

# Modelling the effects of mink and habitat fragmentation on the water vole

S.P. RUSHTON\*, G.W. BARRETO†, R.M. CORMACK‡,  
D.W. MACDONALD† and R. FULLER§

\*Centre for Land Use and Water Resources Research, University of Newcastle upon Tyne, Newcastle NE1 7RU, UK; †Wildlife and Conservation Research Unit, University of Oxford, Oxford, UK; ‡The Mathematical Institute, University of St Andrews, St Andrews KY16 9SS, UK; and §Institute of Terrestrial Ecology, Monks Wood, Huntingdon, UK

## Summary

1. The decline of the water vole *Arvicola terrestris* in the UK has been attributed to the spread of the introduced American mink *Mustela vison*. Understanding the causes and dynamics of this decline is vital to water vole conservation. We investigated the dynamics of water voles in relation to habitat fragmentation and mink predation using an individual-based spatially explicit model of population dynamics on the River Windrush, Oxfordshire, UK.

2. A sensitivity analysis was undertaken using values for life-history parameters drawn from known ranges using Latin hypercube sampling. Partial correlation coefficients were used to estimate how the predicted size of water vole population and extinction were determined by the life-history parameters. The model was then validated by comparing model predictions with observed distributions of water voles.

3. The effects of mink predation and habitat fragmentation on the future viability of water vole populations on the River Windrush were analysed after artificially manipulating habitat fragmentation on the river and running the model in the presence and absence of mink predation.

4. The match between predicted and observed distributions was significantly related to home range requirement and high reproductive success. At low fragmentation, home range requirement was the most important influence on the number of populations. Reproductive output, and adult and juvenile mortality, became increasingly important with increased fragmentation. At high levels of fragmentation demographic stochasticity had a large influence on population size.

5. We deduce that the importance of demography in determining population persistence will depend on the level of fragmentation. Additionally, life-history parameters that are crucial to the viability of water vole populations can only be identified in the context of the landscape in which populations are found.

6. The extinction of water vole on the River Windrush became more likely as habitat fragmentation and mink predation increased. Mink predation effectively doubled the probability of extinction over that arising from fragmentation alone.

7. These simulations indicate that extant populations on the Windrush are now so fragmented that populations may not be viable even in the absence of mink predation. We assessed the extent of habitat restoration necessary to ensure population persistence on the River Windrush and considered developments of the model for use in water vole conservation.

**Key-words:** GIS, habitat fragmentation, individual-based, mink predation, spatial model.

*Journal of Applied Ecology* (2000) **37**, 475–490

## Introduction

In Britain, the water vole *Arvicola terrestris* L. is a riparian species that favours rivers with well vegetated banks (Lawton & Woodroffe 1991; Strachan & Jefferies 1993) and emergent vegetation (Strachan & Jefferies 1993). The species was once widespread in most riparian habitats but has undergone rapid decline in the UK over the last 90 years (Jefferies, Morris & Mulleneux 1989; Strachan & Jefferies 1993). Two factors may be responsible for this decline: changes in habitat, and predation due to feral American mink *Mustela vison* Schreber.

The most important changes in habitat have arisen as a result of changes in land use. Prior to 1940, one-third of the farmland in the UK was covered by rough semi-natural vegetation used for extensive cattle grazing (Parry, Hossett & Wright 1992). In the subsequent 60 years there has been a move away from these extensive agricultural practices. Semi-natural vegetation along river systems favoured by water voles has been subjected progressively to changes in both the type and intensity of land use. Many semi-natural grasslands were used for arable agriculture or managed to provide productive rye grass swards for stock rearing. In many rivers in southern England there has been progressive intensification of land use right up to the waters' edge, resulting in a fragmentation of semi-natural vegetation. The effects of these habitat changes on water voles have not been fully elucidated but it is known that intensively managed land adjacent to rivers is not favoured by the water vole (Barreto, Macdonald & Strachan 1998a) and rivers bordered by land intensively managed for agriculture are generally not preferred (Strachan & Jefferies 1993).

