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Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach

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Summary

1. An integrated Geographical Information System (GIS)-Spatially Explicit Population Dynamics Model (SEPM) for investigating the dynamics of red squirrel *Sciurus vulgaris* and grey squirrel *S. carolinensis* populations in different landscapes is described.

2. Using the model, we simulated processes of reproduction, mortality and dispersal in individual populations of squirrels in habitat blocks identified within a GIS. We modelled dispersal as a process whereby individual animals moved between blocks of habitat separated by areas of unsuitable habitat. An interference model simulating the effects of competition between the grey and red squirrels was incorporated where both species occupied the same habitat blocks.

3. The model was used to investigate the spread of grey squirrels and its impact on the distribution of red squirrels in Norfolk, UK, where historical information on the decline in the red squirrel and the expansion of the grey squirrel were available.

4. We examined the effect of a range of life history scenarios differing in terms of adult mortality, juvenile mortality, fecundity, habitat carrying capacity and maximum dispersal distances. Model predictions were closest to the observed expansion of the grey squirrel and decline in the red squirrel when mortality was lower and fecundity higher than the averages recorded for the grey squirrel in the United Kingdom.

Key-words: Britain, interspecific competition, *Sciurus vulgaris*, population dynamics models, wildlife management.

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Introduction

Understanding the causes of changes in the distribution of species is a central theme of landscape ecology. It is also essential for the practical conservation of endangered species and the control of pests. The red squirrel *Sciurus vulgaris* L. and the grey squirrel *S. carolinensis* Gmelin. are species that utilize similar habitats. The first is a threatened native species, whilst the second is an exotic pest. Historical data indicate that the decline in the distribution of the first species has coincided with the expansion in the distribution of the second (Reynolds 1985; Usher, Crawford & Banwell 1992). It has been suggested that the decline in the red squirrel is linked to the spread of the grey squirrel; with the grey acting as a competitor or as a vector of a disease to which red squirrels are susceptible and greys are not (Reynolds 1985; Sainsbury & Gurnell 1995). There have been other hypotheses linked to food quality (Kenward & Holm 1993) and environmental change (Reynolds 1985), and there is evidence that both species may coexist in some landscapes without any apparent decline in the population of the red squirrel (Shorten 1953; Gurnell & Pepper 1993).

Whilst the habitats of woodland preferred by both species of squirrels are usually temporally stable and spatially well defined, predicting their distributions is not simply a case of ‘find a wood, find a squirrel’. Previous research has shown that the relationship between the distribution of the two species and landscape structure is more complex. The habitats used by squirrels in the UK are distributed as fragments throughout the landscape. Squirrels are highly mobile and may disperse readily through such landscapes (Gurnell 1987), moving from one block of habitat to another as food becomes available (Lurz, Garson & Rushton 1995). They may integrate their habitat requirements taking components of several habitats into their home ranges if there is not sufficient of the preferred habitat available. Red squirrels are thought to be adapted for living in conifer forests and are more arboreal than grey squirrels (Kenward & Tonkin 1986). Grey squirrels, in contrast, prefer broadleaf woodland, but also utilize suburban habitats where they are fed by people. Grey squirrels will also colonize conifer woodlands, but it has been suggested that they generally occur there at lower densities and appear to depend on the availability of broadleaves nearby. Both squirrel species may incorporate areas of unsuitable habitat within their home ranges (Andren & Delin 1994; Lurz *et al.* 1995).

This complexity in habitat use and the lack of information of how the two species interact means that predicting the ultimate distribution of both squirrel species is difficult. The only practical approach under these circumstances is through modelling. There are essentially two approaches; the first is to use associative models that attempt to relate the occurrence of squirrels to habitat and other environmental features that can be mapped, and the second is to use population dynamics models that attempt to derive distribution patterns from models of the underlying population processes that determine them.

Associative modelling approaches have been used to relate the incidence of both red and grey squirrels to the availability of suitable habitats. Logistic regression was used by Fitzgibbon (1993) to determine the relationship between woodland size, isolation and the incidence of grey squirrels. Van Apeldoorn, Celada & Nieuwenhuizen (1994) and Celada *et al.* (1994) used a similar approach to predict the occurrence of red squirrels in fragmented habitats, and Lurz *et al.* (1995) to investigate the effects of tree species composition on the population densities of red squirrels in conifer plantations. Whilst these models can be used to predict the distribution of squirrels in the landscapes for which they were developed, they may be of limited value in other landscapes particularly if the squirrels' relationship with the landscape changes. Wiens (1989) concluded that predators, competitors, spatial and temporal changes in the habitats utilized, and time lags in response may all limit the use of associative approaches in predicting bird distributions. These factors are all likely to be of importance in determining the response of squirrels to landscape structure, and models that simulate the life history processes that determine where the animals are in the landscape are therefore more appropriate.

There has been considerable interest in the development of modelling approaches for investigating the dynamics of populations in fragmented habitats. Much of the strategic research (*sensu* May 1973) in metapopulation dynamics has been based on analytical approaches (e.g. Hanksi 1991). Strategic modelling approaches of this type are useful in developing theory, but they are of limited value for those with a tactical interest in mammal populations in real landscapes for a number of reasons. First, real landscapes are so highly heterogeneous that analytical modelling approaches are not possible (Fahrig 1990). Where these approaches have been used to investigate the spatial dynamics of squirrel populations (Okubo *et al.* 1989) these have been under a restricted range of (often unrealistic) boundary conditions in homogeneous landscapes. Secondly, and probably in keeping with most populations (Harrison 1994), squirrels are unlikely to exist in true metapopulations and cannot be modelled as such (Van Apeldoorn *et al.* 1994). Squirrel populations are more likely to exist as 'mainland-island populations' where extinctions in suitable habitats may occur, but overall persistence is ensured by virtue of a 'mainland' population. Alternatively, they may exist as 'patchy populations' where the habitat utilized occurs at a spatial resolution of a finer grain than that of the animal itself. They may also exist as 'non-equilibrium metapopulations' where populations are totally isolated from each other. At the scale of the UK, there are red squirrel populations which are clearly non-equilibrium, in that isolated areas of distribution occur, for example, in the Brecklands of Norfolk and on the Isle of Wight. The former population is some hundreds of kilometres away from the nearest red squirrel population in Lancashire, whilst the latter is an island population where grey squirrels were never introduced. The extent to which populations may be patchy or non-equilibrium metapopulations at smaller scales is not known.

More tactical modelling approaches have been developed such as spatially explicit population modelling (SEPM) (Dunning *et al.* 1995). The purpose of SEPMs is to investigate the complex interactions between landscape structure and population dynamics. The methodology is based on a systematic approach that simulates the impacts of variations in the values of demographic parameters such as birth, death and dispersal probabilities on the distribution of individuals and populations in real landscapes. It is clear that more 'tactical' approaches that link deterministic models of life history processes with the spatial distribution of the habitats in which animals are found, are likely to be most suited for investigating the distribution of squirrels in the landscape of the UK. Despite widespread recognition of the need for such approaches (Norton & Possingham 1993), their development and application has not been rapid (Harrison 1994). In this paper we develop a generalised integrated GIS-spatial population dynamics model for red and grey squirrels. We use the model to investigate the distribution of these species in one area, Norfolk, UK, for which the distribution and abundance of the habitats used by squirrels are known. Norfolk was colonized by the grey squirrel in the 1960s and subsequently red squirrels declined. Published distribution data for this area (Reynolds 1985) are used to validate the model.

Methods

STUDY AREA

The study area comprised 8100 km^2 of south-eastern England containing the county of Norfolk, a 90 × 90 km square with corners of the National Grid 650 000, 560 000, 260 000 and 350 000. This is a low-land landscape comprising the catchments of the rivers Yare, Bure and Waveney where, historically, red squirrels were widely distributed, and where the historical spread of the grey squirrel and an associated decline of the red squirrel have been documented (Reynolds 1985).

SQUIRREL HABITATS

The major habitats utilized by red and grey squirrels are broadleaf and conifer woodland. In this study, suburban habitats were also considered suitable for occupation by grey squirrel. The distribution of these habitats in the study area was highly fragmented with broadleaf and conifer woodland and suburban habitats comprising 3·3, 2·7 and 6·8% of the total land area, respectively.

