carrying capacities. The change in family habitat requirement from 3km to 3.6km altered the number of patches able to support at least one family from 94 to 66, and the number able to support more than one family from 20 to 11. At the family habitat requirement of 2km the number of patches able to support at

least one beaver family remained the same as at 3km as the minimum habitat requirement of 3km in the initial habitat analysis was not altered. The number of patches able to support more than one family increased to 39.

Parameter	Custom-built model	Vortex analyses
Maximum dispersal distance (km)	4 - 80	50
Family habitat requirement (km)	2.0 - 3.6	3.0
Mean Litter Size	1 - 3	3
Proportion of females breeding	0.5 - 0.7	0.31, 0.63
Adult mortality	0.063 - 0.077	0.07
Sub-adult mortality	0.063 - 0.077	0.07
Yearling mortality	0.44 - 0.55	0.5
Juvenile mortality	0.29 - 0.36	0.33
Dispersal mortality	0.40 - 0.80	0.6

Table 5.1. Values of life history and habitat parameters used in the two modelling approaches to predict beaver persistence in Scotland (based on Nolet and Baveco 1996, see text). For the custom-built model parameter values in 50 replicates were selected from the range shown, for the vortex analyses 100 replicates were conducted with constant parameter values.

The proportion of females breeding each year was varied between 50% and 70% (these values approximate field data for an established population in Germany (63%) and are higher than estimates obtained from a translocated population in the Netherlands (31%) (Nolet and Baveco 1996). The low values in the Dutch population have been suggested as being either a result of poor habitat, pollution or a temporary response to translocation (Nolet and Baveco 1996). Dispersal mortality rates were varied between 40% and 80%. We were unable to find any published dispersal mortality estimates so these figures were chosen to represent a plausible range.

5.2.1.5 Assessing the affect of release scenario

The effects of initial release size and the number of release sites on the viability of populations of beaver were investigated by running the population viability model with a range of reintroduction sites and size of population released at each site. Sites were selected at random from the 94 predicted to be available in the 40,000km^2 of the study area. Fifty release scenarios were generated, each consisting of a randomly selected number of release sites between 1 and 10, and a randomly selected release population size (for each site) between 2 and 20. For each release scenario the model was run 50 times (2500 model runs) using the parameter combinations generated by the LHS methodology. The 50 parameter combinations were considered to be representative of the range that would be likely to occur in beaver populations in the field and the number of times the population went extinct was taken as a measure of population viability. To predict the result of an initial release followed by supplementation, a further 2500 model runs were conducted. These were the same as the single release scenario runs except that the initial release was repeated over the first five years.

The number of extinctions in each series of 50 parameter combinations was used as a dependant variable in separate GLMs for the single release and multiple release scenarios. The number of release sites and population release size were used as the independent variables in a logistic regression with a binomial error structure. This is similar to the method of sensitivity analysis for population viability models suggested by McCarthy et al. (1995). The GLM analyses were conducted in GLIM.

To determine whether releases targeted at the largest habitat patches were predicted to behave much differently from the random patch choice scenarios three additional sets of 50 model runs were conducted. In each of these three sets of runs 20 animals were introduced to one of the three largest patches identified in the habitat analysis.

5.2.1.6 Sensitivity Analysis

The sensitivity of the population dynamics model to input parameters was investigated by taking three of the single release scenarios and, within each, relating the total size and number of populations after 30 years, to input parameter values. A low, medium and high release scenario were chosen for the sensitivity analysis (Low release, 7

animals released in 1 patch; medium release, 7 animals released in 3 patches; high release, 15 animals released in 8 patches). Total population size and number of populations after 30 years were used as the dependant variables in a GLMs with a poisson error structure.

5.2.2 Application of a generic software package to analyse population viability (Vortex)

Vortex models the births and deaths of individuals as sequential events governed by separate probabilities (Lacy 1993). In this respect it is very similar to the custom-built model described above. In Vortex there is the option either to model a population as a single entity or as a collection of sub-populations. In the single population option, mixing is random such that any male can mate with any female. In the multiple sub-population option, animals can breed only within the sub-population, movement of animals between populations is determined by defined dispersal rates. Whereas in the custom-built model the movement of animals through unsuitable breeding habitat is modelled explicitly, in Vortex it is represented by pre-defined probability values.

Previous use of Vortex to analyse the viability of the beaver in Scotland considered all animals as part of a single randomly mixing population (Macdonald et al. 1995). The spatial structuring of populations is an important component of their viability, particularly in fragmented landscapes (e.g. Gilpin and Soule 1986; Lindenmayer and Lacy 1995a,b,c). Here we perform two Vortex analyses to outline how different representations of the spatial population structure influence viability predictions. In the first beaver were represented as a single population, the carrying capacity determined by summing the carrying capacities of all suitable habitat blocks in the 40,000 km^2 study area. The second considered a subdivided population consisting of sub populations with their own carrying capacities, linked by distance dependant dispersal. As a generic software package there are certain limitations in the ability of Vortex to represent the social system of the beaver. Within these constraints the simulations presented here are tailored as closely as possible to the beaver and potentially important limitations are discussed.

Life history parameters were set to the mean values used in the custom-built model (Table 5.1). Two natality scenarios were modelled, in the high natality runs the proportion of females breeding was set to 63.4%, based on an established German population, and within the values of 50-70% used in the custom-built model. In the low natality runs the proportion of breeding females was set to 31% based on a translocated Dutch population (Nolet and Baveco 1996). Environmental variation was incorporated as the standard deviation in mortality rates and the standard deviation in the proportion of pairs breeding (Nolet and Baveco 1996). Environmental variation in mortality and natality rates were set to be correlated. In the sub-divided population model correlation in EV between populations was arbitrarily set to 0.5. Inbreeding depression was not included and density dependence was not modelled except that populations were truncated if carrying capacity was reached. Introduced animals were assumed to be aged 7 (the average adult age of the German source population for the Dutch re-introduction was 7.5 (Heidecke 1984 in Nolet and Baveco 1996).

5.2.2.1 Representing beaver social structure in Vortex

It was not possible to represent explicitly the family structure of beaver (an adult bonded pair, kits, yearlings and sub adults) within Vortex. Patch carrying capacities (in number of beaver families supportable at the mean habitat requirement of 3km) were taken from the habitat analysis conducted for the custom-built model. The number of family groups was then multiplied by 5 (mean family group size) to obtain a carrying capacity estimate. This has the disadvantage that no constraints are placed upon the composition of family groups. This is likely to cause more errors in the sub-divided population runs and particularly in the small patches where by chance you could end up, for example, with families composed entirely of one sex or entirely of sub adults.

5.2.2.2 Spatial structure in the two series of Vortex runs

Following this methodology it was predicted that the 94 habitat blocks could support 136 family groups, giving an estimated carrying capacity of 680 animals. For the single population runs the carrying capacity was set at 680. Runs were conducted with starting populations of 20 animals under high and low natality scenarios.

The current version of Vortex (version 8.02 was used for this analysis) can handle a maximum of 50 sub-populations. As the habitat analysis identified 94 separate habitat

patches that were potentially capable of supporting one or more beaver families not all could be modelled as separate populations. To get around this problem the distance between all patches was calculated so that patches close to each other could be amalgamated for input into Vortex. It was found that if patches closer together than 9km were amalgamated the number of new patches was 46. The carrying capacities (in number of beaver families supportable) for the amalgamated patches were calculated by adding the carrying capacities of each of the constituent patches (thus this does not allow for a beaver family to live between more than one patch). Each amalgamated patch was assigned a centroid co-ordinate that was midway between the centroids of all of the constituent patches. Figure 5.2b shows the spatial location of amalgamated patch centroids and figure 5.3b shows the size distribution of the amalgamated patches. Subsequent use of the word patch with regard to the Vortex analyses, refers to these amalgamated patches.

Only sub-adults (2 year olds) were allowed to disperse (the same as in the custom-built model). Dispersal was modelled as occurring only after sub-populations reached carrying capacity (by setting the dispersal threshold ratio of population density divided by carrying capacity to 1). Vortex uses a dispersal matrix to define dispersal between patches. The values within this matrix define the probability of dispersal from each patch to every other patch. The dispersal matrix was derived by first calculating the distance between each of the patch centroids. Then, for each patch the identity and number of patches that were within the defined maximum dispersal distance were calculated. A maximum dispersal distance of 50km was used in this analysis. In the final step a dispersal probability was calculated for each patch as the reciprocal of the number of patches within dispersal range, and this value was used as the probability of dispersal from the patch to each other reachable patch. Thus animals were assumed to have an equal probability of dispersing to all reachable patches, providing they were below carrying capacity. Within Vortex a patch within the dispersal distance is chosen randomly and if this is already at carrying capacity another is chosen, this process is repeated up to ten times and if a patch below carrying capacity is still not found the animal dies. This combination of the dispersal threshold and the dispersal probabilities used mean that once a population reaches carrying capacity, all 'excess' sub-adults disperse to one of the patches within the maximum dispersal distance (or die if they do

not locate one that is below carrying capacity). Dispersal mortality was set at 60%, the mean of the range used in the custom-built model.

Runs were conducted under high and low natality scenarios for 20 animals introduced between the 4 largest patches (i.e. 5 animals in each patch). Additional runs were conducted under the high natality scenario for 20 animals introduced to the largest patch, and for 20 animals introduced between 4 of the smallest patches. All Vortex runs were conducted for 100 years, outputs at 10 yearly intervals allowed comparison with the custom-built model 30 year predictions.

5.3 Results

5.3.1 Results of the custom-built GIS-population dynamics model

5.3.1.1 The affects of release scenario on predicted population persistence

The results of GLMs relating the probability of extinction to variation in the number of populations released and the size of release population for single and repeat release scenarios are shown in Table 5.2. All models were significant, with the size of population released and the number of animals in each release population explaining 38% and 32% of the total deviance in predicted extinction rate, for the single and repeat release scenarios respectively. In both scenarios the number of populations released was more important in explaining the deviance in extinction rates than was the size of population released.

Variable	Single release estimate (se)	Repeated release estimate (se)
Number of release sites	- 0.290 (0.017)	- 0.351 (0.020)
Size of release populations	- 0.116 (0.009)	- 0.100 (0.009)
Deviance explained by both parameters (%)	38	32
Deviance explained by number of sites alone (%)	23	20
Deviance explained by release pop. size alone (%)	13	3
Null deviance	1358	1182

Table 5.2. Parameter estimates and standard errors for GLMs relating proportion of custom-built model runs ending in extinction after 30 years to the number of release sites and size of release populations. Fifty runs with different model parameter values were conducted for each of fifty release scenarios for a single release and repeated release over five years. A Binomial error model was used.

5.3.1.2 Predicting population persistence, change in patch occupation and population size

The GLMs relating extinction probability to the size and number of reintroduced populations were used to evaluate the likelihood of success of reintroduction schemes. Dr. M. Cooper (SNH, *pers. comm.*) suggested that a population of 20 animals was the current practical limit to the number of animals that could be collected in any one year for use in a release scheme. Predicted likelihoods of population persistence in the 40000km^2 of the study area for schemes based on releasing a total of 20 animals are shown in Table 5.3. Also shown are estimates for release populations of 50 and 100 animals. The highest persistence probabilities were predicted for scenarios with the highest number of populations rather than the greatest number of animals. For all permutations of 20 total animals released in randomly chosen patches the likelihood of persistence to 30 years was predicted to be in the range 0.24 - 0.38. The probability of persistence was predicted to be higher in the repeat release scenario in the range 0.36 -

0.62. Even a repeated release of 10 animals to each of 10 patches (500 animals in total) resulted in a predicted probability of persistence of less than 1 (0.91). In contrast, all three sets of runs in which 20 animals were introduced to one of the three largest patches resulted in a predicted persistence probability of 1.

		Predicted Probability of Persistence	
Number of populations	Size of population	Single Release	Repeated releases over 5 years
2	10	0.24	0.36
4	5	0.24	0.41
5	4	0.28	0.47
7	3	0.38	0.62
10	5	0.65	0.85
5	10	0.43	0.62
10	10	0.77	0.91

Table 5.3. Predicted probabilities of population persistence to 30 years generated by the GLMs derived from the custom-built population dynamics and dispersal model. Different sized populations of beaver released at different numbers of randomly chosen sites in Scotland.

Of all the runs in which the number of animals and patches were chosen randomly, only a very small percentage resulted in an increase in the number of patches occupied after 30 years (2.4% of the single release runs and 3.8% of the multiple release runs). For the runs in which 20 animals were introduced to one of the three largest patches the percentage of runs that resulted in an increase in the number of patches occupied was higher, but still relatively low at 12.7%. For each of the three scenarios the mean increase in patch occupation, for those runs that did increase, was less than 3 patches. Thus, for all of the custom-built model runs there was little increase in patch occupation. For each of the three sets of runs (single release, multiple release and release to the large patches) the mean total population of beavers after 30 years was less than 20.

5.3.1.3 Sensitivity Analysis

The sensitivity of predicted beaver population size and number of populations to variations in input parameters are shown in Table 5.4. This shows the three release scenarios for which model sensitivity was assessed. A greater amount of the deviance in model predictions is explained under the high release scenario (61 - 70% as compared to 38 - 44%). Of the parameters that were significantly related to model outputs all acted in the direction that would be expected, habitat requirements and mortality parameters had a negative effect on outputs, fecundity and the proportion of females breeding had a positive effect. Habitat requirement and fecundity had the greatest affect on the two model outputs across all three release scenarios. In the high release scenario these two parameters alone were significantly related to outputs, additional parameters, including the proportion of females breeding and mortality values, were significant in certain of the other scenarios.

	Low release		Medium release		High release	
Parameter	pop. size	no. pops.	pop. size	no. pops.	pop. size	no. pops.
Dispersal distance	0.5	0.1	1.0	1.0	1.0	0.1
Family habitat requirement	5.0 ***	2.0 *	6.0 ***	2.0 *	9.2 ***	2.8 **
Mean fecundity	5.2 ***	2.9 **	8.6 ***	4.2 ***	7.4 ***	1.8 *
Females breeding	0.4	0.0	2.7 *	1.3	1.0	0.2
Adult mortality	4.4 ***	2.2 *	2.5 *	1.2	0.8	0.1
Yearling mortality	0.8	0.6	1.6	0.9	0.1	0.1
Sub-adult mortality	2.1 *	1.1	0.9	0.2	0.1	0.1
Juvenile mortality	0.6	0.4	0.3	0.2	0.6	0.4
Dispersal mortality	1.8 *	0.9	1.4	0.9	0.8	0.1
Deviance explained (%)	**38**	**40**	**44**	**40**	**77**	**61**
Residual deviance	152	35	268	62	49	9
Null deviance	247	58	478	104	216	23

* p<0.05, ** p<0.01, *** p<0.005

Table 5.4. Approximate t values (one-sided test) for GLMs relating the total size (pop. size) and number of populations (no. pops.) after 30 years to parameters in the custom-built model. Fifty runs with different model parameter values were conducted for each of three single release scenarios. (Low release, 7 animals released in 1 patch; medium release, 7 animals released in 3 patches; high release, 15 animals released in 8 patches). A poisson error model was used.

5.3.2 Results of Vortex analyses

When the whole area was represented as a single randomly mixing population, mean population size increased under both natality scenarios (Fig. 5.4a). Population sizes increased very rapidly under the high natality scenario, and reached carrying capacity within 50 years. Probability of population persistence over 100 years was 1 when natality was high and 0.77 when natality was low (Fig. 5.4b).