The decline of the water vole has also been linked to the spread of American mink (Jefferies, Morris & Mulleneux 1989). The American mink was originally introduced into the UK during the late 1920s, when it was farmed for its fur. Individuals escaped from farms and the species rapidly became established in the 1950s along river systems (Dunstone 1993). A number of studies have cited mink as a possible cause of decline of water vole and other riparian wildlife. Mink are known to cause high levels of mortality in ralliformes (Ferrerias & Macdonald 1999), and Barreto *et al.* (1998b) and Barreto, Macdonald & Strachan (1998a) reported a decline in the incidence of water vole in the Thames river system. This decline was strongly and negatively correlated with the presence of mink. Strachan *et al.* (1998) reported a similar decline in water voles in relation to colonization by mink on two rivers in Leicestershire, and Woodroffe, Lawton & Davidson (1990) on rivers in Yorkshire. The Biodiversity Action Plan drawn up by UK government agencies charged with conserving the water vole (HMSO 1995) concluded

that there was a need for research particularly on the role of habitat loss and mink predation in the decline of this species.

One obvious approach was to relate the distribution of the water vole to its habitat and the changing distribution of mink using a statistical model. Such models could then be used in implementing tactical conservation plans for the species. Barreto *et al.* (1998b) adopted a logistic modelling approach relating incidence of water voles to measured habitat characteristics. They showed that the factors determining distribution of water voles in the Thames catchment changed through time in relation to the presence of mink. They concluded, however, that the relationships between water vole and habitat were dependent more on the historical colonization of mink populations on the river than on any inherent effects of the variables themselves. Thus the variables that were significant predictors of water vole incidence in the presence of mink were those habitat features that occurred in areas where mink were not established. Each model therefore provided only a snapshot of the observed relationship between water vole and habitat at the time it was taken. Models of this type cannot be used in tactical conservation because the species-habitat relationship may be spurious and because they are effectively static. Furthermore, simple analyses of this form do not take into account the effects of delayed population responses to habitat loss caused by fragmentation (Kareiva & Wennergren 1995), which have been cited as a potential cause of the decline of this species.

Spatially explicit population dynamics models predict the distribution of a species in the landscape on the basis of interactions between the landscape structure and individual behavioural processes such as home range behaviour, territoriality and dispersal and the life-history processes of births and deaths. In these models the habitat data act as spatial reference points on which the populations processes occur, and the distribution of organisms amongst habitats emerges as the model is run. They are inevitably much more complex than statistical methods because they attempt to simulate individual processes, but they offer a potential route for investigating species with dynamic distributions. These models have been used to investigate the distributions of other species of conservation and pest significance (Akcakaya, McCarthy & Pearce 1995; Liu, Dunning & Pulliam 1995; Rushton *et al.* 1997; Rushton *et al.* 1999). We developed a spatially explicit population dynamics model and used it to investigate the dynamics of populations of water vole in a river system in the southern UK where mink are in the process of colonizing. We investigated the potential effects of mink predation and habitat fragmentation on the future viability of water vole populations along the river and considered the

implications of the results for water vole conservation.

## Methods

### STUDY SITE

The study site, in the UK, comprised a  $20 \times 30$  km area of the River Thames catchment containing the lower reaches of the River Windrush and its tributaries. This is the section running between National Grid reference 408580 229930 in the north and NGR 429910 211060 in the south. A complete census of the water vole populations of the River Windrush (but not the tributaries) was undertaken by field survey between June and September 1996. The river bank was walked along both sides and water voles recorded as being present if they were seen or if evidence of their presence (latrines, footprints and food remains) were recorded. The distribution of water voles along the river section was then stored as a raster map in the Geographical Resource Analysis Support System (GRASS) geographical information system (GIS) (Westervelt *et al.* 1990)