THE SIMULATION MODEL

Overall structure

The model for simulating the landscape distribution of red and grey squirrel populations in landscapes has two main components. The first is a geographical information system (GIS) which stores environmental, habitat and animal population information. This system undertakes data manipulation and abstraction, and provides inputs for the second component. The second consists of programs simulating the population dynamics of each squirrel species, and their interactions and dispersal within the GIS-held landscape. The geographical information system used to store and retrieve habitat information and model output was GRASS (Westervelt *et al.* 1990). The population dynamics programs were written in the programming language C and integrated with the GIS component.

Defining habitat suitability, habitat use and carrying capacity of habitat blocks

The land surface was divided into areas of habitat used by each squirrel species and areas of non-habitat through which animals could move when dispersing. Identification of habitat suitable for occupation by red and grey squirrels within the landscape was undertaken in the GIS. Suitable habitats were defined as broadleaf and conifer woodland, and suburban areas as recognized by categories of the Institute of Terrestrial Ecology classification of Landsat satellite imagery (Fuller, Groom & Jones 1994). Red squirrels were assumed to utilize conifer and broadleaf woodland habitats. Grey squirrels were assumed to inhabit suburban and broadleaf woodland, and conifer woodland to a depth of 500 m, that shared a boundary with either broadleaf woodland or suburban habitats. Red squirrels are known to favour conifer over broadleaf woodland (Corbet & Harris 1991; Wauters & Dhondt 1987). Grey squirrels favour broadleaf woodland and particularly those with large seed producing trees (Fitzgibbon 1993). They are also known to utilize gardens and parks in suburban habitats (Corbert & Harris 1991). Whilst there is no published data on squirrel densities or home ranging behaviour, it has been suggested that grey squirrels will utilize conifer woodland when this is adjacent to other suitable habitat (Gurnell 1987). Both red and grey squirrels are also known to utilize small fragments of suitable habitat (Verboom & Van Apeldoorn 1990; Fitzgibbon 1993; Wauters, Matthysen & Dhondt 1994), but it is clear that such small areas do not constitute the sole range of animals that use them. Rather, they form components of ranges which contain other woodlands.

The size, composition and distribution of habitat blocks was used to identify blocks of suitable habitat in which squirrels of each species could be found. The minimum area capable of supporting a population of each species was selected on the basis of published relationships between habitat block size and the incidence of populations for areas where woodland habitats were fragmented.

In the case of the grey squirrel, Fitzgibbon (1993) showed that a minimum area of greater than 6 ha was necessary to ensure the presence of dreys in woodland without hazel *Corylus avellara* or beech *Fagus sylvatica*. Where hazel and beech were present in woods, the equivalent area was between 3 and 4 ha. Celada *et al.* (1994) produced a similar relationship for the incidence of red squirrel in broadleaf woodland and in this case only woodlands of size greater than 22 ha had a 99% chance of red squirrels being present, whilst those of 6 ha or more had an 89% probability. Similar relationships between conifer woodland size and the incidence of red squirrels have been derived (Van Apeldoorn *et al.* 1994), but these have been for complex, closely fragmented habitats. In this model, the minimum size of habitat block considered suitable for occupation by grey squirrels was set at 6·25 ha and the minimum size occupiable by red squirrels was assumed to be 12·5 ha (after Lurz 1995). Since squirrels may occupy blocks of habitat which contain fragments of non-suitable habitat (Verboom & Van Apeldoorn 1990; Bright 1993; Andren & Delin 1994). Andren & Delin (1994) recorded non-suitable habitat as comprising up to 12% of the home ranges of female red squirrels they studied in fragmented habitats in Scandinavia. We allowed blocks of habitat that were deemed suitable for occupation by squirrels to comprise up to 12% non-suitable habitat.

The carrying capacities of each block of habitat in the landscape for each species were calculated on the basis of published estimates of core range size and the extent of overlap observed in home range use. The minimum amount of space required by a squirrel was assumed to be related to its home range. This was expressed as the number of core areas (defined as 70% of all recorded observations within a home range, following Wauters & Dhondt 1992) that could be fitted into the habitat block. The minimum core area size for a red squirrel was assumed to be 2·3 ha as recorded in conifer woodlands by Wauters & Dhondt (1992). Equivalent data for the grey squirrel were not available so were derived from estimates of home range. Sixty per cent core ranges of grey squirrels range between 28 and 30% of total home range (after Corbert & Harris 1991). Total home ranges have been recorded between 5 and 11 ha in the UK (Gurnell 1987). This suggests a core range for the grey squirrel of *c.* 2·3 ha, similar to that of the red squirrel.

Since squirrels do not occupy home ranges exclusively, a species packing factor was calculated which allowed for the fact that individual core ranges in squirrels can overlap. This factor scaled the population estimate up for each habitat block on the basis of how many core ranges it could contain and how much overlap was allowed between ranges. The species packing factor was estimated from the literature. In the case of red squirrels, there is considerable variation in overlap. In the study population of Wauters & Dhondt (1992), the average overlap per animal was *c.* 10%. This gives a species packing factor of 1·1. In the case of the grey squirrel the extent of overlap in home ranges in the UK has not been quantified, although evidence from Thompson (1978) for Canada indicates that similar overlap between several individuals within habitat blocks is possible. Equivalent data on overlap of core areas in grey squirrels were not available so, whilst this may be higher than that recorded for the red squirrel, the same species packing factor as that of the red squirrel was used in the model.

The extent to which woodlands are suitable for occupation by squirrels depends on their composition. In the case of grey squirrels, smaller woods with seed bearing trees are more likely to support squirrels than larger woods without (Fitzgibbon 1993). Similarly, conifer woodlands containing Norway Spruce *Picea abies* or Scots Pine *Pinus sylvestris* contain more red squirrels than do those consisting of Sitka spruce *Picea sitchensis* (Lurz *et al.* 1995). It was not possible to identify the species composition of broadleaf or conifer woodland habitats from the ITE Land Cover Classification. All conifer woodland was considered of equal quality and all broadleaf woodland likewise. Population densities of red squirrels in conifer and broadleaf woodlands differ, however, and this is believed to reflect the temporal availability of food sources in each habitat (Wauters & Dhondt 1992). The core range size in broadleaf woodland has been shown to be one and a half times bigger than that in conifer woodland (Wauters & Dhondt 1992). The difference in quality between conifer and broadleaf habitats for red squirrels was incorporated into the model by scaling the carrying capacity of habitat blocks for broadleaf woodland by a factor of 0·6. The effects of habitat composition on squirrel populations were modelled by varying the carrying capacity of the habitat blocks as a model input.

Population dynamics, interspecific interactions, and dispersal of red and grey squirrels in landscapes

Each block of suitable habitat within the landscape was modelled as having separate populations of red and grey squirrels. Squirrel population processes were modelled at integer level, that is fractional individuals of squirrels were not permitted. Each population had its own dynamics which interacted through the processes of dispersal and an indirect form of interspecific competition. For each habitat block, in each year, population size was modelled in terms of the net change due to four factors. These were: gains due to recruitment from breeding and immigration of adults, and losses due to adult and juvenile mortality and emigration. Reproduction in both species of squirrel was assumed to occur in two waves, in early and late spring. All adult females bred once and a further 35% of animals in their second or older years bred twice. Litter size was varied as a model input at run time. Mortality in both species of squirrel was assumed to occur after breeding and was varied as a model input.

Dispersal was modelled as a process occurring once a year in autumn and was assumed to occur as a result of intraspecific competition. Both sexes were assumed to disperse equally. Gurnell (1987) noted that the association between autumn dispersal, food availability and population density suggested that squirrels space themselves out through contest competition. In this model, dispersal was triggered when the density of sub-adults and adults exceeded the core range carrying capacity of the habitat block. Wauters & Dhondt (1993) showed that dispersal amongst red squirrels tends to occur in autumn and spring, and mainly amongst sub-adult/juveniles. Animals of both species were allowed to disperse to blocks of habitat that were at or below the carrying capacity for that species. Accurate information on the dispersal distances of squirrels was not available, although dispersal up to 64 km has been recorded in grey squirrels and maximum daily movements of 2·8 km observed in the red squirrel (Andren & Delin 1994). Maximum dispersal distance was varied as a model input. If there were no suitable habitats available for occupation then dispersers were also assumed to die.