When the whole area was represented as a sub-divided population the predictions were generally less optimistic. Figure 5.4a shows that when 20 animals were introduced to 4 large patches the population increased slowly under a low natality scenario and rapidly under the high natality scenario, although in both cases these increases were slower than when considering a single population of equivalent size. Persistence remained at 1 for the high natality runs, but declined to 0.79 and 0.45 at 30 and 100 years respectively for the low natality runs (Fig. 5.4b).

Figure 5.5 compares the results of three different release scenarios, each of 20 animals, modelling as a subdivided population using high natality parameters. Rate of population increase was highest when five animals were introduced to each of four large patches (reaching around 270 animals by year 30 and 440 by year 100) and lowest when five animals were introduced to each of four small patches (not reaching 50 animals by year 100) (Fig. 5.5a). Population persistence remained at 1 under both large patch scenarios but declined to 0.18 and 0.06 by years 30 and 100 respectively, under the small patch scenario (Fig. 5.5b).

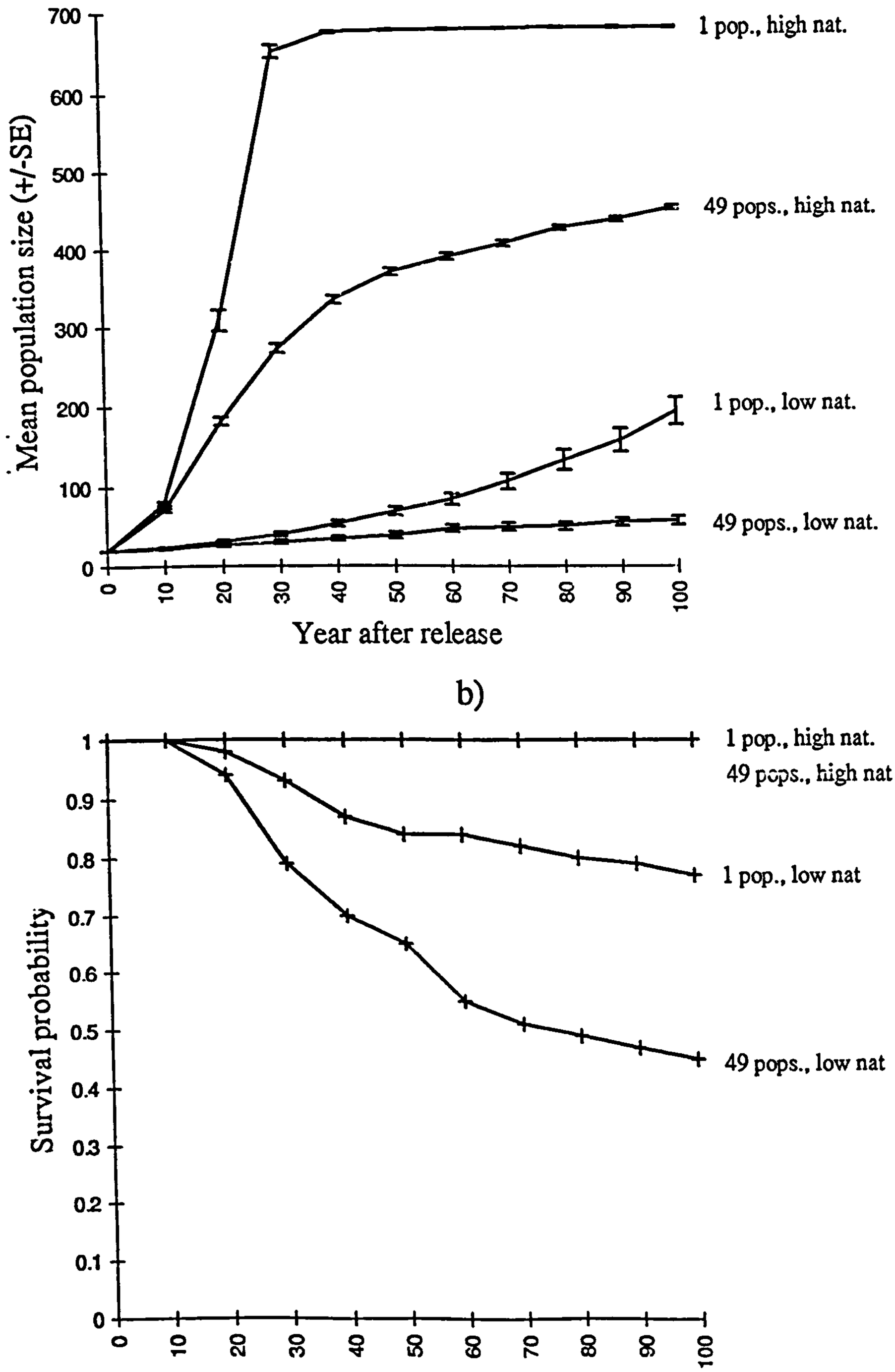


Figure 5.4. Predictions of population size **(a)** and survival probability **(b)** from Vortex runs simulating Beaver re-introduction to Scotland. 1 pop. = population represented as a single randomly mixing population with a carrying capacity of 680. 49 pops. = population represented as 49 sub-populations, carrying capacities sum to 680, dispersal between patches is based on their position in the real landscape.

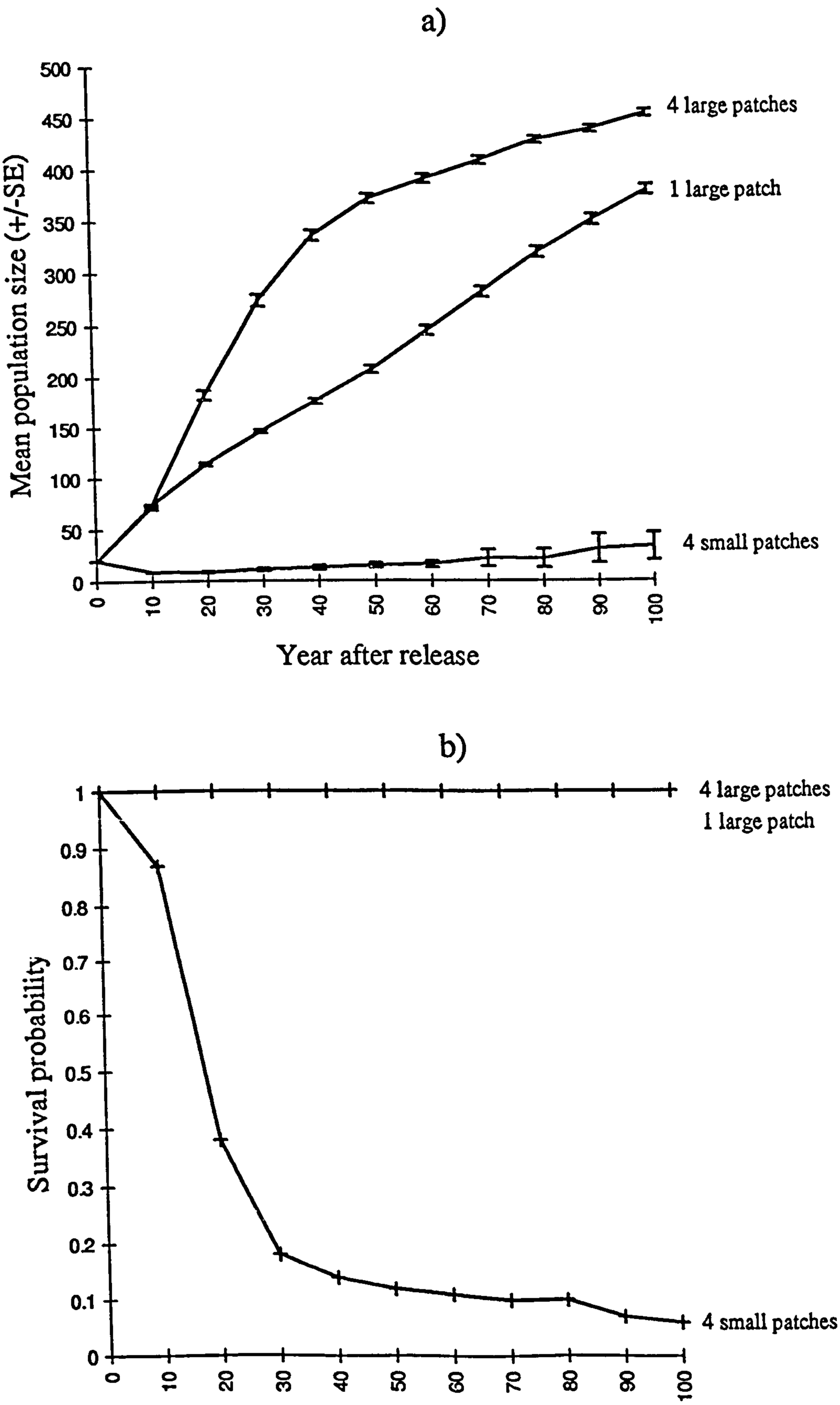


Figure 5.5. Predictions of population size (a) and survival probability (b) from Vortex runs simulating Beaver re-introduction to Scotland. Comparing releases of 20 animals to either 1 large patch, 4 large patches or 4 small patches under a high natality scenario.

5.3.3 Comparing the predictions of the custom-built and Vortex model runs

Table 5.5 shows predicted population size and persistence from the different model runs using high natality parameters. The one thing that is noticeable about the results of the different scenarios and approaches is the diversity in their predictions of population size and persistence. It is possible to split the predictions of the different modelling approaches and scenarios into 4 categories:

a) Prediction of high persistence and large population increase : All of the Vortex, high natality runs, with the exception of those simulating re-introduction to the small patches.

b) Prediction of high persistence and low or negative population change : The custom-built model runs simulating re-introduction to the large patches.

c) Prediction of medium persistence and low or negative population change : Vortex, low natality runs. Custom-built model runs simulating large, repeated releases to multiple randomly chosen patches.

d) Prediction of low persistence and population decline : Custom-built model runs simulating single releases to randomly chosen patches (and those simulating small repeated releases). Vortex, high natality runs simulating re-introduction to small patches.

Model scenario (no. of runs)	Mean no. of animals released	Mean popn. size	Mean change in popn. size	Probability of popn. persistence
Custom-built model Single release of 2-20 animals in 1-10 patches (n=2500)	48	5	- 43	0.43
Custom-built model Repeated releases over 5 years of 2-20 animals in 1-10 patches (n=2500)	297	12	- 285	0.69
Custom-built model Single release of 20 animals in one of the 3 largest patches (n=150)	20	18	- 2	1
Vortex, subdivided popn. Single release of 5 animals in each of 4 small patches (n=100)	20	2	- 18	0.18
Vortex, subdivided popn. Single release of 20 animals in the largest amalgamated patch (n=100)	20	146	126	1
Vortex, single popn.. Single release of 20 animals (n=100)	20	654	634	1

Table 5.5. Comparing predicted population size and persistence after 30 years in different model runs of Beaver re-introduction to Scotland (All with high natality values based on an established German population rather than a translocated Dutch population, Nolet & Baveco, 1996).

5.4 Discussion

The results presented here are initially disconcerting in that the different models produced radically different predictions for similar management scenarios. The difference between the application of Vortex and the custom-built model was illustrated most clearly by the runs that simulated a single release of 20 animals to one of the largest patches; the Vortex runs predicted a mean population of 146 animals after 30 years, whereas the custom-built model predicted a mean population size of just 18 animals. Nevertheless models in wildlife management (as in ecology in general), should be used as problem solving tools rather than taken simply as representations of the truth

(Starfield 1997). A careful analysis of the dependence of model results on model structure and mechanisms can explain the differences observed and advance our understanding of the factors most likely to influence the outcome of a beaver reintroduction to Scotland.

The predominantly negative effect of population subdivision in the Vortex runs is consistent with the conventional wisdom of conservation biology (e.g. Gilpin and Soule 1986) and with previous analyses (Lindenmayer and Lacy 1995a,b,c). In this analysis the difference is most likely to be due to the imposition of an additional source of mortality, dispersal mortality, in the subdivided population runs. Effects of demographic stochasticity, particularly the potential for all the occupants of small patches to be of one sex thus preventing breeding, may also have contributed. This demonstrates the obvious fallacy of representing the beaver population in Scotland as a single panmictic population and how this could lead to an overestimation of the likely success of a reintroduction.

The difference between the predictions of the low and high natality Vortex runs (based on data from an established beaver population in Germany and a translocated population in the Netherlands respectively) is consistent with the predictions made by Nolet and Baveco (1996). Their model predicted a 20% probability of persistence over 100 years under a low natality scenario and a 100% probability of persistence under a high natality scenario. In both cases this is a result of population size remaining lower under the low natality scenario such that the population is more vulnerable to stochastic extinction. The custom-built model runs used predominantly high natality parameters and still predicted very low population spread. Therefore it would appear that for a beaver re-introduction to Scotland to have a reasonable chance of success one of the criteria that will have to be satisfied is for natality rates to exceed the low levels recorded by Nolet and Baveco (1996).

The difference in predicted persistence between introductions to small and large patches was consistent across both modelling approaches. Releases to large patches generally resulted in high persistence probabilities, releases to small patches (and as the majority of patches are small these include most of the custom-built model runs in which release

patches were chosen randomly) resulted in low persistence probabilities. When animals are introduced to small patches, the population can only expand through dispersal to other patches. Dispersal mortality will slow the rate of population growth and thus increase the risk of extinction. In contrast introducing animals to larger patches allows the population to reach a size less vulnerable to extinction without animals having to disperse to new patches. This larger, less vulnerable population can then act as a source of colonists for other patches. This predicts, not surprisingly, that beaver would have a higher probability of persistence and spread in Scotland if releases were targeted at the larger potential release sites.

The poor persistence of most of the custom-built runs was a result of animals being introduced to small patches. The custom-built model runs targeted at the large patches generated predictions of higher persistence but populations were still not predicted to expand in the same way as the equivalent Vortex runs. This difference between Vortex predictions and those made by the custom-built model could be a result of a number of differences between their structures but is most likely a result of the representations of dispersal movements used. In the custom-built model the dispersal process was represented explicitly. Individual animals were simulated as moving through areas suitable for dispersal until either an area suitable for occupation was found, in which case the animal settled there, or the maximum dispersal distance was exceeded, in which case the animal died. The movement algorithm allowed animals to move through 2km squares containing rivers but assumed the animals had no knowledge of the location of patches suitable for occupation. In contrast in the Vortex runs the representation of the dispersal route was not explicit. Instead, individuals had an equal probability of dispersing to any available patches within the pre-defined straight line dispersal distance. The principal difference between these representations of dispersal was that in the custom-built model, individual dispersers might not find a patch even if there was one within the dispersal distance. Re-run of the 50 single release scenarios showed a 9 - 100% (mean 41%) failure of dispersers to locate patches, on top of the dispersal mortality modelled. This additional source of mortality will have restricted the number of animals that reached new patches. This appears to have reduced the probability of a breeding pair from colonising new patches to such an extent that the simulated reintroductions seldom resulted in the establishment of populations beyond

release sites. The representations of dispersal movement in both the custom-built and Vortex runs have little more to support them than a 'standard of plausibility' (Lima and Zollner 1996). Whether or not the beaver spreads across Scotland will depend on the dispersal behaviour of the species in the Scottish landscape and the extent to which it resembles either of these representations.