### WATER VOLE POPULATION DYNAMICS MODEL

The model was an integrated GIS–population dynamics model that linked space use to the incidence of species. The model had two main components. (i) A GIS stored environmental, habitat and animal population information. (ii) An individual-based population dynamics module simulated home range formation, individual life histories and dispersal within the GIS-held landscape. The GIS used to store and retrieve habitat information and display the model output was GRASS (Westervelt *et al.* 1990). The population model was written in the programming language C and integrated with the GIS component through a UNIX-shell environment. The model was stage-structured (Caswell 1989), in so far as discrete stages were recognized in the population, but the life-history processes of mortality, fecundity and dispersal were modelled at the level of the individual within the different age classes in each population.

### DEFINING HABITAT SUITABILITY OF HABITAT BLOCKS IN THE GIS

The water vole is a predominantly riparian species that favours well vegetated habitats that provide food and cover. The animal typically forms linear home ranges along river banks that range from 75 to 300 m in length and into which they tunnel. Habi-

tat inputs for the model were therefore defined as: (i) areas of habitat alongside rivers that could be used by the water vole as home ranges for foraging and breeding; (ii) areas alongside rivers through which animals could move when dispersing, but which they could not exploit for home ranges; and (iii) areas away from rivers that water vole were assumed not to enter.

Suitable habitats for foraging and breeding were defined on the basis of the distribution of marsh and rough grassland areas as recognized by categories of the Institute of Terrestrial Ecology (ITE) land cover map (derived from a classification of Landsat satellite imagery; Fuller, Groom & Jones 1994) and a river network derived from the 1:250000 Ordnance Survey map. Available habitat in the landscape was predicted in terms of units of  $25 \times 25$  m (the scale of resolution of the ITE land cover map) lying on the river network. This was achieved by overlaying the land cover map with a rasterized river network. All contiguous  $25 \times 25$ -m cells (pixels) of habitat were then aggregated to form habitat blocks. Cells were included within blocks where these abutted the block on at least one of their sides. This will have underestimated the size of linear habitat blocks where these were composed primarily of cells that abutted each other at corners. Suitable habitats for dispersal were defined as all other habitats in the ITE land cover map that were adjacent to the river but which were not suitable for foraging and breeding. It was assumed that all other habitats away from the river could not be used in any way by water voles. A second data set comprising the distribution of marsh and rough grassland habitats in areas where populations of water vole were observed along the River Windrush was also collated in order to analyse the viability of the extant populations of water vole on the river. In both cases the size and National Grid coordinates of these blocks of habitat along the river were then used as inputs to the population dynamics model.

Dispersal habitat in the landscape was stored as a two-dimensional grid of cells at the scale of  $200 \times 200$ -m blocks, with cells through which animals could disperse categorized as 1 and others classed as zero. There were two reasons for adopting this scale rather than the 25-m cell size used in defining the foraging and breeding habitat. First, when animals dispersed it was assumed that they would disperse greater distances than a home range, therefore modelling dispersal at subhome range scales was considered to be inappropriate. Secondly, adopting a 200-m scale greatly increased the speed at which individual dispersal steps could be modelled.

In order to ensure that animals dispersing through the landscape at the larger scale could detect habitats suitable for occupation at the smaller scale, a data file relating the incidence of habitat blocks for occupation to the cells within the dispersal map was

created and used as an input to the population dynamics model.

#### POPULATION DYNAMICS AND DISPERSAL OF WATER VOLE IN LANDSCAPES

Each block of suitable habitat within the landscape was modelled as having separate populations of water vole. Each population had separate dynamics that interacted through the process of dispersal. For each block of habitat, in each year, population size was modelled in terms of the net change due to four factors. These were gains from recruitment from breeding and immigration of subadults from other habitat blocks and losses due to adult and juvenile mortality and emigration.