Dispersing grey squirrels were allowed to invade habitat blocks that were occupied by red squirrels provided that they were suitable and within range of the site of their birth. If dispersing grey squirrels successfully invaded a habitat block occupied by red squirrels and survived until the next season, they were assumed to be capable of competing with that species. In the presence of grey squirrels, the breeding success and carrying capacity of the habitat for red squirrels was assumed to be reduced in direct and linear proportion to the population size of grey squirrels and the habitat block carrying capacity. Thus, for example, if the grey squirrel population was at $x\%$ of the carrying capacity of the habitat block for this species, the reproductive success of red squirrels was reduced by $x\%$ and the number of adults by $x\%$ and the carrying capacity of the habitat for red squirrels reduced by $x\%$. This model effectively assumes that red squirrels suffer interference competition from grey squirrels. Gurnell & Pepper (1993) suggested that red squirrels may not obtain sufficient food to survive or reproduce in the presence of grey squirrels, but evidence for the existence of interspecific competition is not clear cut. A flow diagram illustrating the population dynamics processes in the model is shown in Fig. 1.

Sensitivity analysis of the population models to input parameters

The sensitivity of the population dynamics model to the input parameters was investigated by analysing the spatial dynamics of each squirrel species individually in the landscape of Norfolk.

In the first instance, the model was run for red squirrels in the absence of grey squirrels to evaluate the extent to which populations of red squirrels could persist within the landscape. In essence, this meant establishing populations of red squirrels at each suitable habitat site and then running the model for 16 years, under a range of life history scenarios. Secondly, the dynamics of invasion by the grey squirrel in the absence of the red were investigated by running the model after introducing grey squirrel populations at invasion foci corresponding to the known distribution in Norfolk in 1965/1966. Four levels of fecundity, four levels of mortality; two maximum dispersal distances, and two levels of carrying capacity were investigated for both the red and grey squirrel (see Table 1). The two levels of carrying capacity were imposed to simulate variations that could arise in the core range or the quality of the habitat present. All permutations of fecundity, mortality, dispersal distance and carrying capacity were investigated, giving a total of 64 scenarios for each species. The fecundity and mortality levels used in the model encompass the ranges considered by Gurnell (1987) to represent good and average seed years for squirrels.

Analysis of the dynamics of invasion of Norfolk by grey squirrels and its consequences for populations of the red squirrel

The impact of invasion of grey squirrels on the distribution of the red squirrel in Norfolk was investigated by running red and grey squirrel models together, and incorporating the interspecific competition outline above. The initial populations for the red and grey squirrel were based on the observed distribution in 1965/1966. In the case of the red squirrel all available habitat in squares observed to be occupied was allocated an established population at the carrying capacity for the habitat. The fecundity, mortality and dispersal distances used for the grey squirrel were based on those of the sensitivity analysis run which produced the closest match between predicted distributions and those observed in the field from 1965/1966 to 1981. These were two high fecundity-low mortality scenarios of four and five pups per litter with adult: juvenile mortality of 10:50%, run at both the high and low carrying capacity scenarios, and with 10 and 20 km maximum dispersal distances; making a total of eight different life history combinations. The scenarios used for the red squirrel were: fecundity at three pups per litter at adult:juvenile mortalities of 25:58% and 40:75%. These were run under both the high and low carrying capacity scenarios with a maximum dispersal distance of 10 km, making a total of four life history combinations. These combinations represent low mortality and average mortality scenarios for the red squirrel. Each scenario for the grey squirrel was run in combination with all the possible scenarios for the red squirrel giving a total of 32 runs.

Each of the 32 runs was validated by comparing the predicted distribution of populations of red and grey squirrels in the Norfolk study area with the published data of Reynolds (1985). The data in Reynolds (1985) detail records for both species in 5-km squares of the National Grid in the county of Norfolk. Maps at equivalent spatial resolution were created by scaling up the model output at 50 m resolution to 5-km blocks of the National Grid using the GRASS GIS. For each year of a model run the following information was abstracted from the maps:

(1) total number of 5-km squares predicted and observed to be occupied (a);

(2) total number of 5-km squares not predicted and not observed to be occupied (b).

From each map in each year of each model run the simple matching coefficient (SMC) indicating the proportion of squares correctly predicted to be populated or non-populated by red squirrels was calculated:

$$\text{SMC} = (a + b)/\text{total number 5-km squares in Norfolk}$$

Results

SQUIRREL HABITATS

The mean number of 50 × 50-m parcels of habitat in each area of contiguous habitat in the Norfolk study

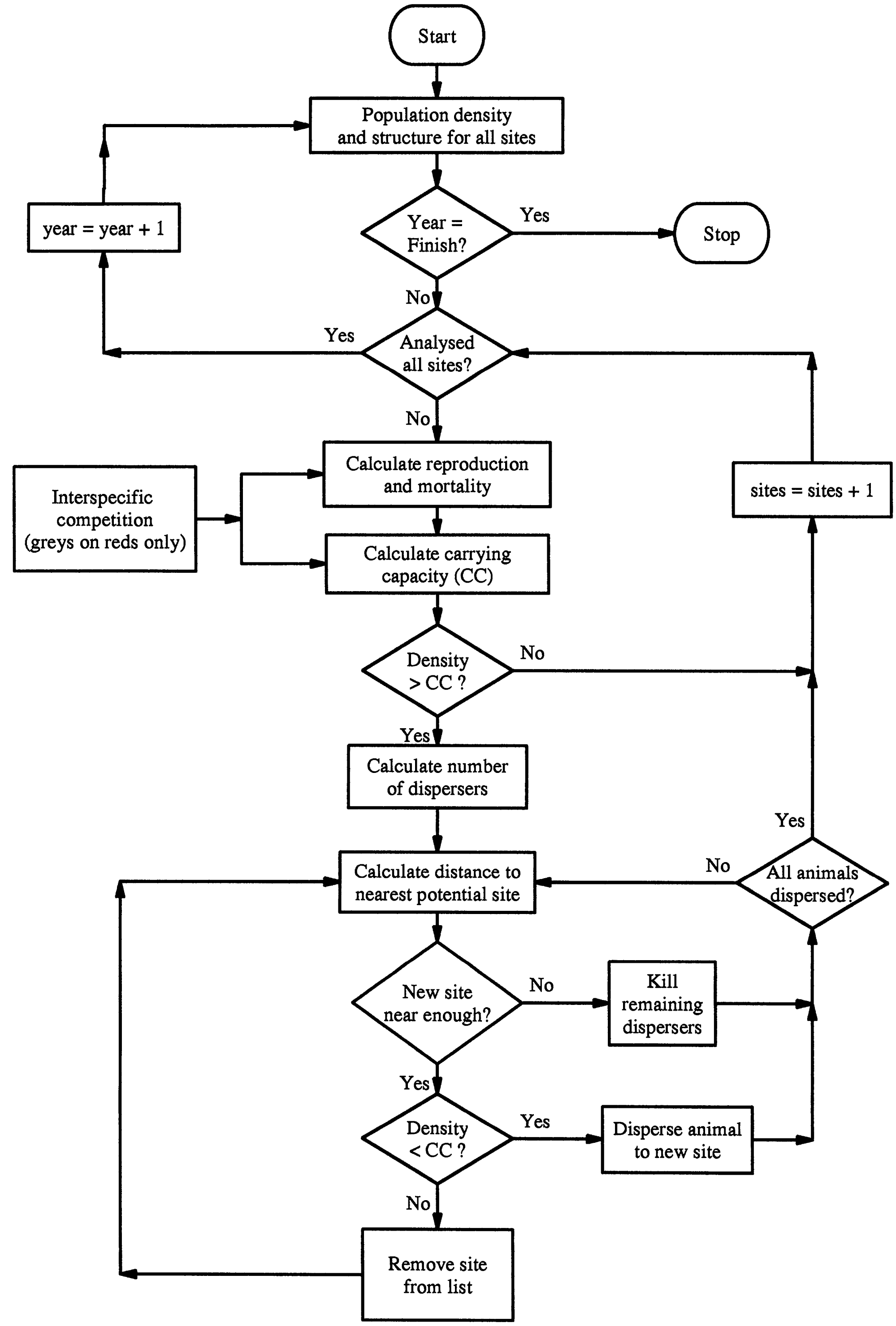

Fig. 1. Flow chart showing the structure of the population dynamics model for red and grey squirrels.