The other differences between the structures of the custom-built model and the Vortex runs do not present such a convincing explanation for the differences in predictions. Vortex is unable to represent beaver social structure as realistically as the custom-built model. The Vortex runs might be expected to be overly optimistic as they potentially allow more than one female within a family group to breed. However the Vortex runs are also potentially overly pessimistic as the carrying capacity of small patches could be reached with all males or all females. This would stop other migrants from settling and therefore prevent breeding within the patch. Another difference between the approaches was the amalgamation of patches for the Vortex analysis. This might be expected to lead to increased patch persistence due to increased carrying capacities, but is unlikely to explain the increased population spread as the amalgamation of patches resulted in increased inter patch distances.

The sensitivity analysis of the custom-built model runs showed that a greater proportion of the variance in model outputs was explained by the variation in parameter values under a high release scenario as compared to a medium or low one. This suggests that stochastic events are more important under the lower release scenarios, as would be expected from the lower population sizes (e.g. Gilpin and Soule 1986). Family habitat requirement and mean fecundity were the most important predictors of model outputs across the three scenarios. It should be realised, however, that just because these parameters had the greatest effect on the predictions of the custom-built model presented here does not necessarily mean that they will be the most important factors in determining the success or otherwise of a proposed beaver reintroduction. As outlined above, it appears that the representation of dispersal movement caused the custom-built model runs to predict very little population spread. As the pattern of low spread was consistent across all custom-built model runs there was little variation to explain. Under

alternative representations of dispersal causing higher spread (such as that used in the Vortex runs) other factors may be more important.

In the analysis of the influence of release scenario on population persistence the number of populations released was shown to be more important than the size of release populations. Again this is only relevant to the model results of low population spread. It could have been caused by the larger number of release sites leading to a higher probability of a reintroduction to one of the larger patches. Under different conditions of release site choice or alternative dispersal scenarios the number of release populations will not necessarily be more important than the size of each release. Similarly the repeat release scenarios generated slightly higher persistences than the single release ones but did not make a difference to population spread. The low population spread in all custom-built model runs precludes us from making recommendations about which release protocol would offer the greatest potential for population spread.

The predictions generated by both modelling approaches should be considered in light of the simplifications and uncertainties that were a part of the modelling process. The outputs of both models are dependant on the habitat data used as the spatial template for modelling. It was assumed that any sites with deciduous woodland adjacent to rivers were suitable habitats for beaver. This is a gross simplification of the habitat requirements of beaver and there are a number of other factors that could determine how much habitat was actually available. Firstly, it is clear that other characteristics besides vegetation, particularly the flow characteristics of the river and soil type, are important determinants of habitat suitability (see reviews in Gurnell 1997 and Macdonald et al. 1995). Rivers with highly fluctuating flow regimes are unlikely to be suitable for beaver. Beaver also prefer to have access to sites where they can create burrows in soft substrates. It is unlikely that all of the sites used in the model would have suitable hydrological regimes or suitable soils, this would lead to a reduction in the number of areas considered suitable for occupation by beaver from those identified using vegetation alone. Conversely, it was assumed that beaver families needed contiguous blocks of habitat, it is not clear to what extent beaver can utilise spatially separated habitat blocks. If they were capable of using this, then many areas of

fragmented habitat along the river systems could be suitable. The relative importance of these factors is difficult to assess but is likely to play an important role in the fate of the beaver in Scotland.

Dispersal, in both modelling approaches, was set to occur only when a population reached carrying capacity. The beaver is a social animal, thus it is likely that the dispersal response to increased population pressure is plastic and not driven by a simple threshold effect (Hartman 1995). Pre-saturation dispersal could increase the likelihood of the colonisation of new patches but would also increase the overall impact of dispersal mortality on the total population in any one year. Previous modelling studies have shown that under an assumption of density independent dispersal rates non-intuitive dispersal effects can occur (Lindenmayer and Lacy 1995a,b,c). Patches with low carrying capacities are subject to stochastic extinctions. In a network of such patches increasing dispersal rates can increase the extinction rate of source patches and increase the probability that individual dispersers move to unoccupied target patches where they are unable to breed. The greater the number of patches, the less likely dispersers are to arrive at the same patches and the more extreme this effect is likely to be. In such a scenario increased dispersal rates and increased number of patches lead to decreased metapopulation size and viability (Lindenmayer and Lacy 1995a,b,c). Conversely in a network of patches with larger carrying capacities, individual patches are less susceptible to stochastic extinctions and increased dispersal rates and number of patches have a positive effect on metapopulation size and viability (Lindenmayer and Lacy 1995a,b,c). The habitat analysis presented here predicts patch carrying capacities to be generally low, so if beaver dispersal was found to be density independent higher dispersal rates could reduce population persistence.

We did not consider social factors in the choice of settlement patches by dispersers, however it seems plausible that individuals (males particularly) are more likely to settle in patches in which other beavers are already present. Hartman (1994, 1995) documents dispersing beavers having passed by apparently suitable unoccupied habitats following reintroductions in Sweden. This was suggested as being a result of the search for mates. In the models presented here single animals will have settled in unoccupied patches and been unable to breed, active searching for mates could increase viability predictions. In

contrast Hartman (1994, 1995) suggests that long distance dispersal movements in search of mates could lead to the formation of an undercrowded or overdispersed population in which individuals are unlikely to find mates and small isolated patches are vulnerable to extinction. It was suggested that such an Allee effect may have been limited in Sweden by the presence of dispersal barriers between catchments. Similarly it is possible that landscape effects restricting beaver dispersal in Scotland could have initially positive effects on population viability.

It must be stressed that the model runs took no account of local events that could cause catastrophic mortality, for example extreme flooding or pollution incidents. The threat of such events would, depending upon their frequency, reduce the probability of persistence of isolated populations, but should have little effect on the persistence of a large, widely distributed metapopulation. Thus those runs that predicted high population persistence but no spread would be expected to predict low persistence if local catastrophes were included, whereas the persistence predictions of runs predicting a large population spread would be expected to remain high.

The difference between the results of the two approaches and the suggested importance of dispersal results from the incorporation of landscape structure into the assessment of reintroducing a species to a highly fragmented habitat. To our knowledge this paper represents the first published attempt to perform such an analysis. Previously published modelling assessments of reintroductions have considered a single randomly mixing population (Bustamante 1996; Brook et al. 1997; de Jong et al. 1997; Howells and Edwards-Jones 1997), a number of isolated populations (Novellie et al. 1996) or a relatively small number (2 - 6) of linked populations (Southgate and Possingham 1995; Nolet and Baveco 1996; vanEwijk et al. 1997). Akcakaya et al. (1995), Liu et al. (1995) and Macdonald et al. (1998) describe analyses similar to this one where spatially explicit models are applied to real landscape data, but these are for established populations. Lindenmayer and Lacy (1995 a,b,c) explore the effect of population subdivision, but their models are not applied to real landscape data.

The analysis of the viability of a re-introduced population is subtly different to that needed for an established species, in that there is an increased emphasis on the role of

spatial population processes. In a population reintroduction scheme the number of populations to be reintroduced and the number of organisms released is inevitably small for practical reasons. Thus, the modeller is interested not only in the long term viability of the population in the proposed reintroduction sites, but crucially in the ability of the organism to disperse to and colonise new areas. Whilst it may be desirable to incorporate models of dispersal into spatial population dynamics to make these models more realistic, it is not clear how this should be achieved. Dispersal is a behavioural process, modelling the processes that initiate, undertake and complete dispersal is difficult (Lima and Zollner 1996; Wennergren et al. 1995; Ruckelshaus et al. 1997). Indeed the inability to model dispersal behaviour realistically is seen as a critical factor determining the value of individual-based modelling for conservation management (Conroy et al. 1995; Wennergren et al. 1995; Lima and Zollner 1996; Ruckelshaus et al. 1997). We suggest this lack of information regarding dispersal behaviour actually increases the potential value of such models as long as the uncertainty is recognised and accounted for. In addition reintroduction studies represent one of the best opportunities to test representations of dispersal behaviour; the starting locations of all individuals are known, the individuals to be reintroduced can be easily marked and at least initially there should be no confusion about the previous location of animals arriving in new areas. A simulation modelling approach allows the generation of multiple alternative hypotheses that can then be tested by the reintroduction itself and the results fed back to refine future predictions.

Reintroduction programs should go through four stages: investigation of feasibility, preparation, planning and monitoring (Stanley-Price 1989; IUCN 1995). IUCN (1995) recommends the use of modelling techniques as a part of the investigation of feasibility stage and this paper represents such an investigation applied to the beaver in Scotland. We foresee that simulation modelling techniques will also prove useful in the later stages of reintroduction programs. The feasibility investigations can be used to identify potential reintroduction sites which should be investigated more closely in the preparation stage. More detailed habitat information can then be incorporated to more detailed models as a part of the planning stage. More detailed assessments of beaver habitat in Scotland have already been conducted (Macdonald et al. 1997; Webb et al. 1997). Following an initial reintroduction, intensive monitoring of animal behaviour

(e.g. territory sizes, natality rates, habitat use and dispersal behaviour) should be conducted to provide information for the refinement of model parameters. The effect of beavers on their food supply should also be monitored as this may be an important factor determining population growth and viability (Hartman 1994). Model runs based on information collected following the initial reintroduction could then be used to predict population development and direct subsequent management actions. Such an approach is being applied to the beaver reintroduction to the Netherlands (Nolet and Baveco 1996). Modelling could also be used to assist in the identification of 'success indicators' (IUCN 1995), these might take the form of a natality rate that generates a prediction of a certain population persistence or alternatively a threshold population size that a population needs to reach in order to reduce the predicted risk of extinction to below a pre-defined level. This follows the adaptive management approach to reintroductions advocated by Sarrazin and Barbault (1996) and the initial use of reintroductions as a research tool to provide information for later management actions advocated by Southgate and Possingham (1995).

This analysis shows that the uncertainty associated with beaver dispersal behaviour is the principle limitation precluding us from predicting conclusively whether a reintroduced beaver population would be likely to persist in Scotland. Additional information regarding beaver behaviour in similarly fragmented landscapes or the initial dispersal behaviour of a reintroduced population are necessary to refine these predictions.

6. Chapter 6 : Dispersal in Spatially Explicit Population Models

6.1 Introduction

Spatially explicit population models have been advocated as a means of addressing the complexities of population dynamics within heterogeneous landscapes (e.g. Dunning et al. 1995) and have been applied to a number of conservation issues (e.g. Mckelvey et al. 1993; Liu et al. 1995; Rushton et al. 1997). Recently, the utility of such approaches has been questioned due to their representation of the dispersal process (Wennergren et al. 1995; Ruckelshaus et al. 1997).

Ruckelshaus et al. (1997) described a spatially explicit model of animal dispersal in which individuals were simulated as moving randomly within randomly generated fragmented landscapes. For each replicate a single animal was positioned at a randomly chosen patch and moved until it located another patch. This framework was used to show how changing the values of three model inputs (proportion of suitable habitat, maximum dispersal distance and dispersal mortality) effected the fraction of dispersers that successfully located a habitat patch. This model output was termed 'dispersal success'. It was shown that the model was particularly sensitive to the value of dispersal mortality, with differences as low as 8% leading differences in dispersal success of greater than 60%. The first sentence of the abstract stated : 'We evaluated the consequences of parameter errors for predictions of spatially explicit population models'. The inference is that the prediction errors generated by the model are equivalent to the errors that would be expected from spatially explicit population models (SEPMs).

I contest that whilst Ruckelshaus et al. (1997) explored error propagation in a dispersal model, this is not the same as exploring error propagation in a SEPM as no consideration of population processes was included. In a recent review of SEPMs Dunning et al. (1995) define models as : 'spatially explicit when they combine a population simulator with a landscape map that describes the spatial distribution of landscape features'. SEPMs are generally used in conservation biology to predict population abundance, distribution and viability (e.g. Akcakaya et al. 1995; Conroy et al. 1995; Liu et al. 1995; Rushton et al.

1997). In contrast, Ruckelshaus et al. (1997) generated predictions of individual dispersal success. I describe a simple simulation model to illustrate how errors in dispersal success are not equivalent to errors in predicted patch occupancy or predicted population viability. The model used dispersal success as an input and investigated the effect of variation in this parameter on predictions of patch occupancy and population viability.

Space was represented explicitly (sensu Hanski 1994; Hanski and Simberloff 1997) in that each patch was not equally connected to all others. Within SEPMs, the connectivity between habitat patches will be dependent upon the composition of the landscape simulated and the dispersal ability of the species in question. These factors condense down into a matrix of the dispersal probabilities between each patch that will be different for each study. Here I used a simple connectivity parameter that avoided reliance on a single landscape structure.

There has been considerable debate as to whether animals are motivated to disperse when their habitat reaches carrying capacity or whether they do so below carrying capacity (e.g. Stenseth and Lidicker 1992). The former has been termed saturation dispersal and the latter, presaturation, although it has been recognized that it can be difficult to differentiate between them in the field and that motivating factors are inevitably more complex than this simple classification suggests (Lidicker and Stenseth 1992). Previous SEPMs have simulated either saturation (e.g. Pulliam et al. 1992; Liu et al. 1995; Rushton et al. 1997) or presaturation dispersal (e.g. Lahaye et al. 1994; Lindenmayer and Lacy 1995 c). I simulated two dispersal mechanisms, one saturation and the other pre-saturation.

6.2 Model outline

The model simulates the births and deaths of individuals within patches and the dispersal of individuals between patches. The stochastic nature of births and deaths was represented by sampling deviates from a uniform distribution for each individual and each event. The model was run on a yearly time step within which births, deaths and dispersal were simulated in that order (see Fig. 6.1). A sex ratio of 1:1 was assumed, the birth rate was applied to 50% of the individuals in each patch, and litter size was set at a constant 2. In each year the number of individuals in each patch was increased by the number of new young produced.