Water voles have a breeding season that can extend from March to September. They are potentially highly prolific and are capable of producing between two and five litters per year with between four and six young per litter (Corbet & Harris 1993). Reproduction in the water vole was therefore assumed to occur several times a year and was varied as a model input. The number of litters per female and the number of pups produced in each litter were estimated by drawing deviates from a Poisson distribution with a mean varied as a model input (following Akcakaya, McCarthy & Pearce 1995). Mortality in water voles is highly variable but is typified by high juvenile mortality (Macdonald, Mace & Rushton 1997) and a reduced, almost uniform, mortality following recruitment to the adult population (Stoddart 1971). Four types of mortality were used in the model in each population: adult mortality, juvenile mortality, dispersal mortality and predation due to mink. Mortality in adult water voles was assumed to occur after breeding; that in juveniles as they were recruited into the adult population; and that in dispersal when animals were dispersing. Mortality due to mink was applied as a predation rate acting on adults and dispersing animals. Young were assumed not to be predated until they entered the adult class or dispersed as subadults. In reality, female mink may predate juvenile water voles in the nest, but there were no data available to quantify this. Mortality was modelled at the level of the individual for all types. The probability of death for each individual was determined by sampling deviates from a uniform distribution in the range 0–1, with mortality occurring if the deviate was in the range of the mortality for the relevant factor. Thus, for an individual subjected to adult mortality of 40% all deviates in the range 0–0.60 corresponded to the individual surviving, and those greater than 0.6 and up to 1.0 corresponded to it dying. All mortality rates were varied as model inputs.

There is very little information available on dispersal in water voles. They are generally considered

poor dispersers; Stoddart (1970) recorded only one incidence of long distance dispersal and this was only 2.6 km. Males tend to disperse at 4 months of age, and females in the spring (Macdonald, Mace & Rushton 1997). In the model dispersal between water vole populations in the landscape occurred once a year. Only subadults that could not find space in their natal habitat block dispersed. Dispersing animals interrogated the landscape, moving cell-by-cell through the 200-m squares in the dispersal landscape if they contained suitable dispersal habitat. Animals stopped dispersal if they arrived at a place that contained habitat capable of supporting a breeding population. Animals moved on if the suitable habitat was already fully occupied by adults. Animals were not allowed to return in the same direction from which they came unless there was no suitable dispersal habitat ahead of them. Where there was a choice of two or more cells through which dispersal was possible, the animal moved in the direction that was furthest from the last cell occupied (measured in terms of the Euclidean distance between cells). Where there was more than one cell at the same distance, the cell to move into was chosen at random. This dispersal therefore imposed a strong directional component that is not present in a random walk. If there were no suitable habitats available for occupation then dispersing animals died. The maximum distance animals could disperse was varied as a model input.

#### SENSITIVITY ANALYSIS

The sensitivity of the population dynamics model to input parameters was investigated by analysing the proportion of habitat blocks occupied, the total population size and the persistence of populations of water vole over 15 years to variations in the model inputs. A Latin hypercube sampling (LHS) strategy following the methods of Vose (1996) was used to select input parameters for the model from the known or estimated ranges of the different variables in the model. Latin hypercube sampling uses stratified sampling without replacement to select suites of input parameters from known distributions of those variables. In practical terms, the probability distribution for each variable is split into  $n$  intervals of equal probability, where  $n$  is the number of sets/suites of input variables selected. The creation of input variables for a model run proceeds as follows. A random number is used to select an interval and a further random number to determine the position, and hence the value, of the input variable for inclusion in the set. Once selected, an interval cannot be used again. In effect each interval may be used once, but once only, in combination with values of the other variables selected in the same way. The aim was to provide a range of input values for each vari-

**Table 1.** Ranges for each demographic parameter from which samples were drawn by Latin hypercube sampling for use in the sensitivity analysis of the water vole population dynamics model