Table 1. Life history parameters used in the sensitivity analyses of the population dynamics models for the red and grey squirrel

Adult mortality (%)	50	40	25	10
Juvenile mortality (%)	79	75	58	50
Fecundity (young)	2	3	4	5
Maximum dispersal distance (km)	10	20		
Carrying capacity	1·0	0·5		

area as identified from the ITE Land Cover Map for 1989 are shown in Table 2. Also included are summary data describing the separation of habitat blocks in space. Habitats are separated into three types: those assumed to be used by red squirrels exclusively, those used by grey squirrels exclusively and those capable of use by both species. The most obvious feature is the difference in the availability of each habitat type across the region with the greatest abundance in the south-west of the region. This coincides with the area

Table 2. Habitat information for the Norfolk study areas: (a) Size characteristics of habitat blocks. Mean number of 50 × 50 m land parcels making up a block of habitat as used by red and grey squirrels in the study area as derived from the ITE Land Cover Map for 1989

	Red exclusive		Grey exclusive		Shared	
Area	Mean	*n*	Mean	*n*	Mean	*n*
Norfolk	11·1	152	19·3	1144	62·3	571

(b) Spatial separation characteristics of habitat blocks. Mean nearest neighbour distance (m) between blocks usable by each squirrel species. > 10 km = number of habitat blocks in study area with nearest neighbour greater than 10 km away

	All red habitats				All grey habitats			
Area	Mean	SD	*n*	> 10 km	Mean	SD	*n*	> 10 km
Norfolk	1473·3	1843·0	723	3	1352·2	2254·2	522	3

where the grey squirrel was first established in Norfolk in the 1930s and 1940s.

The mean distance between nearest neighbour habitat blocks assumed to be used by each species was less than 2000 m and less than 0·5% of the blocks present were further than 10 km away from an adjacent block (Table 2b). This indicates that nearly all habitat blocks, whilst fragmentary, were within very close proximity to each other. This suggests that inter-habitat blocks distances would be within the range of dispersal of both squirrel species.

SENSITIVITY ANALYSES

Red squirrels

The total number of 5-km grid squares predicted to have populations of red squirrels in Norfolk over 15 years based on a starting population derived from the observed distribution in 1965/1966 are shown in Table 3a and 3b for 64 life history juvenile mortality, fecundity, carrying capacity and dispersal scenarios.

The most obvious feature of these results is that for all runs the model predicted that populations of red squirrels would persist in Norfolk for 15 years in the absence of greys. The number of squares occupied increased with increased fecundity and decreased survivorship. For model runs where fecundity was higher than three pups per female, the number of squares occupied became constant by the fifteenth year of the run. Increased fecundity and decreased mortality increased the number of squares occupied. In the case of the low fecundity, high mortality scenarios the number of squares occupied declined, indicating that the population of red squirrels would eventually become extinct. For scenarios with adult and juvenile mortalities of less than 25 and 75%, respectively, the number of squares occupied reached an upper limit of *c.* 108. Where this limit was reached in any run, the population then appeared to enter a stable cycle, oscillating between 96 and 108 squares occupied in each year. Halving the carrying capacity of the habitat decreased the number of squares occupied under each life history scenario, indicating that fewer sites were occupied when carrying capacity was reduced. Similar biennial cycles were predicted in the high fecundity-low mortality scenarios, but the maximum number of squares occupied was different. The cycling represented successive extinction and recolonization of individual woodland blocks in 5-km squares. Consideration of the individual blocks of habitat present where this occurred showed that extinction and recolonization occurred in habitat blocks that were small and incapable of supporting more than three adults. Increasing the maximum dispersal distance increased the number of squares predicted to be occupied, but the effect was not as important as changing mortality or fecundity, and there was no effect at all in the high fecundity–low mortality scenarios.

In summary, the model predicted that red squirrel populations would persist in Norfolk under all life history scenarios except that where fecundity was below average and mortality was above average, but the number and variation in numbers of squares occupied in each year was dependent on the values of mortality, fecundity, carrying capacity and dispersal distance used.

Grey squirrels

The total number of 5-km grid squares predicted to have populations of grey squirrels in Norfolk over 15 years based on a starting population derived from the observed distribution in 1965/1966 are shown in Table 4a and 4b for 64 life history juvenile mortality, fecundity and dispersal scenarios. Grey squirrels were predicted not to invade Norfolk under any scenario where mortality was 40% per year or greater. Only in those runs for which mortality was less than this was there any increase in the number of 5-km grid squares

Table 3a. The number of 5-km squares in Norfolk remaining occupied by red squirrels under different fecundity, mortality and maximum dispersal distance scenarios. Carrying capacity = 1·0

Mortality		Fecund	2	2	3	3	4	4	5	5
		Dist. (km)	20	10	20	10	20	10	20	10
Adult	Juvenile	Year								
0·5	0·79	1	94	91	98	92	98	96	99	97
		5	53	53	73	73	86	83	93	91
		10	31	31	73	73	83	79	98	91
		15	22	21	74	74	80	78	96	92
0·6	0·75	1	97	91	8	95	99	97	99	97
		5	56	55	92	86	91	89	90	91
		10	47	47	90	88	101	97	107	98
		15	42	41	90	84	97	93	96	96
0·25	0·58	1	99	96	99	97	99	97	99	98
		5	99	94	99	99	99	99	99	99
		10	107	98	108	105	108	106	108	108
		15	99	94	99	99	99	99	99	99
0·10	0·50	1	99	96	99	97	99	98	99	98
		5	99	97	99	99	99	99	99	99
		10	108	106	108	106	108	108	108	108
		15	99	97	99	99	99	99	99	99

Table 3b. The number of 5-km squares in Norfolk remaining occupied by red squirrels under different fecundity, mortality and maximum dispersal distance scenarios. Carrying capacity = 0·5

Mortality		Fecund	2	2	3	3	4	4	5	5
		Dist. (km)	20	10	20	10	20	10	20	10
Adult	Juvenile	Year								
0·50	0·79	1	73	72	95	86	101	92	104	94
		5	36	35	54	53	58	57	75	69
		10	20	19	54	53	57	56	71	69
		15	11	11	54	53	60	59	73	69
0·40	0·75	1	87	80	100	90	104	93	105	94
		5	43	43	62	61	84	77	92	84
		10	31	31	63	60	88	74	88	81
		15	30	30	63	62	93	79	96	88
0·25	0·58	1	105	97	110	100	111	102	111	104
		5	97	87	110	101	111	102	111	105
		10	86	79	88	87	86	87	86	91
		15	97	87	110	101	111	102	111	105
0·10	0·50	1	109	99	111	103	111	104	111	104
		5	109	99	111	104	111	105	111	104
		10	88	86	86	90	86	91	86	92
		15	109	99	111	104	111	105	111	104

occupied by grey squirrels. In those runs where expansion did occur the number of squares occupied increased sigmoidally, reaching an upper asymptote of between 160 and 190 5-km grid squares. The rate of expansion was greatest when fecundity was greater than three young per female. Increased dispersal distance increased the rate at which 5-km squares were colonized, but the effect was not apparent when there were only very few squares colonized. Decreased carrying capacity decreased the number of squares occupied and slowed the rate of predicted expansion of grey squirrels. The observed number of squares occupied by grey squirrels over the same period is shown in Table 5. There were two important differences between the numbers of squares observed to be occupied and the number predicted by the model. First, the observed expansion was not smooth, with a large expansion observed in 1970–71 which was not observed in the model. Secondly, for all model runs expansion was slower in the first few years after 1966 than was actually observed. The model predictions lagged behind the observed by between 3 and 5 years in all cases. This latter may reflect differences in the observed populations of grey squirrel in 1966 and the initial starting conditions used in the model.