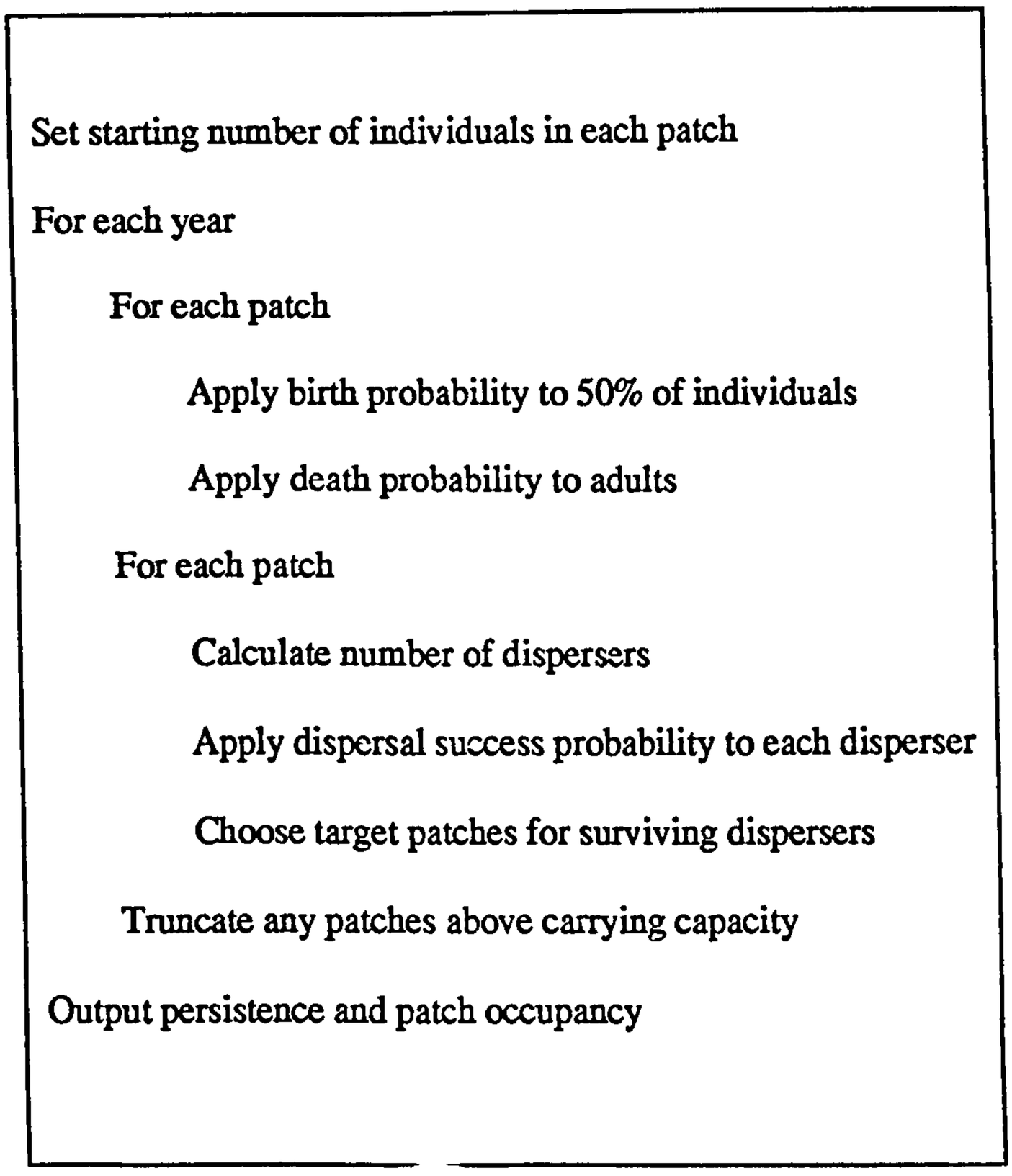


Figure 6.1. Model outline

Two dispersal mechanisms, that differed in the initiation of individual dispersal, were simulated. In the first (saturation dispersal), any individuals in excess of the patch carrying capacity dispersed. In the second (pre-saturation dispersal), a constant dispersal probability of 0.05 was applied to all individuals in each patch in each year. This dispersal probability was chosen to be within the range of values used in previous SEPMs (Lahaye et al. 1994; Lindenmayer and Lacy 1995 a,b,c).

A dispersal success probability was applied to each dispersing individual, those that survived were moved to another patch. To keep the model simple, while not restricting the analysis to a single landscape configuration, each patch was 'connected' to a number of other patches according to a connectivity parameter that could be varied between runs. In practice this was accomplished by giving each patch an identification number and connecting it to all patches plus or minus half of the connectivity value (see Fig. 6.2). For each dispersal event the target patch was chosen randomly from those that were within the

connectivity range and below carrying capacity. If none of the patches within the connectivity range were below carrying capacity, the individual died.

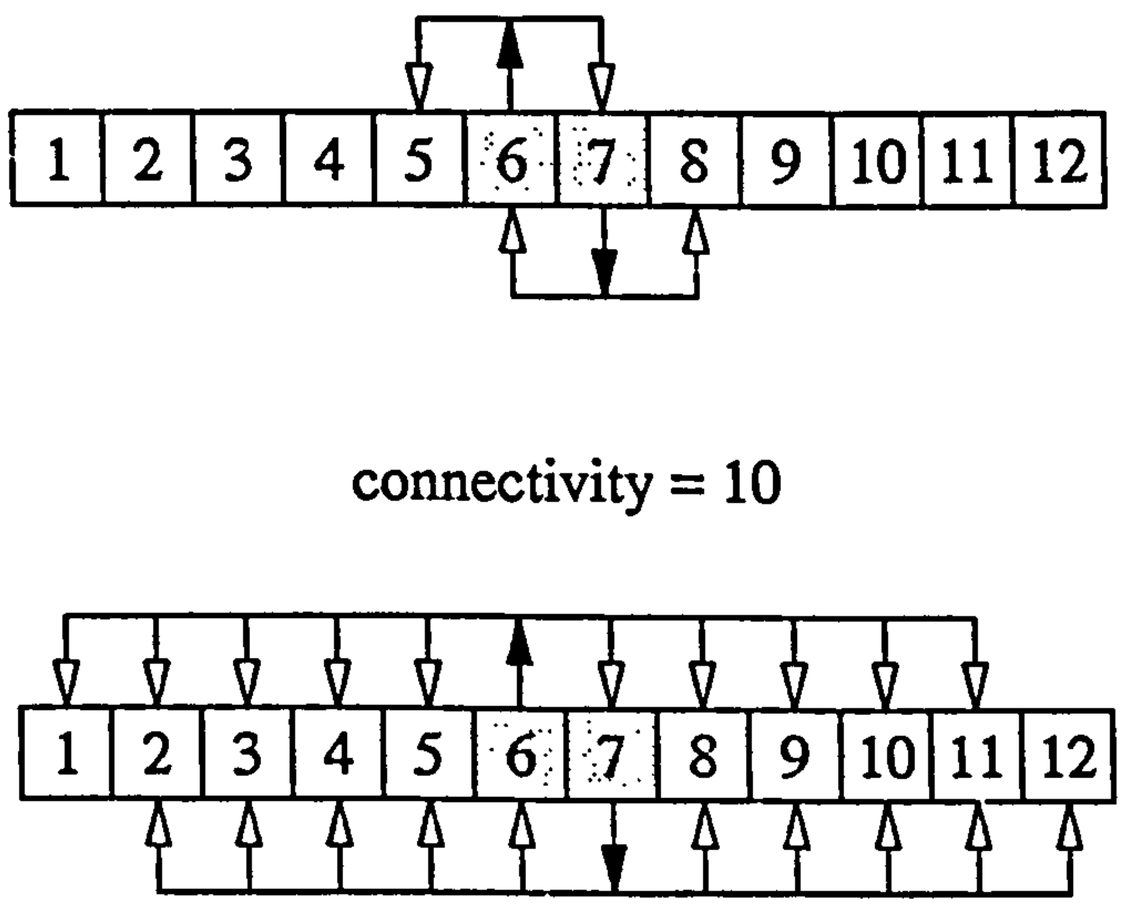


Figure 6.2. Representation of space used in the model. Each square represents a patch, animals dispersing from the shaded patches (indicated with the filled arrows) can move to any of the patches indicated by the open arrows.

At the end of each year any patches above carrying capacity were truncated. Under the saturation dispersal mechanism any individuals in excess of carrying capacity will already have dispersed, so this additional truncation only operates under the presaturation dispersal mechanism.

To investigate the effect of dispersal success under different population growth scenarios the model was run under a range of birth probabilities (0.3 - 0.46) and a constant probability of death (0.3). Due to the simple set up of the simulation the within patch intrinsic growth rate (lambda) in the absence of dispersal behaviour could be calculated as : (probability of birth * 0.5 * litter size) + (1 - probability of death). Thus the demographic rates simulated represent within patch lambdas from 1 to 1.16. A range of dispersal success probabilities (0.2 - 1) were simulated. The model was run for 50 patches with equal carrying capacities, each run was started with 10 animals in each of 10 equally spaced patches. Runs were conducted for connectivity parameters of 2 and 10 and patch

carrying capacities of 10 and 20. Fifty replicates of each parameter combination were conducted and population persistence (proportion of replicates persisting) and mean patch occupancy (including only those runs that had not reached extinction) calculated after 20 and 100 years (a summary of the model runs is given in Table 6.1).

Dispersal Mechanism	Connectivity	Patch carrying capacity	Reporting interval (years)	Within patch intrinsic growth rate (lambda)	Dispersal success
Saturation, Presaturation	2, 10	10, 20	20, 100	1, 1.02, 1.04, 1.06, 1.08, 1.10, 1.12, 1.14, 1.16	0.2, 0.4, 0.6, 0.8, 1

Table 6.1 : Parameter values simulated in the model, 50 replicates were performed for every parameter combination.

6.3 Results

Figures 6.3 to 6.6 show the responses of population persistence and mean patch occupancy to changing lambda and dispersal success for the model runs with a connectivity parameter of two. As expected, the general response is one of increasing persistence and patch occupancy with increasing lambda and dispersal success. This response did, however, vary according to the dispersal initiation mechanism, patch carrying capacity, reporting interval and the relative values of the two parameters themselves.

Populations persisted to 20 years in the majority of replicates, irrespective of the value of dispersal success (Figs. 6.3a - 6.6a). Patch occupancy at year 20 showed an approximately linear response to increasing dispersal success, in all scenarios and across all lambda values (Figs. 6.3b - 6.6b).

Population persistence to 100 years, tended to be low and little effected by dispersal success at low lambda values (Figs. 6.3c - 6.6c). At high lambda values populations

persisted in the majority of replicates, irrespective of dispersal success. At intermediate lambda values, responses of persistence to dispersal success approximated a sigmoid curve, the difference in dispersal success of 0.8 causing a difference in persistence of up to 0.8 (e.g. Fig. 6.6c). The response of patch occupancy at year 100 to lambda and dispersal success (Figs. 6.3d - 6.6d) was similar to the response of persistence, but displaced towards higher lambda values. For example, the runs simulating saturation dispersal with a patch carrying capacity 10, generated a persistence probability of 1 at lambda 1.12, irrespective of the level of dispersal success (Fig. 6.3c), but patch occupancy varied from 20% to 100% according to the level of dispersal success (Fig. 6.3d).

Within the saturation dispersal runs, increasing patch carrying capacity from 10 to 20 had little effect on persistence and patch occupancy at year 20 (compare Figs. 6.4a, b to 6.3a, b). At year 100 the effect of increased patch carrying capacity was to increase persistence and patch occupancy, and decrease the range of lambda values over which they were sensitive to changes in dispersal success (compare Figs. 6.4c, d to 6.3c, d). The response to patch carrying capacity was similar within the presaturation dispersal runs (Figs. 6.5 and 6.6).

The predictions of the saturation dispersal runs were generally higher than those of the presaturation runs (compare Figs. 6.5, 6.6 to 6.3, 6.4). The results of the saturation runs after 100 years tended to be sensitive to dispersal success across a narrower range of lambda values than the results of the presaturation runs (e.g. compare Figs. 6.4c, d to 6.6c, d).

The results of the simulations using a connectivity parameter of 10 showed a very similar pattern to those using a connectivity of 2 and are not shown here. For a limited range of parameter combinations the simulations using the higher connectivity parameter generated higher predictions of patch occupancy and lower predictions of persistence, but this effect was not greater than 20% and 0.4 respectively.

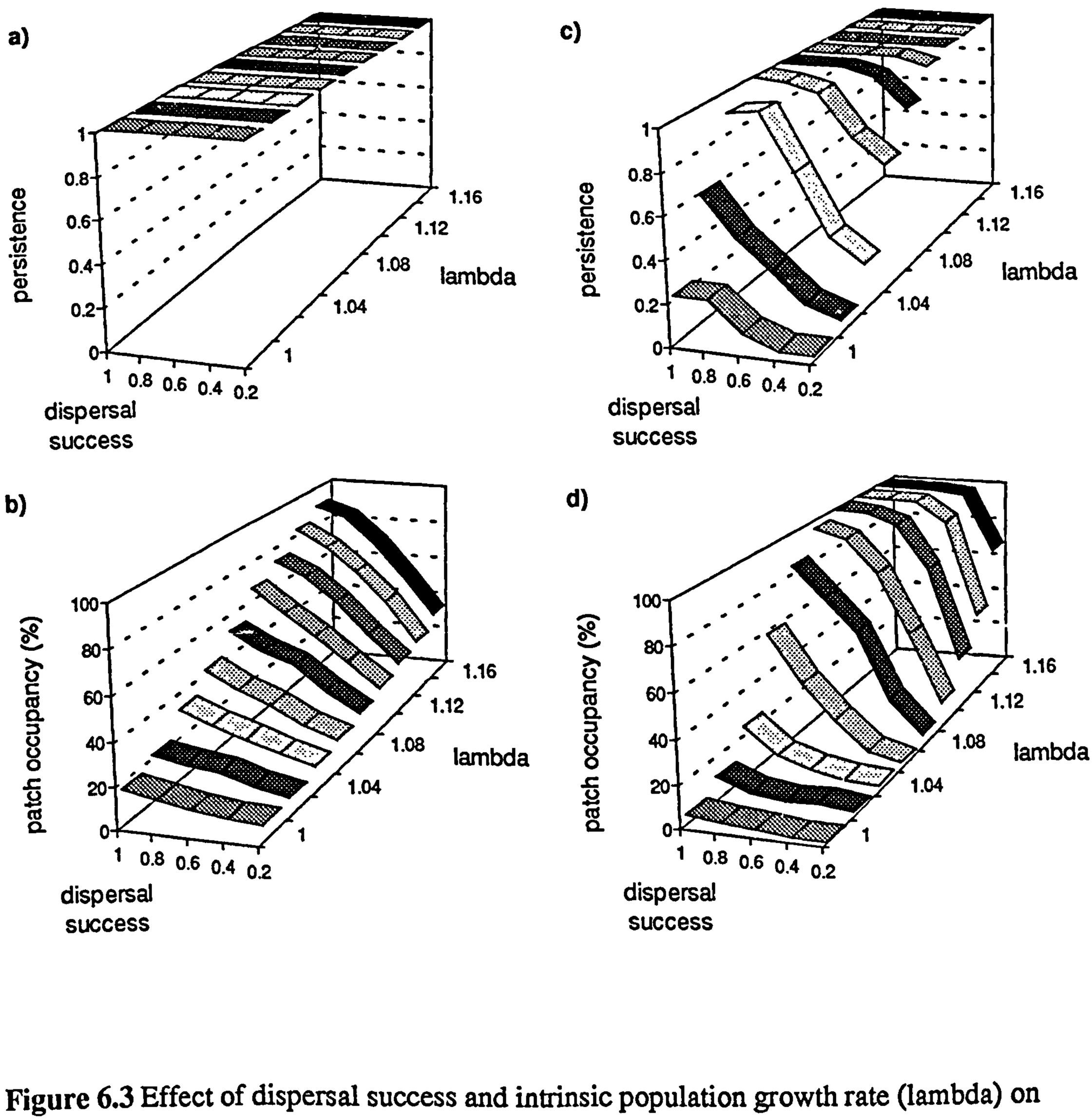


Figure 6.3 Effect of dispersal success and intrinsic population growth rate (lambda) on model predictions using a saturation dispersal mechanism with patch carrying capacities set to 10 and the connectivity parameter set to 2. (a) Population persistence at year 20, (b) Mean patch occupancy at year 20 (SE's < 2), (c) Population persistence at year 100, (d) Mean patch occupancy at year 100 (SE's < 3).