Variable	Minimum	Maximum	Source
Maximum dispersal distance (m)	400	2000	After Stoddart (1970, 1971)
Minimum home range requirement (m)	75	300	Strachan & Jefferies (1993)
Fecundity	2	6	Corbet & Harris (1993)
Litters	1	5	Corbet & Harris (1993)
Adult mortality (%)	40	80	After Stoddart (1970, 1971)
Juvenile mortality (%)	40	80	After Stoddart (1970, 1971)
Dispersal mortality (%)	0	80	—

able that could potentially occur under field conditions. In other words the model would be run a sufficiently large number of times to encompass *all* of the potential range of conditions that occur naturally rather than simply worst and best case scenarios (*sensu* Bart 1995). Seven parameters were considered. These were: (i) maximum dispersal distance, the distance along the river corridor that water voles could disperse; (ii) the carrying capacity of the habitat, expressed as a 'minimum home range requirement' (effectively an inverse measure of carrying capacity), in units of 25 m of suitable habitat alongside the river, the number of blocks of 25 m of river habitat needed for a water vole to form a home range, which effectively placed a lower limit on the size of habitat block that could be occupied by water voles in the river landscape; (iii) fecundity; (iv) mean number of litters per female per year; (v) adult mortality per year; (vi) juvenile mortality per year; (vii) dispersal mortality per year.

In all cases there were insufficient data available to identify the distribution function for each parameter. Furthermore, there were no data available to assess the extent to which each of the life-history parameters was correlated with the others. A uniform distribution was assumed for each variable with upper and lower limits derived from the literature. The range of each parameter from which samples were taken is given in Table 1. In effect, the use of uniform distributions for all of the input variables leads to an overestimate of the size of the likely universe of possible values that each life-history parameter could take, as it is likely to lead to the selection of values for parameters that are near the extremes of their distributions more frequently than would be expected in reality. On the other hand it also ensures that all potential values (within the known range of observed behaviours for each variable) are sampled. In other words, whilst we know that the hyperspace of possible values for each parameter in the model will be larger than reality, we know that reality lies somewhere in that space and not outside it.

A 100 sets of the input parameters were selected and the model was then run for 15 years for each set. The starter population for each run consisted of populations of animals present at carrying capacity in all available habitats in the landscape. For each model run, the total number of available habitats occupied, whether or not the population had gone extinct, and the total population of water voles present in the landscape were output at the end of the 15 years. These data were then correlated with the input variables and partial correlation coefficients were calculated to assess the impact of the individual life-history parameters on the dynamics of the population as simulated by the model.

The analysis was run for five separate 100 sets of data and as one large set of 500 input variations to assess the impacts of varying the number of samples from the LHS and variations in the LHS on the stability of the partial correlation coefficients.

#### COMPARING MODEL OUTPUT TO OBSERVED WATER VOLE DISTRIBUTIONS

The model was run using a range of scenarios with the complete landscape map, and the output was compared with the observed distribution of water voles in the River Windrush study area. Initial starting populations for the model were created by distributing water voles at all available sites within the study area as in the sensitivity analyses. The model was then run 100 times for 15 years with the same sets of the life-history and habitat parameters as used in the sensitivity analysis. For each set the habitat blocks predicted to have water voles present at the end of the 15-year run were then overlaid with a map of the observed distribution of the water vole at the same spatial scale. This produced lists of the number of habitat blocks predicted to have water vole populations in the areas of river where they were observed and where they were not observed during the field survey. Two simple matching coefficients were calculated to compare the observed and predicted incidence of water voles.

These were the simple matching coefficient:

$$\text{SMC} = (a + d)/(a + b + c + d)$$

which includes joint absences, and:

$$\text{Czekanowski coefficient} = 2a/(2a + b + c)$$

which does not; where  $a$  = number of populations both predicted and observed in the landscape;  $b$  = number of populations predicted present but not observed;  $c$  = number of populations observed but not predicted;  $d$  = number of populations both predicted and observed not to be present. In both coefficients a value of 1 represents a perfect match between observed and predicted distributions.