The mean simple matching coefficient and mean to standard deviation ratio for comparing observed and predicted numbers of 5-km squares occupied by grey squirrels for each year over the period 1966–81 for each of the 64 life history scenarios are shown in

Table 4a. The total number of 5-km squares in Norfolk invaded by grey squirrels under different fecundity, mortality and maximum dispersal distance scenarios. Carrying capacity = 1·0

Mortality		Fecund	2	2	3	3	4	4	5	5
		Dist. (km)	20	10	20	10	20	10	20	10
Adult	Juvenile	Year								
0·50	0·79	1	3	3	3	3	3	3	3	3
		5	0	0	1	1	1	1	1	1
		10	0	0	1	1	1	1	1	1
		15	0	0	1	1	1	1	1	1
0·40	0·75	1	3	3	3	3	3	3	3	3
		5	0	0	1	1	1	1	1	1
		10	0	0	1	1	1	1	1	1
		15	0	0	1	1	1	1	1	1
0·25	0·58	1	3	3	3	3	3	3	3	3
		5	1	1	2	2	3	3	7	7
		10	1	1	3	3	8	8	46	39
		15	1	1	8	8	117	65	194	144
0·10	0·50	1	3	3	3	3	3	3	3	3
		5	3	3	3	3	6	6	8	8
		10	4	4	10	10	95	58	147	92
		15	20	20	161	96	196	165	197	188

Table 4b. The total number of 5-km squares in Norfolk invaded by grey squirrels under different fecundity, mortality and maximum dispersal distance scenarios. Carrying capacity = 0·5

Mortality		Fecund	2	2	3	3	4	4	5	5
		Dist. (km)	20	10	20	10	20	10	20	10
Adult	Juvenile	Year								
0·50	0·79	1	3	3	3	3	3	3	3	3
		5	0	0	0	0	0	0	0	0
		10	0	0	0	0	0	0	0	0
		15	0	0	0	0	0	0	0	0
0·40	0·75	1	3	3	3	3	3	3	3	3
		5	0	0	0	0	0	0	1	1
		10	0	0	0	0	0	0	1	1
		15	0	0	0	0	0	0	3	3
0·25	0·58	1	3	3	3	3	3	3	3	3
		5	0	0	2	2	2	2	4	4
		10	0	0	2	2	16	16	70	44
		15	0	0	21	21	126	62	178	121
0·10	0·50	1	3	3	3	3	3	3	3	3
		5	1	1	3	3	4	4	4	4
		10	1	1	7	7	40	35	137	74
		15	1	1	112	66	177	141	171	164

Table 6a and b. For all model runs, the mean simple matching coefficient was greater than 0·61 suggesting that in all cases the model predicted the correct squirrel status for 5-km squares at greater than 60%. This would suggest that the model was reasonably accurate over all possible life history scenarios. In reality, for those model runs where grey squirrel fecundity was less than 3 and adult mortality was 40% or greater per year, grey squirrels were not predicted to invade Norfolk at all. This apparent high match reflects the composition of the simple matching coefficient (which gives equal weighting to matches between squares predicted and observed to have, and squares predicted and observed not to have the squirrel) and the fact that there were many maps with few squares occupied. Thus, in the early years of any one run, the match between observed and predicted maps was very high because the majority of the squares were empty of grey squirrels and scores were high even if the model failed to predict any invasion. A more meaningful measure of the match between model predictions and observations is the measure of the deviation of the mean value of the matching coefficient for each run. A low standard deviation relative to a high mean would indicate a sustained high level of fit of model to observed distributions as these changed over the 15-year sample period. On this basis, the high fecundity-low mortality scenarios provided the best match between predicted and observed squirrel distributions.

Table 5. The number of 5-km grid squares observed to be occupied by red and grey squirrels in the Norfolk study area from 1966 to 1981. Data are derived from Reynolds (1985)

Year	Red squirrels	Grey squirrels
1966	168	5
1967	166	6
1968	166	15
1969	166	22
1970	164	39
1971	163	90
1972	100	98
1973	95	100
1974	83	104
1975	78	103
1976	75	113
1977	71	116
1978	62	121
1979	49	122
1980	41	141
1981	19	150

DYNAMICS OF INVASION OF NORFOLK BY GREY SQUIRRELS AND THEIR CONSEQUENCES FOR POPULATIONS OF THE RED SQUIRREL

The change in the number of 5-km grid squares occupied by red squirrels as they interacted with the expanding grey squirrels under each of the 32 life history-carrying capacity-dispersal distance scenarios are shown in Table 7. In all scenarios the initial number of squares occupied by red squirrels was lower than observed suggesting that the model underestimated the range of the red squirrel in Norfolk. The observed number of squares occupied by red squirrels is shown in Table 5. There was a large decline in the number of squares occupied after 1971, this lagged behind the largest proportional increase in squares occupied by grey squirrels by 1 year. This decline was not observed in the model. The model predicted a range of responses with different lag times, but in all scenarios the number of squares predicted to be occupied by red squirrels declined. The decline in numbers of squares occupied was greatest where grey squirrel fecundity was high and mortality was low, and the carrying capacity for the red squirrel was low. Where mortality for the grey squirrel was increased or the maximum dispersal distance and carrying capacity were decreased, the rate of decline in the number of squares occupied by red squirrels was slower. The mean simple matching coefficients comparing the predicted red squirrel distributions with those observed in the field for each of the 32 scenarios are shown in Table 8. In all models the mean simple matching coefficient was greater than 67%. The mean to standard deviation ratio for all models was greater than that estimated from the grey squirrel models suggesting that the variation in the matching coefficient between years was lower for the red squirrel than for the grey. The five pups per litter low carrying capacity for greys and 25% mortality high carrying capacity for reds scenario had the highest mean simple matching coefficient and the second highest mean to standard deviation ratio indicating that this model run was that which most closely matched the observed change in red squirrel distribution in the field.

Maps showing the observed and predicted distribution of the red and grey squirrel under the scenario which most closely matched that observed in Norfolk over the period 1965/1966 to 1981 are shown in Figs 2 and 3 at 3-year intervals. For the red squirrel, the model appeared to underestimate the distribution of the species at the beginning of the run, but produced distributions similar in form by the end, with populations becoming highly fragmented with centres in the east and south-west by 1981. For the grey squirrel, the model suggested an initially slow spread from the two invasion foci which accelerated towards the end of the run. Spread was more rapid than observed from the north-eastern focus and there was an overall overprediction in the north-west area where observations suggested grey squirrels were not found. This suggests that the model may have over-estimated the availability of grey squirrel habitats in this area. The poor fit of the model predictions for the grey squirrel reflects the time-lag in expansion after the start of the model run and the non-smooth observed expansion in the field from 1970 to 1971.

Discussion

One of the most important aspects of assessing models is the extent to which their output can be validated against data from sources independent of those used in their creation. In this study we used data on the historical distributions of red and grey squirrels in Norfolk over the period 1966–81, as reported in Reynolds (1985) for validating the model. Comparisons of the results of the model with those of Reynolds (1985) show that matches between observed and predicted were by no means perfect. There are several potential sources of error in the model which may have given rise to these mismatches. It is possible that the model was conservative in its estimation of the availability of habitats in Norfolk at the beginning of the study. It was assumed that the habitats available for use by squirrels in 1965/1966 were the same as those represented by the ITE Land Cover Map of 1989. Since there were no data available for the woodland and other habitat covers for 1965/1966, the impact on the model cannot be assessed. Conversely, it is also possible that the sampling/recording of squirrels during these initial years was inaccurate. First, Reynolds (1985) discussed this in some detail. He noted that an intensive survey of squirrels by the Ministry of Agriculture, Fisheries and Foods in 1971 led to a fictitiously high extinction rate for red squirrels from 1971 and 1972, and an apparently high spread of grey

Table 6a. Mean simple matching coefficients comparing observed distribution of grey squirrels in 5-km grid squares in Norfolk with those predicted by the model under a range of fecundity, mortality and maximum dispersal distance scenarios. Mean calculated for 15 maps for the period 1966–81. Carrying capacity = 1·0

	Mortality	Adult	0·50	Juvenile	0·79			
Fecund	2	2	3	3	4	4	5	5
Dist. (km).	20	10	20	10	20	10	20	10
Mean	0·61	0·61	0·61	0·61	0·61	0·61	0·61	0·61
Mean/SD	3·05	3·05	3·09	3·09	3·09	3·09	3·09	3·09
	Mortality	Adult	0·60	Juvenile	0·75			
Fecund	2	2	3	3	4	4	5	5
Dist. (km)	20	10	20	10	20	10	20	10
Mean	0·61	0·61	0·62	0·62	0·62	0·62	0·62	0·62
Mean/SD	3·05	3·05	3·09	3·09	3·09	3·09	3·09	3·09
	Mortality	Adult	0·25	Juvenile	0·58			
Fecund	2	2	3	3	4	4	5	5
Dist. (km)	20	10	20	10	20	10	20	10
mean	0·62	0·62	0·62	0·62	0·64	0·64	0·66	0·65
mean/sd	3·09	3·09	3·16	3·16	3·63	3·55	4·01	3·93
	Mortality	Adult	0·10	Juvenile	0·50			
Fecund	2	2	3	3	4	4	5	5
Dist. (km)	20	10	20	10	20	10	20	10
Mean	0·63	0·62	0·65	0·65	0·67	0·66	0·67	0·67
Mean/SD	3·25	3·25	3·80	3·71	4·17	4·07	4·22	4·38