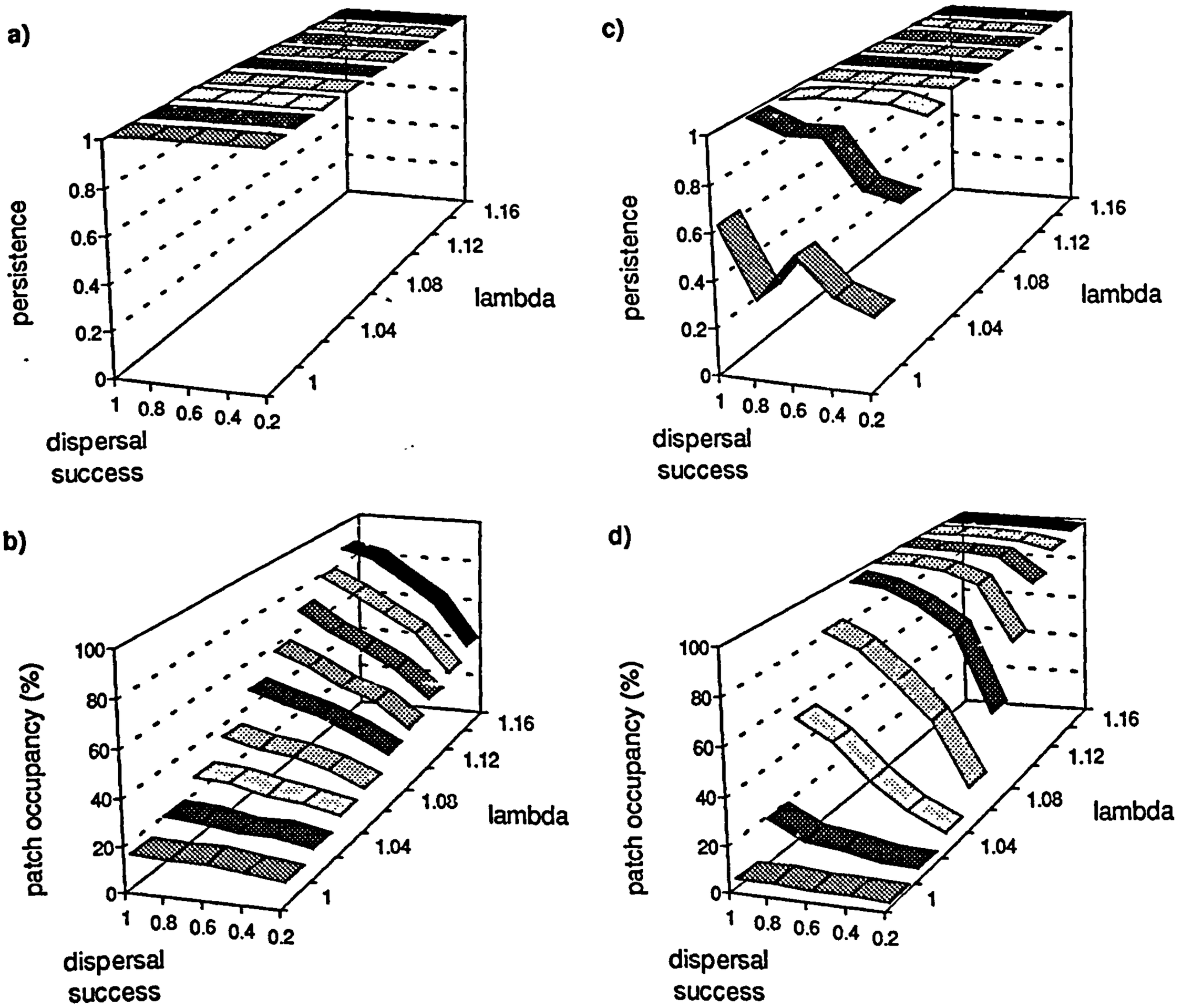


Figure 6.4 Effect of dispersal success and intrinsic population growth rate (lambda) on model predictions using a saturation dispersal mechanism with patch carrying capacities set to 20 and the connectivity parameter set to 2. (a) Population persistence at year 20, (b) Mean patch occupancy at year 20 (SE's < 2), (c) Population persistence at year 100, (d) Mean patch occupancy at year 100 (SE's < 3).

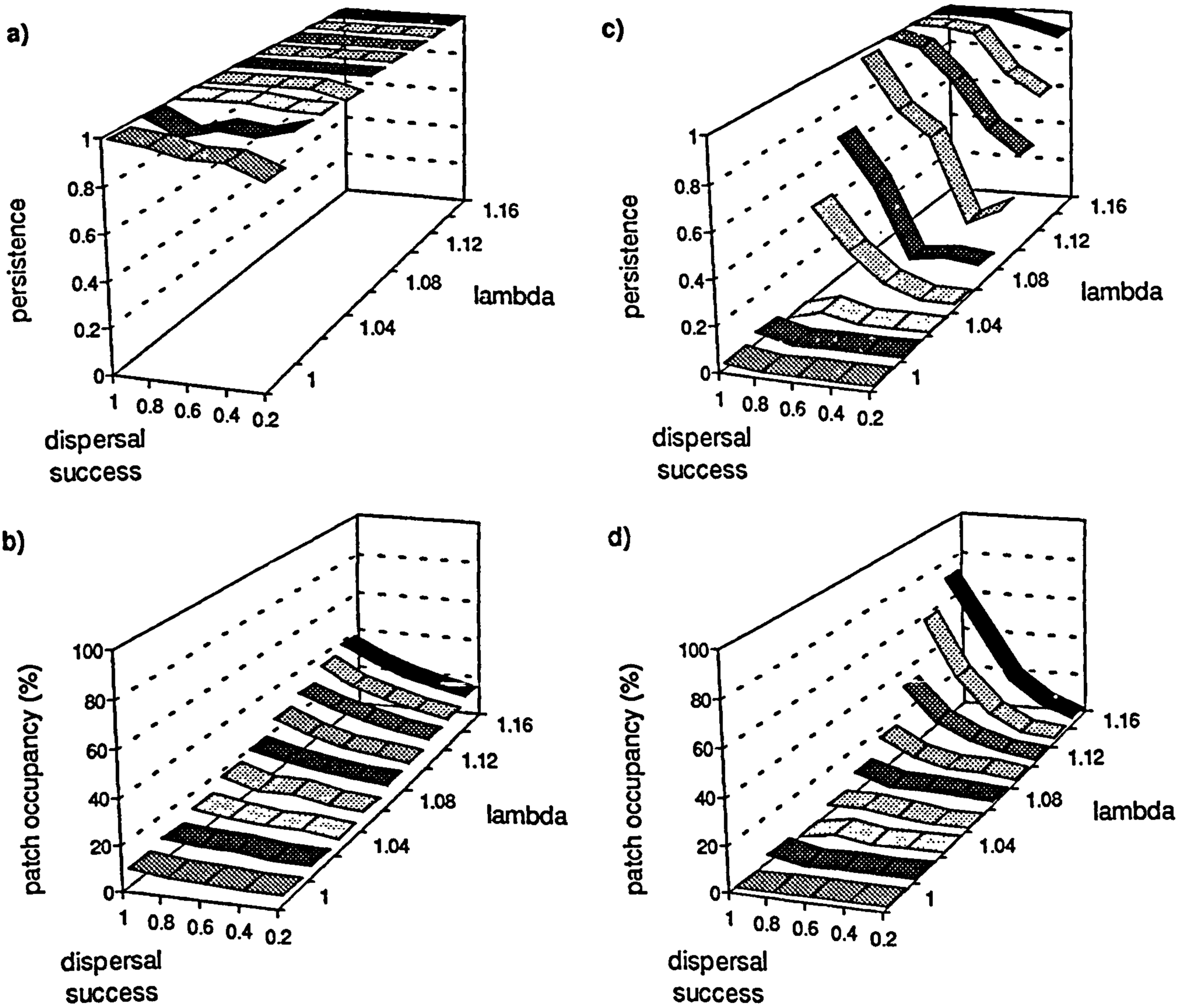


Figure 6.5 Effect of dispersal success and intrinsic population growth rate (lambda) on model predictions using a presaturation dispersal mechanism (dispersal probability 0.05) with patch carrying capacities set to 10 and the connectivity parameter set to 2. (a) Population persistence at year 20, (b) Mean patch occupancy at year 20 (SE's < 2), (c) Population persistence at year 100, (d) Mean patch occupancy at year 100 (SE's < 3).

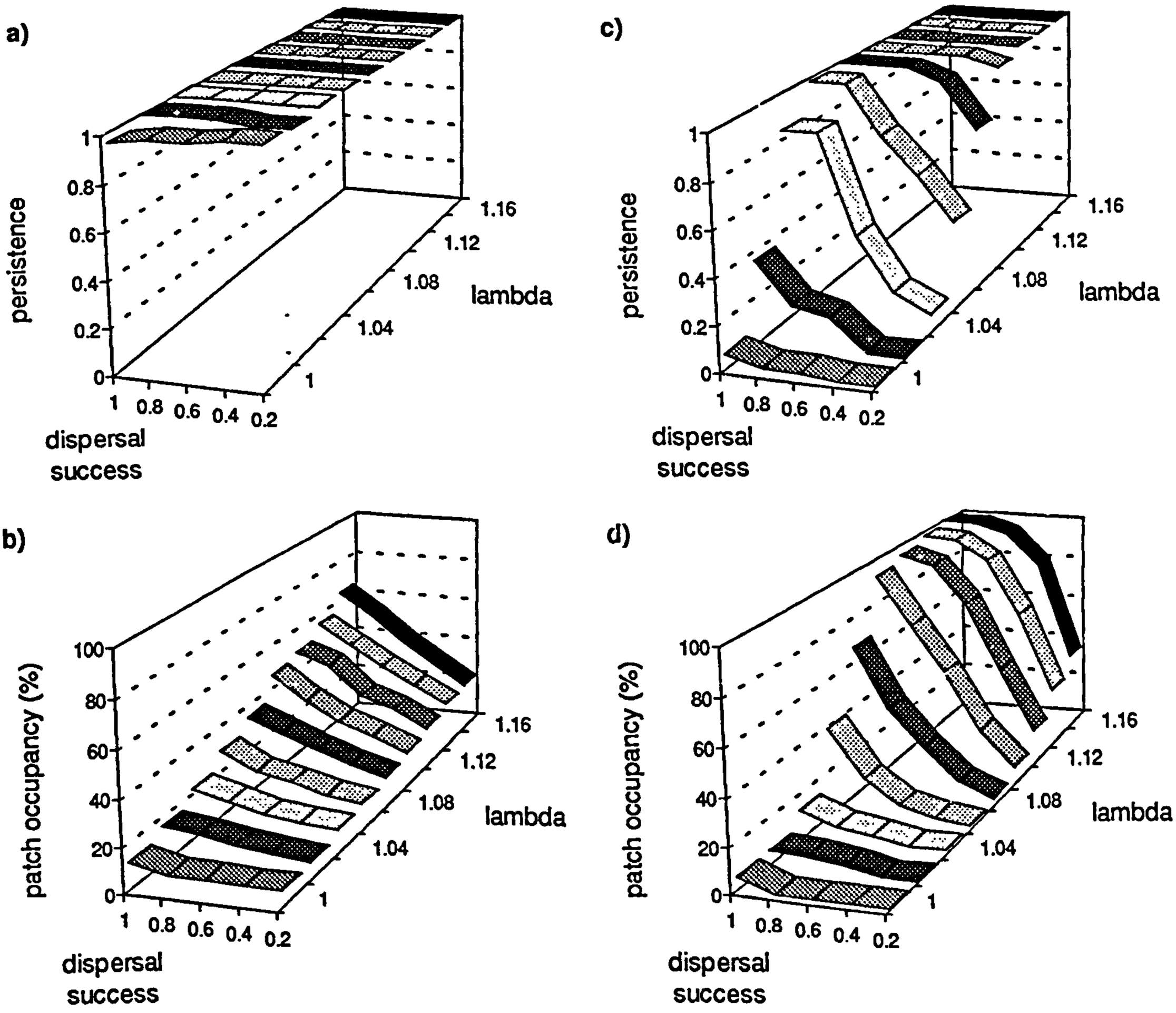


Figure 6.6 Effect of dispersal success and intrinsic population growth rate (lambda) on model predictions using a presaturation dispersal mechanism (dispersal probability 0.05) with patch carrying capacities set to 20 and the connectivity parameter set to 2. (a) Population persistence at year 20, (b) Mean patch occupancy at year 20 (SE's < 2), (c) Population persistence at year 100, (d) Mean patch occupancy at year 100 (SE's < 3).

6.4 Discussion

The model outlined here is a very simple SEPM. It considers a series of patches with equal carrying capacities, each of which is equally connected to a defined number of other patches. Dispersal is represented simply by initiation according to either a saturation or pre-saturation mechanism, applying a dispersal success parameter and moving surviving animals to a randomly chosen connected patch. Nonetheless, the model is based on the balance between intra- and inter-patch processes that is fundamental to SEPMs and to population dynamics in fragmented habitats in general (Hanski 1994).

The results show that dispersal success does not always have a major effect on predicted patch occupancy and population persistence (the conventional outputs of spatially explicit population models, Akcakaya et al. 1995; Conroy et al. 1995; Liu et al. 1995; Rushton et al. 1997). In a detailed SEPM applied to the Bachman's sparrow in a representation of a real landscape, demographic parameters were found to be more important than dispersal parameters (Pulliam et al. 1992; Liu et al. 1995). Similarly the robustness of SEPMs to changing dispersal parameters under qualitatively defined conditions has been suggested (Dunning et al. 1995; Wennergren et al. 1995). The framework presented here goes beyond this and quantifies the relationship between dispersal success and demographic parameters across a selection of landscape and dispersal characteristics.

The range of within patch growth rates for which outputs were particularly sensitive to dispersal success was found to be dependent on the dispersal initiation mechanism, patch carrying capacities and the number of generations simulated. The lower sensitivity to dispersal success of the saturation dispersal simulations, can be explained by the stabilising effect of the saturation mechanism. As patches do not lose dispersers until they have reached carrying capacity, dispersal cannot cause patch extinction. In contrast, under the presaturation mechanism, patches with few individuals can lose dispersers. This could lead to patch extinction and if dispersal success is low, dispersers are unlikely to reach other patches, thus reducing the viability of the population. For both dispersal mechanisms, increasing the patch carrying capacities led to a decreased sensitivity to dispersal success. This can be explained by a decreased susceptibility of larger patches to demographic stochasticity, decreasing the importance of inter-patch transfer.

The effects of dispersal success for a particular lambda value were potentially greater over the longer simulation period, a simple result of the dispersal success probability being applied more often in the longer simulation. However, the range of lambda values over which predictions of patch occupancy were sensitive to the effect of dispersal success was lower over the longer time period. This can be explained by populations that declined or increased at slightly different rates, such that after 20 years they exhibited different patch occupancies, but after 100 years were both either extinct or at saturation.

Increased landscape connectivity led to minor increases in patch occupancy and minor decreases in population persistence. This is consistent with the population becoming spread between more patches in the more connected landscape, and the consequently lower populated patches being more vulnerable to demographic stochasticity.

In more realistic, detailed simulation models these inter-relationships between demographic parameters, landscape composition and dispersal behaviour will inevitably be more complex. The analysis of Ruckelshaus et al. (1997), although used as a criticism of spatially explicit population models, takes dispersal out of the demographic and landscape context.

Although testing sub-components of ecological simulations separately has been advocated in the past (e.g. Conroy et al. 1995; Caswell 1976) it does present problems if used in isolation. Firstly, as a model or model sub-component is never 'true' (Oreskes et al. 1994), it is not clear when a model sub-component, and thus the predictions generated by the whole model, should be rejected. Secondly, separate testing of model sub-components limits the ability to compare the relative importance of parameters that influence more than one sub-component. Ruckelshaus et al. (1997) identify dispersal mortality as more important than landscape classification in their model of the dispersal process. In a SEPM, landscape classification can also effect demographic processes, through an effect on patch carrying capacity. This could increase the importance of landscape classification relative to dispersal mortality within SEPMs.

If model uncertainty is assessed at the scale of application, the level of uncertainty in applied predictions can be attached to those predictions. This then allows the potential utility of the model predictions to be assessed, based upon whether they conform to predefined levels of precision. Testing of model sub-components may be most useful if it is used to generate secondary predictions that can help in the evaluation of the reliability of the primary predictions (Bart 1995). It may also prove useful if used to assess alternative model representations of the same process.