The values of the matching coefficients were then transformed using the arcsin transformation (because they were effectively proportions lying between 0 and 1). These were then correlated with the input variables and partial correlation coefficients calculated in order to assess the impact of the individual life-history parameters on the goodness-of-fit of the model outputs to observed water vole distributions.

#### INVESTIGATING THE EFFECTS OF MINK PREDATION AND HABITAT FRAGMENTATION ON THE POPULATION DYNAMICS OF WATER VOLE

There was no evidence that the study area had been occupied by mink up to June 1997, although mink had been recorded in the catchment in 1976 and they had reappeared in the lower reaches of the catchment in June 1997. In order to investigate the consequences of future mink predation on the population dynamics of the water vole, an extension to the LHS strategy was used to create a mortality factor due to mink input variable. There were no data available on the mortality rate that water voles suffer in the presence of mink, although data from G.R. Barreto (unpublished data) indicate that water vole populations can disappear within 1 year of mink colonizing their habitat, suggesting that mortality may be exceptionally high. Predation by mink was varied as a proportion between 0 and 0.8, included with the same set of mortality and fecundity parameters used in the sensitivity analysis, and the analysis repeated. For each model run the proportion of available habitats occupied and the total population of water voles present in the landscape were output at the end of 15 years. The output parameters were then correlated with the input parameters and partial correlation coefficients were determined to assess the impact of the individual life-history parameters on the dynamics of the population as simulated by the model.

The effects of habitat fragmentation on the viability of water vole populations in the study area in the presence and absence of mink predation were investigated by running the sensitivity analyses with a reduced number of habitats available for occupation by voles. Ten subsets of habitat blocks were created from the total present by stepwise removal of all blocks that were smaller than each of 10 minimum size classes. This created 10 maps in which only blocks above the threshold were present. For each subset of habitat blocks the 100 sets of life-history parameters used in the sensitivity analysis were then used as inputs to the model and the model run for 15 years with water vole populations established at all available blocks at year zero. Each run was equivalent to 10 habitat fragmentation by 100 life-history sets, run for 15 years. In these analyses the 100 sets were assumed to represent the extent of variation in life-history parameters in the field and the extinctions represented the response of the water vole to habitat fragmentation. The analyses were undertaken both with and without mink predation.

In order to investigate the extent to which different life-history and habitat variables had differential effects on the predicted number of populations, partial correlation coefficients were calculated for each level of habitat fragmentation in the model. The proportion of extinctions in each set of 100 runs was used as a response variable, with the level of fragmentation and presence or absence of mink predation as independent variables in a logistic regression to investigate the effects of fragmentation and predation on population extinction.

#### THE VIABILITY OF THE WATER VOLE POPULATION FOR THE EXTANT POPULATION ON THE RIVER WINDRUSH WITH AND WITHOUT MINK PREDATION

In order to assess the future viability of water vole populations along the Windrush, the population model was run using the extant populations and the habitats they occupied as starting conditions. Only blocks of habitat currently occupied by water voles were assumed to be present in the model. The LHS methodology described above was used to create 100 sets of dispersal distance, home range requirement, reproductive output and mortality input scenarios and the model run for 15 years for both the absence of predation and with variable rates of mink predation as used in the analyses above. Extinction of water voles in the landscape in each 15-year run was used as a binary dependent variable, with the life-history data as independent variables in logistic regression to assess the relative importance of each life-history parameter on the probability of extinction with and without mink, following McCarthy & Burgman (1995). The analyses

were undertaken within the GLIM package and manual of Francis, Green & Payne (1993).

## Results

### AVAILABLE HABITATS

The length of the River Windrush and its associated tributaries in the  $20 \times 30$  km grid square comprising the study area was 113.6 km. The length of the River Windrush sampled in the field survey was 20.1 km. There were eight populations along the river where populations were evident, two groups of two of these were very close to each other so the couples were merged to produce six populations. The mean nearest neighbour distance of the six populations of water voles was 4.8 km, with two populations separated by 9.5 km. There was a total of 225 discrete blocks of marshland and rough grassland habitats, of greater than 75 m length, available for water voles in the study area. Of these 107 were along the 20.1 km of river sampled and 22 of these were in areas where water voles were recorded in the field survey. This suggests that there were areas of habitat along the river that were not used by water voles.