Table 6b. Mean simple matching coefficients comparing observed distribution of grey squirrels in 5-km grid squares in Norfolk with those predicted by the model under a range of fecundity, mortality and maximum dispersal distance scenarios. Mean calculated for 15 maps for the period 1966–81. Carrying capacity = 0·5

	Mortality	Adult	0·50	Juvenile	0·79			
Fecund	2	2	3	3	4	4	5	5
Dist. (km)	20	10	20	10	20	10	20	10
Mean	0·61	0·61	0·61	0·61	0·61	0·61	0·61	0·61
Mean/SD	3·05	3·05	3·05	3·05	3·05	3·05	3·05	3·05
	Mortality	Adult	0·60	Juvenile	0·75			
Fecund	2	2	3	3	4	4	5	5
Dist. (km)	20	10	20	10	20	10	20	10
Mean	0·61	0·61	0·61	0·61	0·61	0·61	0·62	0·62
Mean/SD	3·05	3·05	3·05	3·05	3·05	3·05	3·10	3·10
	Mortality	Adult	0·25	Juvenile	0·58			
Fecund	2	2	3	3	4	4	5	5
Dist. (km)	20	10	20	10	20	10	20	10
Mean	0·61	0·61	0·62	0·62	0·64	0·64	0·67	0·65
Mean/SD	3·05	3·05	3·26	3·26	3·55	3·55	4·18	4·06
	Mortality	Adult	0·10	Juvenile	0·50			
Fecund	2	2	3	3	4	4	5	5
Dist. (km)	20	10	20	10	20	10	20	10
Mean	0·62	0·62	0·64	0·64	0·67	0·67	0·68	0·68
Mean/SD	3·10	3·10	3·76	3·55	4·46	4·46	4·53	4·53

squirrels over the period 1970–71. These two factors are major contributors to the poor match between the observed and predicted distribution patterns for both species. Secondly, the records or sightings for squirrels in each year may not have represented the presence of established populations. Records may represent the

Table 7. The predicted number of 5-km grid squares in Norfolk remaining occupied by red squirrels following invasion by grey squirrels under a range of life history scenarios for each species

Grey fec	4	4	4	4	4	4	4	4
Red fec	3	3	3	3	3	3	3	3
Grey mort	0·10	0·10	0·10	0·10	0·10	0·10	0·10	0·10
Red mort	0·25	0·25	0·25	0·25	0·40	0·40	0·40	0·40
Grey cc	High	Low	High	Low	High	Low	High	Low
Red cc	High	Low	Low	High	High	Low	Low	High
Grey dd	20	20	20	20	20	20	20	20
Red dd	10	10	10	10	10	10	10	10
Year 1	97	100	100	97	95	90	88	95
2	105	86	86	105	95	70	70	95
3	99	84	84	99	84	68	68	84
4	105	84	84	105	90	60	60	90
5	99	85	85	99	87	57	58	86
6	105	83	83	105	83	59	59	83
7	98	84	83	98	87	58	58	88
8	102	80	81	101	80	55	58	78
9	89	81	78	94	77	52	52	79
10	81	73	62	96	63	49	44	77
11	63	62	53	72	51	40	33	62
12	49	44	36	63	34	32	26	42
13	41	29	25	41	25	18	16	26
14	40	22	22	41	20	13	12	22
15	36	24	21	36	18	12	11	20
Grey dd	10	10	10	10	10	10	10	10
Red dd	10	10	10	10	10	10	10	10
Year 1	97	100	100	97	95	90	88	95
2	105	86	86	105	95	70	70	95
3	99	84	84	99	84	68	68	84
4	105	84	84	105	90	60	60	90
5	99	85	85	99	87	57	58	86
6	105	83	83	105	83	59	59	83
7	98	84	83	98	87	58	58	88
8	102	80	81	101	80	55	58	78
9	89	81	78	94	77	52	52	79
10	93	76	72	97	73	51	49	79
11	79	75	66	84	64	46	41	72
12	77	61	58	85	53	43	39	61
13	66	56	53	68	50	37	33	56
14	61	48	41	68	39	30	27	42
15	46	43	33	52	31	24	18	37
Grey fec	5	5	5	5	5	5	5	5
Red fec	3	3	3	3	3	3	3	3
Grey mort	0·10	0·10	0·10	0·10	0·10	0·10	0·10	0·10
Red mort	0·25	0·25	0·25	0·25	0·40	0·40	0·40	0·40
Grey cc	High	Low	High	Low	High	Low	High	Low
Red cc	High	Low	Low	High	High	Low	Low	High
Grey dd	20	20	20	20	20	20	20	20
Red dd	10	10	10	10	10	10	10	10
Year 1	97	100	100	97	95	90	88	95
2	105	86	86	105	95	70	70	95
3	99	84	84	99	84	68	68	84
4	105	83	84	105	91	59	60	90
5	98	84	84	98	85	58	57	86
6	104	82	83	103	83	59	59	82
7	94	81	81	94	84	55	52	84
8	96	77	73	99	72	52	49	76
9	72	65	61	74	59	41	42	64
10	56	43	40	58	41	28	29	42
11	44	27	31	40	32	16	21	26
12	40	22	23	40	22	13	12	22
13	36	22	21	37	18	11	11	19
14	38	19	19	38	18	11	11	18
15	36	22	22	36	18	11	11	18

Table 7—*Continued.*

Grey dd	10	10	10	10	10	10	10	10
Red dd	10	10	10	10	10	10	10	10
Year 1	97	100	100	97	95	90	88	95
2	105	86	86	105	95	70	70	95
3	99	84	84	99	84	68	68	84
4	105	83	84	105	91	59	60	90
5	98	84	84	98	85	58	57	86
6	104	82	83	103	83	59	59	82
7	94	81	81	94	84	55	52	84
8	97	77	76	99	74	51	51	76
9	82	73	72	82	72	45	49	72
10	81	62	59	84	63	42	43	66
11	69	58	57	69	56	37	37	57
12	64	46	43	65	45	30	32	42
13	45	40	32	52	31	24	19	36
14	46	31	26	53	25	18	15	32
15	39	29	25	41	24	15	14	25

Grey = grey squirrel; Red = red squirrel; fec = fecundity; mort = mortality adult; cc = carrying capacity; dd = dispersal distance.

Table 8. Mean simple matching coefficients comparing maps of the predicted distribution of the red squirrel in 5-km squares in Norfolk under different life history scenarios and the observed distribution of red squirrels for the period 1966–81

Grey fec	4	4	4	4	4	4	4	4
Red fec	3	3	3	3	3	3	3	3
Grey mort	0·10	0·10	0·10	0·10	0·10	0·10	0·10	0·10
Red mort	0·25	0·25	0·25	0·25	0·40	0·40	0·40	0·40
Grey cc	High	Low	High	Low	High	Low	High	Low
Red cc	High	Low	Low	High	High	Low	Low	High
Grey dd	20	20	20	20	20	20	20	20
Red dd	10	10	10	10	10	10	10	10
Mean	0·69	0·68	0·69	0·68	0·69	0·68	0·68	0·69
Mean/SD	8·62	6·80	6·90	8·62	6·90	5·23	5·23	6·90
Grey dd	10	10	10	10	10	10	10	10
Red dd	10	10	10	10	10	10	10	10
Mean	0·67	0·67	0·67	0·66	0·68	0·67	0·67	0·67
Mean/SD	11·16	8·37	8·37	13·20	8·50	5·58	5·15	8·37
Grey fec	5	5	5	5	5	5	5	5
Red fec	3	3	3	3	3	3	3	3
Grey mort	0·10	0·10	0·10	0·10	0·10	0·10	0·10	0·10
Red mort	0·25	0·25	0·25	0·25	0·40	0·40	0·40	0·40
Grey cc	High	Low	High	Low	High	Low	High	Low
Red cc	High	Low	Low	High	High	Low	Low	High
Grey dd	20	20	20	20	20	20	20	20
Red dd	10	10	10	10	10	10	10	10
Mean	0·70	0·69	0·69	0·70	0·69	0·68	0·67	0·69
Mean/SD	8·75	6·90	6·27	11·42	6·90	5·23	5·23	6·90
Grey dd	10	10	10	10	10	10	10	10
Red dd	10	10	10	10	10	10	10	10
Mean	0·68	0·69	0·68	0·68	0·69	0·68	0·67	0·69
Mean/SD	9·71	6·90	6·80	9·71	6·90	5·23	5·15	6·90

Grey = grey squirrel; Red = red squirrel; fec = fecundity; mort = mortality adult; cc = carrying capacity; dd = dispersal distance.

presence of transient individuals. Comparisons of such data with those of the model, which represented established populations as sites with two or more adults present, may have therefore been invalid.