Ruckelshaus et al. (1997) made the point that there are currently insufficient data available to model dispersal behaviour at the scale they did. This is indeed well supported by the results presented. However little evidence was produced to support the contention that the model of dispersal presented is broadly generalisable. Dispersal was simulated using a random walk, which will have created tortuous paths involving occasional revisiting of previously visited cells. Dispersal mortality was simulated by taking a published mortality rate and dividing it to generate a per step probability of death. This assumes a linear relationship between mortality risk and the number of dispersal steps taken at the scale simulated. For conservation biology the important question is whether the high sensitivity of dispersal success to small changes in the risk of dispersal mortality is a feature of natural systems or an artifact of the simulation methodology. To address this question two alternative hypotheses can be formulated :

Hypothesis 1 : The representation of dispersal used was a faithful representation of the dispersal process at that scale. Dispersal mortality is linearly related to dispersal distance and dispersal paths are largely random. Small differences in susceptibility to dispersal mortality (maybe characteristic of one species in two different regions) cause large differences in dispersal success.

Hypothesis 2 : The representation of dispersal used was a poor representation of dispersal at that scale. Dispersal mortality is not linearly related to dispersal distance, dispersal paths are poorly represented by a random walk. Small differences in susceptibility to dispersal mortality do not cause large differences in dispersal success.

If the first hypothesis is accepted then fine scale models of animal dispersal may be necessary to predict population behaviour for species and landscapes in which dispersal success is likely to be important (i.e. within the parameter space identified by the simulations presented here). If the second hypothesis is accepted then fine scale dispersal models may be an unnecessary component of SEPMs and would be more usefully replaced by a coarser scale representation of dispersal. There is already a range of scales at which dispersal is modeled within SEPMs. At the coarser end of the scale, the population viability analysis software package, Vortex (Lacy et al.1995), allows dispersal to be represented simply as probabilities of movement between each patch in each year. A similar approach was used by Lahaye et al. (1994) and Lindenmayer and Lacy (1995 c). At the finer end of the scale Pulliam et al. (1992) simulated juvenile Bachmans sparrows as stepping between 2.5 ha cells, moving to habitable cells where possible, randomly choosing between neighboring habitable cells if there was more than one and moving in a straight line through contiguous areas of unsuitable cells.

In order to address the issue of the appropriate scale at which to simulate dispersal there should be a continued development of both fine and coarse scale dispersal models in tandem with the field data on which to base and test them (Conroy 1995; Lima and Zollner 1996). The development of new modeling approaches and the collection of further data should not be treated as alternatives. For conservation applications dispersal behaviour needs to be modeled within the demographic and landscape context to assess whether our lack of knowledge is likely to cause unacceptable uncertainty in the predictions of spatially explicit population models.

7. Chapter 7 : Discussion : Issues relating to modelling the spatial distribution of mammals

In this thesis I have outlined the scales at which mammals interact with space and reviewed modelling approaches applicable to the spatial distribution of mammals. I have demonstrated the application of a selection of these modelling approaches. In this discussion I summarise the model results and then go on to discuss potential future work to build on that described here. I conclude with a general discussion of the relative merits of different modelling approaches and some recommendations regarding the future use of models to explain and predict the spatial distribution of mammals.

In chapter 3, the attempt to extrapolate from individual energetic requirements and the distribution of food to individual space use and spacing patterns yielded a number of straightforward predictions. Patterns of range area and range overlap generated were negatively related to food density. A positive correlation between range area and overlap was attributed to two mechanisms; firstly that larger ranges were more likely to overlap by chance and secondly that overlapped ranges were likely to be larger to compensate for the effects of depletion competition. The model provides a framework for investigating individual home ranging behaviour and its influence on spacing patterns.

Application of a model to the distribution of badger main setts, based on habitat suitability rules derived from the literature and a predefined minimum distance between setts, proved unsatisfactory. Empirical sett density data were within the range predicted for one, high density area, but not for the other lower density area. The poor reliability of the data for the low density area, precludes rejecting the methodology outright, but other factors suggest that it might not be reliable. Among these the spatial distribution of setts in the high density area was less regular than that predicted by the model and there is not an obvious objective way of deriving the 'minimum inter-sett distance' parameter when applying the model to unsurveyed

areas. In the analyses presented here this parameter was derived from the literature for the high density area and from a nearby study area for the low density area. It seems likely that social spacing mechanisms in the badger are dependant upon local scale factors not represented by this methodology (Kruuk 1989). A simple associative model based on national survey data (Cresswell et al. 1992), performed well in one area but not in the other. The poor performance in the high density area was likely a result of applying the model across a much smaller area than that over which it was developed.

Application of two similar individual based, spatially explicit population models to the proposed reintroduction of the beaver to Scotland generated contrasting predictions. A custom built model, using an explicit representation of dispersal, predicted little or no population spread. Use of a generic PVA package with an implicit representation of dispersal predicted rapid population spread. A high rate of dispersal failure in the custom built model was identified as the most likely cause of this disparity. A sensitivity analysis of the custom built model indicated minimal effects of demographic and habitat suitability as poor dispersal success lead to little variation in model predictions.

Development of a simple generalised SEPM allowed the interaction between demographic and dispersal processes to be investigated. Predictions of population persistence and patch occupancy were shown to be sensitive to changes in dispersal success across a restricted range of demographic parameters. Variation in dispersal success tended to have a greater effect under pre-saturation rather than saturation dispersal, at lower patch carrying capacities and over longer time periods.

Table 7.1 summarises the attributes of the different process-based models applied in chapters 3 to 6. None of the models used represented all of : foraging movements, dispersal movements and reproduction. Elements of each approach could potentially be built into some form of hierarchy of models, as advocated by Murdoch et al. (1992) and deRoos and Sabelis (1995), in order to extrapolate from fine scale processes to patterns at larger scales. A foraging model as in chapter 3 could potentially be used to predict patch carrying capacities for incorporation into models

such as those described in chapters 5 and 6. For territorial species a space pre-emption model such as that described in chapter 4, might be a necessary intermediate step between these approaches. However the present uncertainty regarding landscape level behavioural mechanisms (e.g. Lima and Zollner 1996), particularly at the lower end of this hierarchy limits the utility of such an approach. More research on foraging, territorial and dispersal behaviour is required before there is likely to be much success in developing a model based on all of three of these to predict the spatial distribution of mammals.

Model attributes (rep. = representation)	**chapter 3,** squirrel foraging model	**chapter 4,** badger space pre-emption model	**chapter 5,** beaver custom built model	**chapter 5,** beaver Vortex PVA model	**chapter 6,** general SEPM
rep. of space	explicit, heterogeneous	realistic, heterogeneous	realistic, 3 categories	explicit, binomial	explicit, binomial
rep. of foraging movements	explicit	no	no	no	no
rep. of dispersal movements.	no	no	explicit, saturation	implicit, saturation	implicit, saturation & presaturation
rep. of reproduction	no	no	yes	yes	yes
inputs (c.c.s = carrying capacities)	food distribution, drey positions, movement & energetic rules	land use map, sett site suitability rules, minimum inter-sett distance	land use map, colony habitat requirements, demographic parameters, dispersal rules	patch c.c.s, inter-patch distances, demographic rates, dispersal rules	patch c.c.s, connectivity, dispersal rules
outputs	distribution of foragers over days to months	distribution of main setts at saturation	popn. persistence & mean patch occupancy at yearly intervals	as for beaver custom built model	as for beaver custom built model
theoretical/applied (t/a)	t	a	a	a	t

Table 7.1 : Summary of process based methodologies employed in the thesis

Future distribution patterns of the red squirrel, badger and beaver will inevitably result from an interaction of processes operating at the different scales outlined in chapter 1. However, the relative importance of particular scales and processes is

likely to differ. I will now consider this for each of the three species, and discuss the extent to which the modelling approaches described in the thesis may be extended to predict spatial distributions into the future.

For the red squirrel, foraging movements within habitats are likely to be an important component of its interaction with the grey squirrel, but the mechanisms involved in the displacement of the red by the grey are as yet poorly understood. Assuming a simple displacement of reds by greys, the dispersal movements of greys will be among the most important factors in the distribution of reds (Okubo et al. 1989; Rushton et al. 1997). The model described by Rushton et al. (1997) provides a means of extrapolating from assumed interactions of red and grey squirrels to predict regional and national distribution patterns. The model described in chapter 3 offers a means of investigating the interaction between reds and greys and potentially of generating parameters to fit into the larger scale model. The first of these is a more realistic goal in the short term.

The model, despite being potentially very complex, is only applied to a relatively simple situation here. The model represents individuals that forage according to a memory map of food availability and predefined movement rules. However, the model was only applied to a uniform landscape and using a single movement rule. In addition the model potentially produces a range of outputs that can be tested against field data, e.g. activity period, body weight and distance moved, yet only forager positions were analysed. The other potential outputs are outlined in appendix 2 (South et al. 1997). Further model development and testing can proceed in two complimentary directions. Firstly, a largely theoretical approach could be followed, with the development and testing of alternative movement rules in a range of landscapes (somewhat similar to the approach taken by Turner et al. 1993 for nomadic herbivores). Secondly a more empirical approach could be followed, parameterising the model more closely to a field situation and comparing model predictions and observations.

For the badger, foraging movements and territorial interactions are likely to determine maximum densities within an area, but understanding of this mechanism

is poor. There is evidence that badger densities in Britain are currently increasing due to recent reductions in persecution (Wilson et al. 1997). Long distance dispersal movements (greater than the width of a single territory) may play an important role in the colonisation of large areas, such as East Anglia, where populations are absent or very sparse due to extreme past persecution. At a smaller scale, short distance dispersal movements may play an important role in the recolonisation or boosting of local areas of low badger density, but the ubiquitous distribution of the badger is likely to make this a difficult process to study. The questionable nature of the representation of badger spacing behaviour used in the space pre-emption model described in chapter 4, limits the potential utility of this approach for both applied and theoretical purposes. It is not clear what methodology holds the most promise for predicting badger distributions, except that more data over contiguous areas is required if more realistic models are to be developed and tested.

The survival and reproduction of an initial release of beaver to Scotland will be dependent upon the success of their foraging movements. To some extent this will be an unknown quantity until beavers are actually released. If beaver prove able to forage successfully within Scottish habitat fragments, then dispersal movements will play a vital role in the viability of the beaver population in Scotland. The beaver models, presented in chapter 5, were identified as a preliminary analysis of potential viability in Scotland. Greater confidence could be placed in predictions if an effort was made to consider habitat suitability in more detail. This would require looking at beaver habitat use in a landscape that is as close as possible to proposed reintroduction sites in Scotland. A modified classification of habitat suitability and requirements could be incorporated into the existing model, providing that there were the habitat data to support it. The chapter identified dispersal as the major factor likely to lead to success or failure of the reintroduction program, should it go ahead. Data on dispersal is notoriously difficult to obtain (Wennegren et al. 1995; Ruckelshaus et al. 1997) These problems are compounded by the fact that the beaver has been absent from Scotland for 500 years. However a reintroduction of the beaver to the fragmented Scottish landscape is likely to provide an ideal opportunity to study the dispersal process and feed the results back into future models and predictions.

Spatially explicit models applied to real landscapes have been criticised for including more complexity than there is the understanding to support (e.g. Kareiva and Wennergren 1995). There is a danger that the mechanisms by which model outputs are generated will not be understood and that the models become black boxes that do little to increase our understanding of system behaviour. Indeed, this is a danger encountered by most modelling approaches. One way of countering this is to develop simpler models that are based on the same processes. The behaviour of the simple model can then be investigated more fully and compared to the behaviour of the more complex landscape model. Attempts could be made to attribute differences between predictions of the simple and complex models to particular features of the landscape. Under certain conditions spatial population dynamics may be explainable by general factors (i.e. the balance between inter- and intra-patch processes due to average patch size, connectivity, demographic rates and dispersal success). In contrast in certain landscapes spatial population dynamics may be governed by more specific factors e.g. one unusually large population that acts as a mainland, or a lack of connectance between some patches that acts to divide the population (Harrison 1994).

The model described in chapter 6 is effectively a simplified version of those described in chapter 5. Parameters could be set to mimic aspects of the beaver models. This would enable determination of whether the predictions generated by the custom built and Vortex models were a straightforward result of average patch sizes, demographic and dispersal success parameters, or whether they were largely dependant upon particular features of the patch network to which the models were applied.

At a more general level, three recent publications indicate the range of philosophies of ecological modelling (Peters 1991; Starfield 1997; Murdoch et al. 1992). Peters (1991) advocated that, in order for ecology to become a truly predictive science, ecologists should concentrate on empirically derived associative models rather than attempting to gain a mechanistic understanding. Of simulation models he said (p117) :

'By examining simulation models, one can show that mechanistic approaches do not realistically depict nature, but do offer a complexity which confounds specification of the model, propagates error, and renders the goal of the simulation too vast to be effective and too vague to be stated.'
Peters (1991).

In contrast Murdoch et al. (1992) advocated the development of individual-based models centred on the representation of mechanisms. They suggested that testability and generality can be combined by starting with complex models containing much system detail and progressively removing detail to develop simpler, general models. Testing the progressively simpler models should enable identification of the loss of predictive capacity accompanying the simplification. A similar approach was advocated by deRoos and Sabelis (1995).

In between these extremes Starfield (1997), advocated a pragmatic, management oriented approach to modelling, with models used as problem solving tools. He suggested that models be kept small and simple enough to be used and understood by wildlife managers. He also suggested that, in a management context where decisions have to be based on something, models could actually be more useful when data were lacking. This contrasts with the complex starting models advocated by Murdoch et al. (1992) and the models based entirely on empirical data advocated by Peters (1991).

Peters' (1991) concentration on empirical relationships and shunning of mechanistic explanations has been criticised elsewhere (e.g. Weiner 1993). Weiner (1993) and Conroy et al. (1995) have argued that mechanistic explanation can generate more general and robust predictions than obtainable from merely applying empirical relationships. It does seem that some mechanistic simulations (e.g. Folse et al. 1989; Wolff 1994) are so complex that a complete understanding of the interactions going on within the model is unlikely. Also, as pointed out by Peters (1991), there is no guarantee that the complexity generated by the model is the same or similar to the

complexity exhibited in nature. Nevertheless deconstruction of such simulations does offer prospects for increasing our understanding that would not be possible by studying natural systems in their entirety or by restricting modelling attempts to a very simple level. Where problems are likely to arise is if the results of complex models (or even simple models that are poorly understood) are applied to management issues. A difference should be recognised between models developed to increase general understanding and models developed to make predictions for a particular management issue (e.g. Holling 1966; May 1974; Caswell 1976). Although it has been recognised that these aims may be complementary (e.g. Conroy 1995) the danger occurs when they are confused :

> 'There is commonly a gap in the chain of logic stretching from a simple thought experiment to a management action. It skips at the point where a qualitative conclusion is applied in quantitative form to a specific problem. The constants of a model (which itself may or may not be structurally appropriate) are assigned values, often by guessing, and the output presented as a specific management recommendation.'
>
> Caughley (1994).

If the aim of a model is to increase understanding of a system then it can never be verified, validated or proved true (Caswell 1976; Oreskes et al. 1994; Bart 1995). A model that aims to make quantitative predictions applicable to a particular system can be assessed by the proportion of predictions that are within certain range of observed values. However, independent data are often unavailable at the scale at which a model is applied. In such a case model testing may be better directed at a models assumptions than its predictions (Oreskes et al. 1994; Bart 1995; Starfield 1997).