Whilst it is obvious that there was a reasonable match between the observed and predicted distributions of both squirrel species, this does not constitute a critical assessment of this modelling approach. It is possible, for instance, that the results may have arisen from fortuitous selection of the correct values for the input variables. Indeed, by using a scatter-gun approach, whereby the whole range of possible life history scenarios was modelled it is in some sense inevitable that a match between model predictions and the observed squirrel distributions would be found. It is also not surprising that the

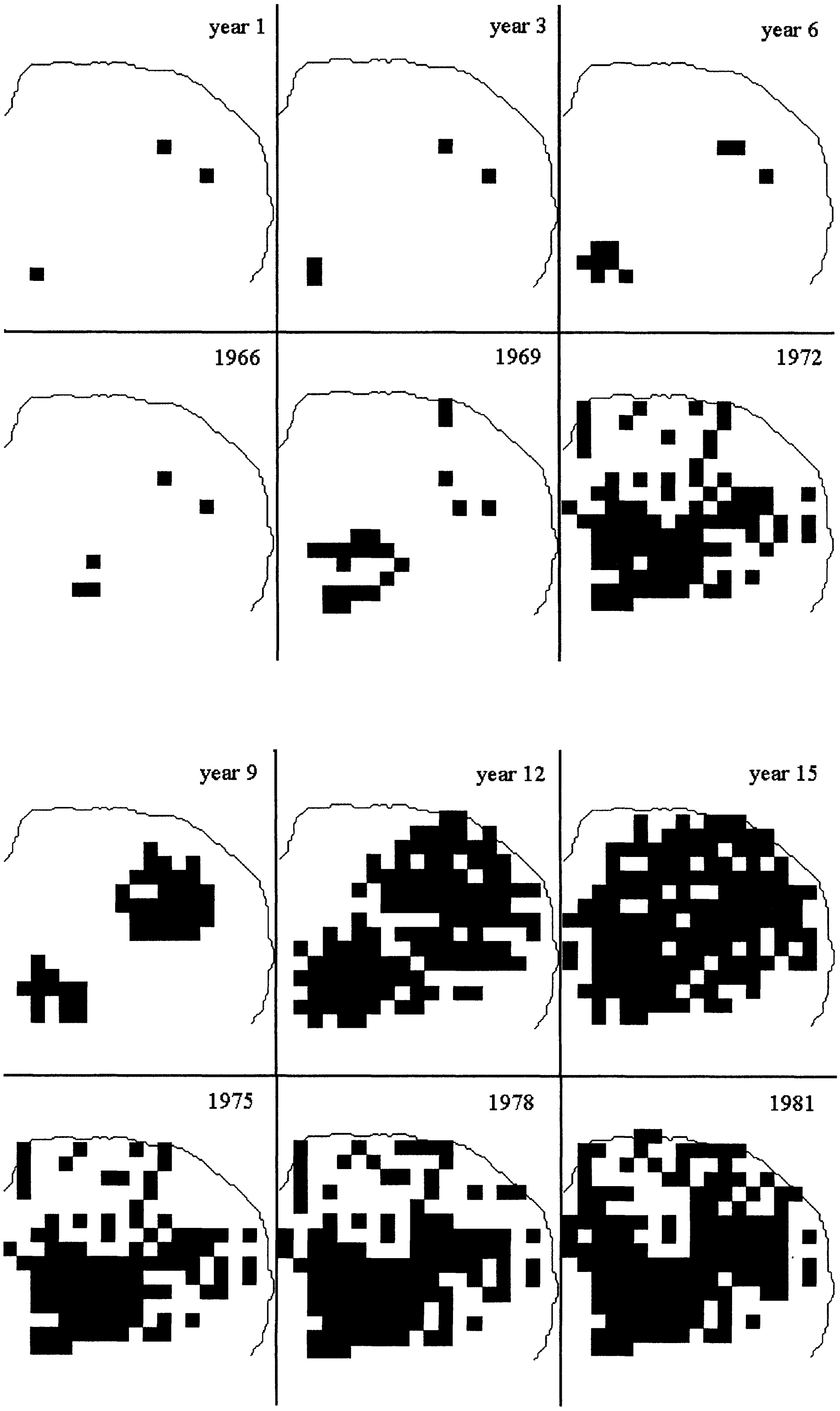

Fig. 2. Changes in the number of 5-km squares occupied by grey squirrels in Norfolk as predicted by the model over 16 years. Adult mortality = 10%, juvenile mortality = 50%. Starting populations were based on observed distribution of grey squirrels in Norfolk in 1966. Fecundity was held constant at five pups for the first brood and three for the second, maximum dispersal distance was 10 km. Carrying capacity = 50% (see text). Observed changes in the number of squares occupied over the period 1966–81 are included for comparison.

sensitivity analyses showed that the effects of varying the life history, carrying capacity and dispersal distance parameter inputs for both squirrel species were for the most part predictable. In the case of the grey squirrel, decreased mortality, increased fecundity, increased carrying capacity and increased maximum dispersal distance, increased the rate at which the species colonized Norfolk. Varying the same para-