To minimise these problems mentioned above, Bart (1995) advocated a comprehensive protocol for the evaluation of individual-based models. This included a detailed model description, analysis of model reliability at the levels of a) structural assumptions, b) parameter values, c) secondary predictions and d) primary

predictions, and presentation of best and worst case scenarios spanning the range of plausible outcomes. It was suggested that this should be produced and peer reviewed prior to predictions being used to direct management decisions.

7.1 General Conclusions

I have outlined the interactions of mammals with space and the vast array of models that have been developed to represent different aspects of these interactions. I have shown that extrapolating from individual level processes is far from straightforward and that more research is required on the behavioural ecology of animal spacing before predictions can be made with confidence. I have also shown that caution needs to be exercised in the use of model predictions, as even relatively similar approaches can generate disparate predictions.

It is inevitable that a wide range of modelling approaches will continue to be applied to the spatial distribution of mammals. This can be healthy as long as increased efforts are made to put models in the context of each other and not to rely on the predictions of a single approach. Continued efforts should be made to test models at multiple scales, but it should be recognised that correspondence between predictions and observations does not guarantee a model to be a robust representation of the truth (e.g. Oreskes et al. 1994). A closer union of modelling and field approaches can only increase our understanding of the factors determining the spatial distribution of mammals and increase our ability to predict it. The uncertainty that will continue to accompany such predictions must be communicated when models are used in an applied setting.

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Appendix 1 : Derivation of Energetic Parameters used in Chapter 3

(i) Deriving the relative energetic costs of different activities

The metabolic rate in running squirrels is 1.4 - 2.8 times the resting metabolic rate (Wunder and Morrison, 1974 in Gurnell, 1987). As the active metabolic rate will be slightly higher than the resting metabolic rate the moving metabolic rate was estimated at 1.6 times the active metabolic rate. Minimum metabolic rates measured in the drey are 82% of the basal metabolic rate (Pauls, 1981 in Reynolds, 1985). As the basal metabolic rate is lower than the active metabolic rate, an estimate for the metabolic rate in the nest of 80% of active metabolic rate was used. Therefore the relative costs of different activities were modelled as : moving = 1.6 : active (eating or searching within a cell) = 1 : in a refuge = 0.8.

(ii) Deriving the absolute energetic costs and benefits of different activities

Monthly activity periods for red squirrels in North West England for June to February have been reported as 11.2, 8.7, 4.8 (mean = 8.2) hours (Tonkin, 1983 in Gurnell, 1987). Over this time the average time spent travelling is 8% (approx. 0.7 hours). Therefore the approximate time budget over 24 hours is moving = 0.7 hours, active = 7.3 hours, in drey = 16 hours. The three activities must balance the minimum energy requirement of 335 kJ (80 kCal, Grönwall, 1982). This energy balance can be solved to give the following energetic costs per hour : moving 25.26 kJ, active 15.79 kJ, in a refuge 12.63 kJ. These result in the following costs per time step : moving 0.029 kJ, active 0.018 kJ, in a refuge 0.014 kJ. In the uncertainty analysis values were taken from a range 10% above and below these estimates.

Estimates for the energetic benefit of a single pine cone vary between 3.84 kJ (Grodzinski and Sawick-Kapusta, 1970) and 2.85 kJ (Grönwall, 1982, obtained by dividing the average daily energy intake of 356 kJ by the average daily cone consumption of 125).

(iii) Converting energetics costs and benefits to weight losses and gains

Energetic costs and benefits were converted to weight losses or gains assuming a constant energy value per gram of body weight. In reality the energetic costs of the loss or gain of bodymass will be dependant on what is being metabolised or deposited (Robbins, 1993). It is mainly fat, protein, and water that are involved in weight change and these have approximately the following energy values per gram respectively, 38.1 kJ (9.1 kcal), 22.6 kJ (5.4 kcal) and 0 (Robbins, 1993). An estimate of 29.3 kJ (7kcal) per gram was made for the energetic value of a change in bodymass of 1 g based on an approximate composition of 50% fat and 50% protein.

Appendix 2 : South, A.B., Lurz, P.W.W. & Rushton, S.P. (1997) Simulating foraging movements of red squirrels (*Sciurus vulgaris*) to generate hypotheses regarding spacing patterns. In *The Conservation of Red Squirrels* (ed. J. Gurnell and P. W. W. Lurz). People's Trust for Endangered Species, London.

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Simulating foraging movements of red squirrels *Sciurus vulgaris* to generate hypotheses regarding spacing patterns

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Summary

A model simulating daily red squirrel (*Sciurus vulgaris*) foraging in a Scots pine (*Pinus sylvestris*) plantation is presented. Individual foragers move between cells in a hexagonal grid. The foragers exist in a number of behavioural states and have a 'memory map' of cone availability. Energetics and food consumption are explicitly modelled. The model presented here is one of a series of models to investigate the implications of plausible foraging behaviours. These models allow the range of possible spacing behaviours to be more closely defined and the generation of alternative hypotheses that can then be tested. Outputs from the model are compared with observed squirrel behaviour in the field.

Key-words: individual based model, energetics, spatially explicit, home range, behaviour, *Sciurus vulgaris*.

Introduction

Identification of the relationship between red squirrel (*Sciurus vulgaris*) densities and habitat structure is necessary if we are to be able to predict squirrel abundance in changing landscapes (Wauters *et al.* 1994). Animal density within an area is determined by the balance between births, deaths, immigration and emigration. The way that animals space themselves out influences these four processes and the social system exhibited determines the nature of this influence. In a strictly territorial system population densities need not be directly related to food availability as the size of defended areas may be determined by other factors such as avoidance of infanticide (Wolff 1997). If there are no territorial interactions between individuals, exploitation competition may limit population densities through an absolute shortage of food or through the inability of animals to utilise available food (Andrewartha & Birch 1954). The latter case can occur as food depletion by other foragers compromises the knowledge of the spatial location of food held by individuals.

In the UK the red squirrel exhibits a spacing pattern of overlapping home ranges (Lurz 1995, Tonkin 1983) although this does not necessarily mean that there are no territorial interactions (see Maher & Lott 1995). Space use in tree squirrels has been shown to vary depending on habitat type, the sex of the animal, the time of year and changes in food abundance (Smith 1968; Koford 1982; Benson 1980; Kenward 1985; Gurnel 1984, 1987; Wauters & Dhondt 1992). Wauters & Dhondt (1992) showed that spacing behaviour in European red squirrels was influenced by habitat quality with seasonal changes in range size relating to sexual activity, as well as changes in food abundance. Similar changes in home range size were also observed for red squirrels in the North of England (Lurz & Garson in press; Lurz, Garson & Wauters 1997), although site fidelity, space use and dispersal behaviour differed due to large variations in tree seed availability.

To predict spacing behaviour in novel landscapes, it is necessary to understand the mechanisms leading to the behaviour. Here we develop a model of squirrel foraging behaviour that includes no

territorial interactions or ranging related to sexual activity. The main inter-action between individuals in the model is caused by the depletion of food supplies. The model is being developed systematically, effectively creating a series of working hypotheses and the results of the models are then being compared to field data to test these hypotheses.

The model presented here, based upon a Scots pine (*Pinus sylvestris*) plantation, represents one of these working hypotheses. In such a habitat cones are the major source of food from June in one year (green cones) until March the following year when the seeds are shed (Tittensor 1970; Wauters & Dhondt 1987; Wauters, Swinnen & Dhondt 1992).

Methods

The model simulates squirrel foraging for each day for the period from June to March. It is based upon individual foragers that move between cells in a hexagonal grid. The foragers exist in a number of behavioural states and have a 'memory map' of food availability (cones). The major behavioural states are:- moving towards food, eating, hungry exploring, satiated exploring, moving towards a drey, resting in a drey, and dead. Transitions between behavioural states are summarised in Figure 1. Energetics and food consumption are explicitly modelled. Parameters used, their values and sources are outlined in Table 1.

Each day is divided up into time steps of two minutes, approximately the time taken to search for and consume a single pine cone within a pine tree (Moller 1983). Within each time step an individual either consumes a single cone, moves (up to a defined maximum distance), assesses a previously unvisited cell or rests in a drey. The number of time steps available in each day is determined by a function that calculates daylight hours according to the day of the year.

The animals start the season at an average weight. Each activity has a defined energetic cost per time step and cones have a defined energetic benefit and both of these are converted to weight losses or gains assuming a constant energy value per gram of body weight (Robbins 1993). Thus an individual's change in weight within a single time step is determined by the balance between weight lost due to maintenance and activity, and weight gain if a cone is consumed. Animals die if they go below a defined minimum body weight, and stop eating to prevent them from exceeding a defined maximum body weight. Alternatively death could be considered as emigration from the area as the net effect is the same.

A landscape of 25 ha (500 m x 500 m) is represented as a grid of 10000 hexagonal cells each representing 25 m^2. Food availability within this grid is a variable input with parameters determining the total amount of food, the maximum and minimum food values per cell and the aggregation of food cells. In the simulations presented here, cone availability was generated to simulate that observed at Spadeadam Forest in 1993 (Lurz 1995). In any one run cone availability is generated at the beginning of the season and depleted through the season by the action of the foragers.

Eight foragers are simulated, approximating the density of 0.33 squirrels per ha estimated for Spadeadam (Lurz 1995). A defined number of dreys per animal are positioned randomly in the landscape at the beginning of each run. To our knowledge, there has not been a comprehensive analysis of the spatial distribution of squirrel dreys. Positioning the dreys randomly allows multiple simulation runs to be conducted without dependence on one spatial pattern of drey locations. Each animal starts the first day of the season at a randomly chosen drey and knows the locations of all dreys in the landscape. If an animal is still active 20 minutes before the end of daylight it moves to the nearest drey. If this drey is already occupied it moves to the next nearest until it finds one that is unoccupied. Each animal can stay in any one of the dreys in the landscape providing it is unoccupied when the animal arrives there.

Animals start the season with no knowledge of food availability in the landscape. At this stage and at any other time during the simulation when an animal has no knowledge of food availability it switches to the 'hungry exploring' state. In this state the animal moves to the closest cell that it

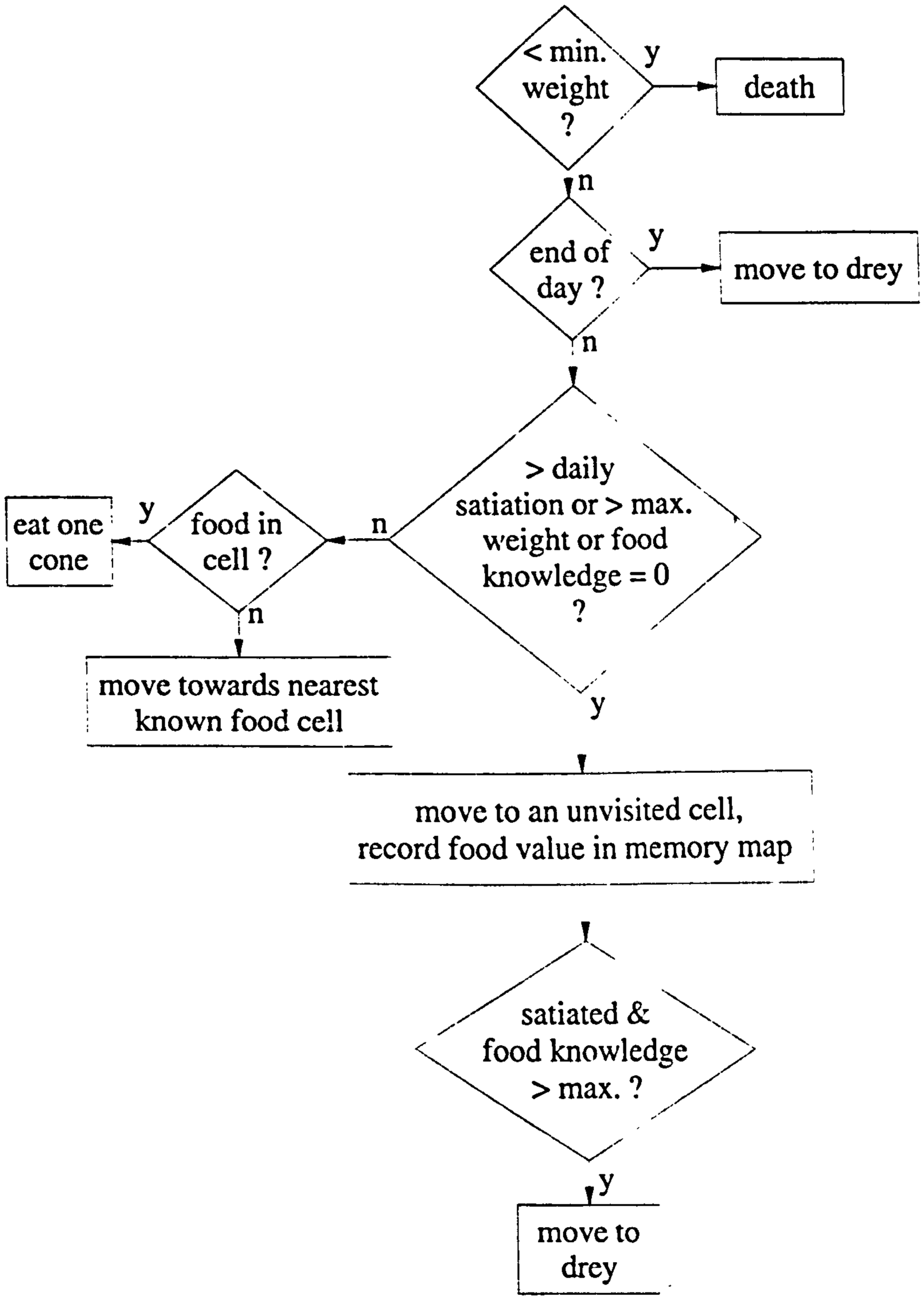

Figure 1. Main transitions between behavioural states for each individual in each time step. Each individual effectively works through the chart and enters the next time step when it can go no further. At each time step individuals move in a random order to stop any one individual having a time advantage over any other.

has not visited that season. If there are two or more equidistant cells the animal moves to the one that is closest to the drey it started from that day. The animal spends a defined number of time steps (search time) assessing the value of the new cell. After this, if the cell contains cones, the animal switches to the 'eating' state, otherwise it remains in the 'hungry exploring' state and moves to another unvisited cell in the next time step.

In the 'eating' state an animal consumes one cone per time step. The animal remains in the occupied cell until the food is depleted to zero or the animal changes state on reaching satiation or the end of the day. A functional response relating consumption rate to cone density could have been incorporated into the model but evidence from studies of captive fox squirrels (*Sciurus niger*) suggests that consumption rate does not vary considerably with cone density (Steele & Weigl 1992).

An animal with knowledge of available food in the landscape (and not currently occupying a cell containing food and not satiated) moves towards the nearest food cell in its memory. Animals can move a maximum number of cells per time step, determined by a maximum travel speed parameter. An animal that reaches daily satiation, determined by the maximum number of cones

Table 1. Model Parameters.