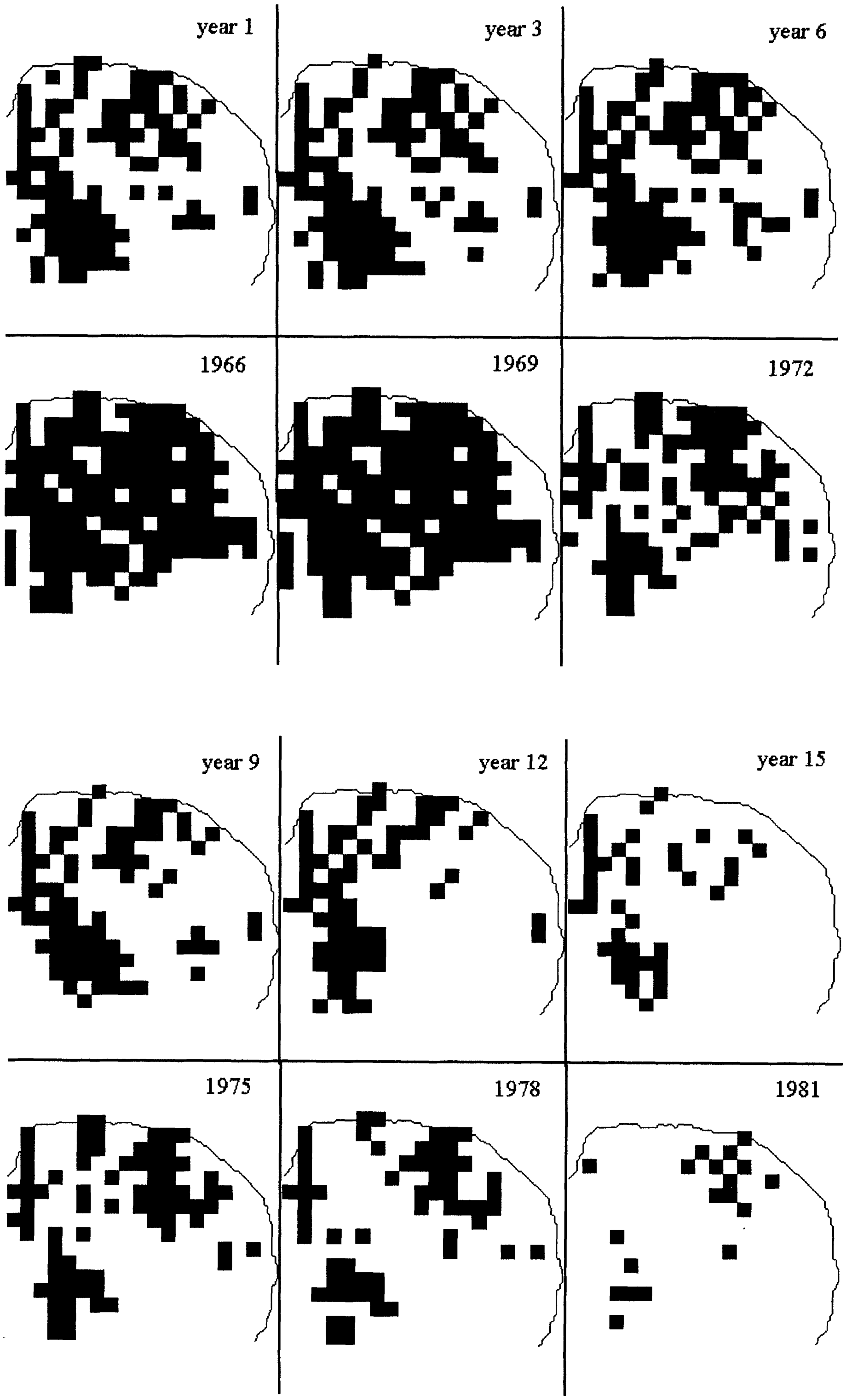

Fig. 3. Changes in the number of 5-km squares occupied by red squirrels in Norfolk as predicted by the model over 16 years. Adult mortality = 25%, juvenile mortality = 75%. Starting populations were based on observed distribution of red squirrels in Norfolk in 1966. Fecundity was held constant at three pups per brood, maximum dispersal distance was 10 km. Carrying capacity = 100% (see text). Observed changes in the number of squares occupied over the period 1966–81 are included for comparison.

meters in the same way for the red squirrel, increased the number of habitats occupied by the species in all years. Where survival and fecundity were higher, more 5-km squares had populations present. In terms of the populations in these squares, this meant that smaller habitat blocks were being occupied by squirrels than at lower fecundity, dispersal and higher mortality levels. The inference is that small habitat blocks in squares with sparse habitat could not maintain breeding populations without their being repeatedly invaded from other squares with a net surplus of squirrels to disperse. In effect, the model demonstrated a simple form of metapopulation behaviour for red squirrels when grey squirrels were excluded. Of greater interest, however, is the fact that the sensitivity analyses showed that the grey squirrel could not have invaded Norfolk without populations having a lower than average mortality and increased reproductive output (*sensu* Gurnell 1987) over the period during which invasion occurred. There are two possible reasons for this. It is possible that the process of dispersal and the factors determining it were not modelled accurately. SEPMs differ from other population modelling approaches in that they include dispersal. It is an implicit assumption of any SEPM that it is possible to model the animal's perception of the landscape through which it is dispersing. The paucity of data on the behaviour of animals and their mortality during the dispersal process is generally considered to be a factor determining the accuracy of SEPMs (Wennergren, Ruckelhaus & Kareiva 1995). In this study, dispersal was only assumed to occur in those habitat blocks where there was insufficient space available for each squirrel to have a core range, that is, it was assumed to be saturation dispersal (Stenseth 1984). Whilst there is considerable evidence that competition for space is a major factor determining dispersal of young squirrels (Wauters & Dhondt 1993; Wauters *et al.* 1994), space use is highly variable, and core ranges are known to expand and contract in relation to a variety of factors. Of these, the availability of food and the population density of surrounding squirrels are known to be important factors determining range size in both red (Wauters & Dhondt 1992) and grey squirrels (Kenward 1985). Core range size was fixed in this model at one of two levels. This meant that dispersal was an all-or-nothing (step-response) when populations exceeded the space available for them in each habitat block. At high population densities, a fixed core range may have been too rigid and over-emphasised dispersal by underestimating the carrying capacity for individual blocks of habitat. Conversely, since dispersal was considered to be saturation in type and only triggered when populations exceeded the space available for them, dispersal at low population densities may have been underestimated. Clearly, the saturation density of squirrels will have a significant impact on the rate of spread of grey squirrels, with higher values in the model leading to a slower spread as individual habitat blocks take longer to fill to saturation. It is obvious that more subtle dispersal-core range response relationships are required to make the dispersal component of this model more realistic. These relationships need to take cognisance of the factors which cause young squirrels to leave the maternal home range, as well as the mechanisms by which squirrels find, move to and occupy new sites, since there is considerable evidence that this is also dependent on the site of birth (Wauters & Dhondt 1993). Secondly, the average values for squirrel mortality and fecundity recorded in the literature (Gurnell 1987) may not have been those experienced by grey squirrel populations in Norfolk from 1965 to 1981. It is possible that the values given for grey squirrel mortality and fecundity by Gurnell (1987), represent measures determined from studies of established populations rather than those at the boundary of an invasion front. Populations of grey squirrels at the edge of an invasion front are likely to experience different conditions to those of an established population in that population densities will be low and probably subject to less intraspecific competition.

The model estimated mortality and fecundity in populations using average values from the literature and it effectively assumed that all of the habitats in Norfolk were of equal quality and were equally capable of supporting populations of squirrels. There is abundant evidence that different conifer species produce cones at different intervals (Lurz *et al.* 1995) and that the quality of these cones as food for red squirrels also differs (Hibberd 1991). In this model, the conifer forest was assumed to be of equivalent quality to Scots pine. This species retains its cones and tends to cone in most years. It is likely that much of the conifer woodland present in the study area was plantations of Sitka spruce, Norway spruce or Corsican Pine *Pinus nigra*. Neither of the first two of these species cone every year. Furthermore, Sitka does not provide as good a food resource for squirrels as Scots pine (Lurz *et al.* 1995). Thus, the model will have over-estimated population densities, particularly for red squirrels, by exaggerating carrying capacity, survival and fecundity in individual habitat blocks. Lurz *et al.* (1995) showed that such plantations generally had lower population densities of red squirrels than those containing other species. In addition, it is possible that the minimum woodland size for supporting red squirrels may have been too high, as Kenward and Holm (1993) recorded 6 ha as the minimum occupied habitat block on Furzey Island. The effect of this would be to cut out small areas of woodland that may have supported populations with the net effect of accelerating the rate of decline of red squirrels.

The model assumed also that factors beside intraspecific competition for space and dispersal were unimportant in determining the dynamics of squirrel populations; factors such as outbreaks of parapoxvirus disease which are known to influence the survival of squirrel populations were not included. This disease has been suggested as a cause of the decline in red squirrels (Reynolds 1985) and is considered to be a threat to the success of re-introduction schemes (Sainsbury & Gurnell 1995). The model needs extending to include a disease component to assess the significance of this disease on the output. One obvious consequence is that the extinction of red squirrels could arise as a result of the presence of infected *transient* individual grey squirrels (i.e. non-established populations). This would give rise to the loss of red squirrels in 5-km squares before greys are detected in them as noted by Reynolds (1985). In addition to the non-inclusion of variations in habitat quality, the effects of density independent factors such as between-year variations in weather on squirrel mortality and reproductive success were also not included. Whilst the model was developed to include all of these forms of variation, there were no data available to use as inputs. The effects of temporal variability in any of the modelled processes have to be considered carefully. It is clear that the longer any model run is, the greater will be the chance that unusual years, e.g. harsh winters or differences in coning, will fall within the model run period. Furthermore, since the outputs of populations size and distribution from each year provide the inputs for the next, it is clear that errors arising from temporal variation are likely to compound as the model is run for progressively longer periods.

Given these considerations, what are the conclusions that can be drawn from this study? First, it is obvious that the model was capable of emulating historical expansion in the distribution of grey squirrels within the Norfolk landscape with reasonable accuracy. Secondly, and more interestingly, the results also suggested that inclusion of a simple model of interference competition between red and grey squirrels was sufficient to explain the decline of the red squirrel in Norfolk as the grey squirrel expanded its range. Okubo *et al.* (1989) used an aspatial, but analytical, modelling approach to investigate the spatial dynamics of both species and concluded, in common with this study, that interference competition alone was a sufficient mechanism to explain the decline in distribution of red squirrels. Whilst the model may have predicted the observed changes in distribution of both squirrel species in Norfolk it is unclear whether or not this model has a general application in areas other than that for which it was created. This model clearly needs evaluating in other areas before its utility can be assessed.

At a more general level, it is clear that whilst the modelling framework developed in this study is very simple, it has succeeded in highlighting areas where further research on squirrel ecology is required. More importantly, it is also obvious that this modelling approach could be quite easily generalized to investigate the spatial population dynamics of other mammals for which the habitat requirements and life history processes are understood. It seems obvious that approaches of this type that link modelling of population dynamics with the spatial distribution of the habitats in which species are found will have considerable potential for use in conservation and wildlife management in the future.

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