Model Parameters	Values used		Source
Food value of a single pine cone (kJ)	2.85		Grönwall (1982)
Cone density (per m^2)	low	1	Lurz (1995)
Max., mean and min. body weight (g)	350, 320, 260		Lurz (1995)
Energetic costs of daily activities (kJ/hour)	in nest	12.63	estimates based on Grönwall (1982), Gurnell (1987)
	active	15.79	
	travelling	25.26	
Energy content of squirrel body tissue (kJ/g)	29		estimate based on Robbins (1993)
Time to find and consume a cone (minutes)	2		Moller (1983)
Max. travel speed (m per min.)	50		Lurz (pers. obs.)
Dreys per animal	2.5		Lurz (1995)
Daily satiation (cones)	150		Grönwall (1982)
Time taken to assess food value of a previously unvisited cell (minutes)	10		estimate

that can be consumed in a day, or reaches its maximum body weight, switches to the 'satiated exploring' state. This is equivalent to the 'hungry exploring' state except that the animal does not switch to 'eating' on encountering food. If the animal obtains knowledge of enough food to support it until the end of the season (an upper threshold to food knowledge) it stops exploring and moves to an unoccupied drey. The rationale behind the 'satiated exploration' state is that it allows animals to build up a knowledge of food availability in the landscape. Without this component all animals tend to die early as they experience extended periodswhen they are unable to find food. During the 'satiated exploration' state each animal develops a unique memory map of food availability in the landscape dependant upon where it has been. At each time step the memory map of each animal is not complete and also contains inacuracies due to depletion by other animals. This was thought to be a more accurate representation of the information stored by an animal than perfect knowledge. The upper threshold to food knowledge was put in to stop animals from exploring for every hour of available daylight as this is seldom observed in the field (Reynolds 1985).

For each simulation run the following outputs were generated:- daily cone consumption, daily distance moved, daily activity period and variation in body-weight over the season. Additionally, animal locations were sampled once a day for 30 days to emulate a radio tracking study of space use. For one run of the model a minimum convex polygon (MCP) and 70% core area (based on recalculated arithmetic mean) were calculated for January using Ranges V (Kenward & Hodder 1995). This was compared with radio-telemetry data for female squirrels, collected in pine-dominated plantations at Spadeadam Forest, Cumbria in 1993 (Lurz 1995). Females only were used in this comparison as male ranges are principally determined by sexual activity rather than food availability (Wauters & Dhondt 1992).

The model was written in C and run on a UNIX workstation. The GIS GRASS (Westervelt *et al.* 1990) was used to display output maps.

Results

Ten model runs were performed each starting with eight individuals. The number of individuals that 'survived' the whole season ranged from one to three. At the start of the season each animal rapidly gained weight to reach the maximum (Figure 2a) (the level in the graph is slightly lower than the defined maximum body weight because weight was recorded at the beginning of the day, and some weight was lost since the last feeding episode on the previous day). The rapid weight gain is caused by each animal initially consuming cones at the maximum rate of 150 per day (Figure 2b) leading to a large positive energy balance each day. Once animals reached their maximum body weight, cone consumption dropped to about 100 cones per day and body weight stayed close to the maximum for most of the season. Occasional decreases in body weight occurred when animals failed to locate a sufficient number of cones.

Activity patterns and distances travelled were variable (Figures 2c & 2d). Activity periods followed the curve of available daylight hours for some animals in some time periods (Figure 2c) indicating that they utilised all available daylight on some days. Such periods of high activity occurred at the start of the season and following drops in cone consumption. The minimum activity period of about two hours corresponded to the time taken to eat the daily food requirement if the location of sufficient cones was known. Travel distances averaged approximately 200 m per day but occasionally reached distances of up to 1500 m. The peaks in distance travelled follow drops in cone consumption (Figures 2b & 2d).

For the one run of the model for which home ranges were estimated (for January) space use was relatively discrete with home ranges (Figure. 3) and core areas separated from each other. The MCP and core area estimates were smaller in the model than those observed for females in the field (MCP, model: 0.4 - 5 ha, field: 3 - 20 ha, Core area, model: 0.1 - 2.6 ha, field: 0.6 - 6.8 ha).

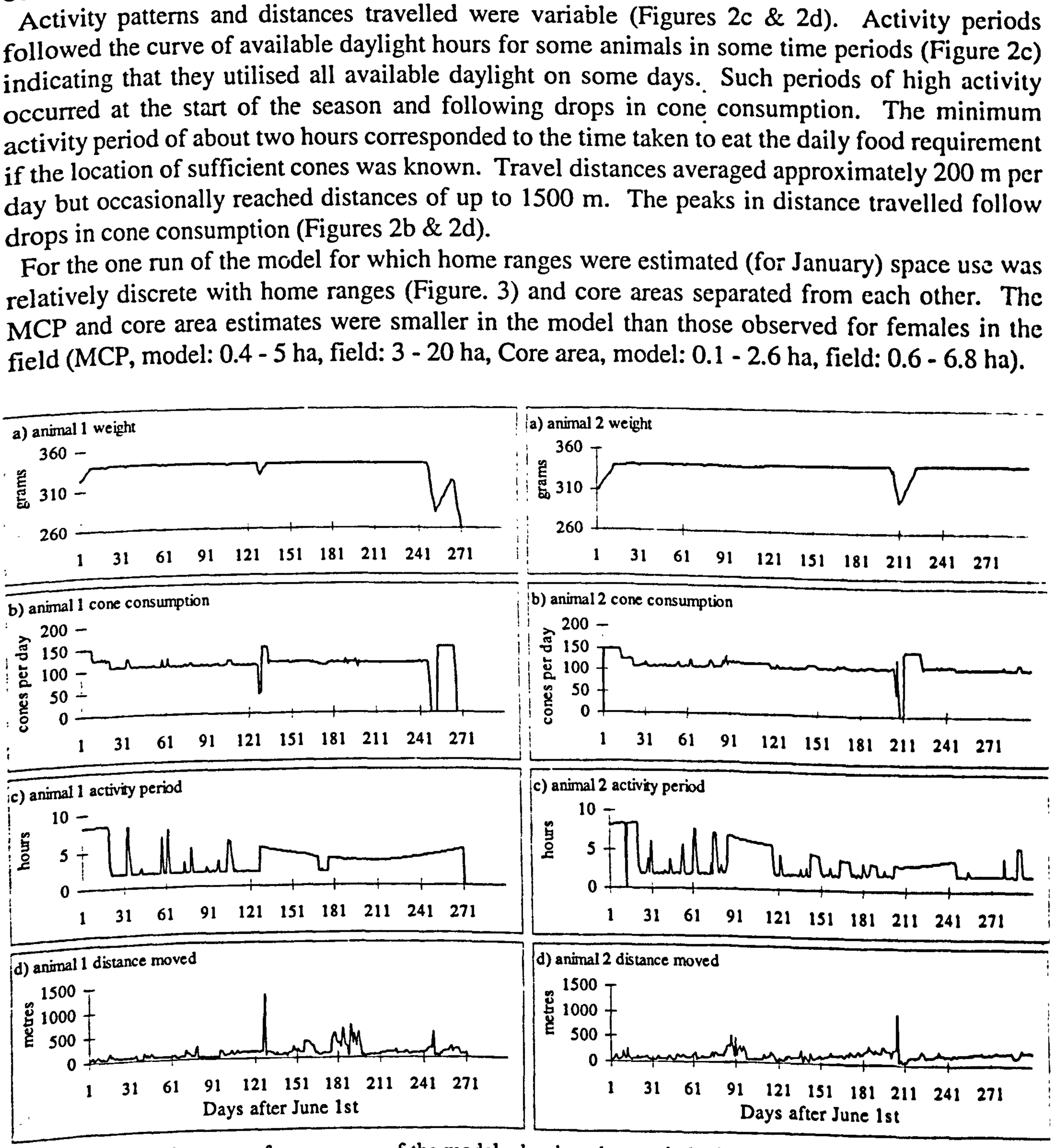

Figure 2. Example outputs from one run of the model, charting changes in body weight, cone consumption, activity patterns, and distance travelled per day for two of the eight squirrels.

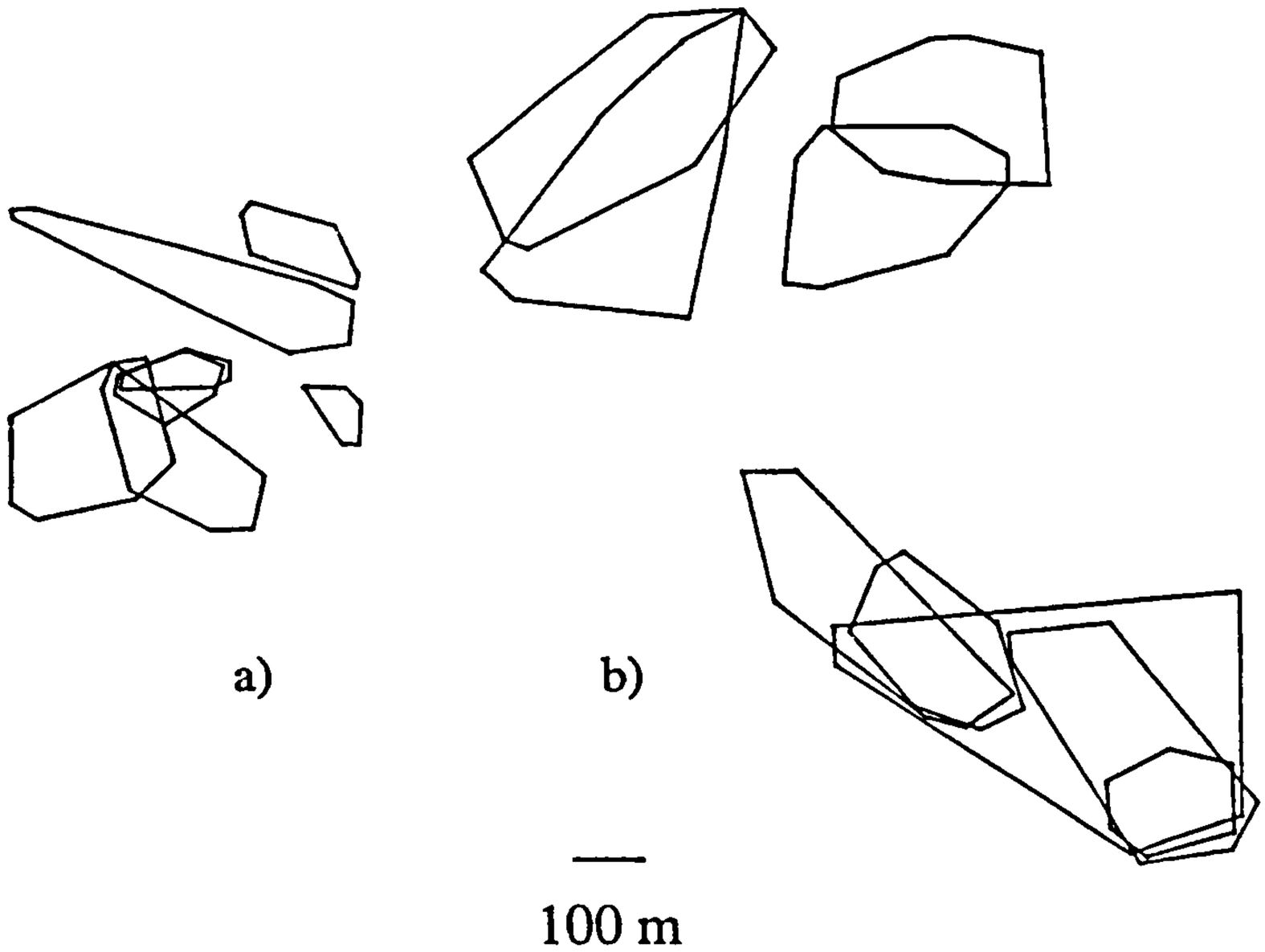

Figure 3. MCP range estimates for January. (a) Output from one run of the model (b) Spadeadam Forest radio-telemetry data (females).

Discussion

The fact that simulated squirrels died early in the season indicates that although food is available, they are unable to find it. Whether this occurs in the wild or whether this is an artefact of the model needs further investigation. A high turnover of squirrels was observed in Spadeadam (Lurz 1995) so the high rate of total mortality generated by the model (i.e. real mortality or emigration) is not inconsistent with field data. In the model, squirrels started the season with no knowledge of food availability. Although this will be the case for new arrivals, squirrels living in an area can monitor cone development prior to its availability as the pine cone crop for one year is visible as developing conelets in the preceding year (Lurz *pers. comm.*). The model could be used to investigate the relationship between prior knowledge of cone availability and squirrel survival. The model also does not yet take account of secondary food items or caching behaviour which have been shown to be important in times of low seed food availability (Gurnell 1983). Caching behaviour increases survival in the wild (Wauters, Suhonen & Dhondt 1995) and the high mortality caused by a relatively short number of days over which squirrels were unable to find food points to the possible importance of hoards. Hoarding and exploring are alternative potential strategies to survive local food shortages. The model could be used to investigate the ecological significance of exploring and hoarding, and their importance in energetic terms.

In Spadeadam squirrels maintained a stable body weight (~320 g), and changes generally were associated with sexual activity (Lurz 1995). Body weights generated by the model, although stable, were about 30 g higher than this. As none of the energetic drains of breeding, sexual activity or bad weather were included in the model it is perhaps not surprising that the animals tend to stay close to maximum body weight.

The January MCP range estimates generated by the model were smaller than those estimated for females at Spadeadam. Perhaps it would be more instructive to compare range sizes generated by the model to 70% core ranges estimated from field studies as these have been suggested to be determined primarily by foraging activity, whereas MCP range estimates include courtship chases and exploring activity (Tonkin 1983, Wauters & Dhondt 1992). Model generated MCP ranges were of a similar magnitude to 70% core areas estimated at Spadeadam. Changes in range size

associated with sexual activity often are associated with increased range overlap (Wauters & Dhondt 1992; Lurz, Garson & Wauters 1997) and thus have little effect on the density of animals within an area. Therefore this aspect of spacing behaviour may need to be factored out when looking for a relationship between food and squirrel density.

Perhaps the most tentative component of the model is that used to determine the exploratory behaviour of squirrels. The way that this is represented has a major effect on the model outputs. The problem is that there is little behavioural information available at the appropriate spatial and temporal scales. This adaptive modelling approach allows different plausible scenarios to be tested. In the scenario modelled here animals explore systematically outwards from temporarily occupied dens and do not re-explore previously visited areas. Alternative scenarios that could be modelled include animals making occasional explorations further afield and animals returning to previously explored areas enabling them to keep track of depletion by other individuals. The model can also be altered to incorporate other behaviours such as caching, leaving food cells before they are entirely depleted or territorial defence.

In addition to the uncertainty regarding behavioural mechanisms there are uncertainties regarding the values of some of the energetics parameters used in the model. For example the energy value of a single pine cone was set at 2.85 kJ in the model, derived from Grönwall (1982), whereas Wauters, Swinnen & Dhondt (1992) use a value of 3.54 kJ, derived from Grodzinski & Sawicka-Kapusta (1970). A sensitivity analysis is required to determine whether predicted behaviours are consistent across the range of reasonable parameter estimates.

With these reservations in mind, the pattern of space use generated by one run of the model for one month suggests that the spatial distribution of home ranges in Spadeadam could result solely from resource depletion rather than territorial defence. Further runs of the model are necessary to confirm this suggestion. Resource depletion, rather than territorial defence, recently has been postulated as a factor determining ranging patterns in the European badger (Stewart, Anderson & Macdonald 1997).

The model presented here is one of a series being developed to investigate the implications of plausible foraging behaviours. This approach allows the range of possible spacing behaviours to be more closely defined and the generation of alternative hypotheses that can then be tested. It can also be used to identify which individual level behavioural parameters are likely to be most important at the population scale. The results presented here are a preliminary application of the model. We will continue to investigate relationships between food availability, foraging and spacing behaviour through further model development and testing.

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