The total area of available habitat in the Windrush study area was predicted to be 34.5 ha in a river corridor of 100.5 ha. Assuming that the minimum home range size for a water vole is 75 m (Stoddart 1970), this equates to a maximum supportable population of 184 animals in the Windrush study area, or approximately nine animals per km of river. Trapping (Macdonald, Mace & Rushton 1997) in the largest section of river known to have water voles indicated that the observed density of water voles in blocks of habitat was 13 animals per km.

### SENSITIVITY ANALYSIS

Partial correlation coefficients relating the life-history inputs to the model output were similar for the five sets of 100 runs. There was some variation in

the partial correlation coefficients for the life-history parameters between replicates (with ranges between 2% and 15% around the mean value for the three most important variables), but the rank order of these variables was the same in each run, for all but one run. The results of the analysis of the data set comprising 500 runs were little different to those of the individual 100 runs, with the rank order remaining the same. This suggests that 100 runs were adequate to provide a consistent estimate of the impacts of the different life-history parameters on the output of the model. Partial correlation coefficients relating the effects of varying the life-history and habitat parameters to the total number of populations and the total population size of the landscape are shown in Table 2 for one set of 100 runs. *F*-values for each coefficient are included. There were significant partial correlation coefficients for all variables except adult mortality and dispersal mortality for the analyses of the predicted number of populations. The same was also true for the analyses considering the total population of animals, except that maximum dispersal distance was not significant. These results suggest that the individual input variables contribute significantly (in their own right) to both the predicted number of populations and the total population of animals predicted by the model. The most highly significant variables of all were the minimum home range requirement variable and the number of broods per year.

### COMPARING MODEL PREDICTIONS WITH THE OBSERVED DISTRIBUTIONS OF WATER VOLE

The simple matching coefficient between observed distribution of water voles and the model predictions varied between 0.53 and 0.80 (mean 0.766, SE 0.004), suggesting that the model predictions were good for parts of the range of input parameters modelled. The goodness-of-fit was more apparent than real, however, as for model runs where all

**Table 2.** Partial correlation coefficients (*pr*) and associated *F*-values relating the predicted total number of habitat blocks occupied and total predicted water vole population along the River Windrush to the values of different life-history parameters used in each model run, with no sink mortality ( $n = 100$ )

Variable	Total number of habitat blocks		Total population	
	<i>pr</i>	<i>F</i>	<i>pr</i>	<i>F</i>
Maximum dispersal distance	0.22	4.65	0.17	2.67
Home range requirement	-0.77	135.56	-0.74	111.43
Fecundity	0.41	18.87	0.30	9.48
Broods	0.56	43.65	0.44	21.84
Adult mortality	-0.20	3.79	-0.18	2.97
Juvenile mortality	-0.37	14.94	-0.33	11.12
Dispersal mortality	-0.0	0.03	0.00	0.00

Critical value of  $P < 0.05$  for  $F(1,93) = 3.95$ .

populations went extinct the coefficient was 0.8. This reflects the large impact of the not predicted: not observed count in all analyses. Values of the Czekanowski coefficient varied between 0 and 0.46. The model predicted populations in areas where they were not observed as well as failing to predict populations in some blocks of habitat where they had been observed. The proportions of available habitat predicted to be occupied by water vole in inhabited and in uninhabited areas were calculated for each model run. These data were arcsin transformed to normality and a paired *t*-test undertaken on the differences between proportions of habitats predicted to be occupied in water vole inhabited and uninhabited areas. Over all model runs, there was a significantly higher proportion of habitat blocks predicted to be occupied by the model in the areas where water voles were observed than where they were not ( $t=2.51$ ,  $P < 0.007$ ). This suggests that those areas observed to have water voles in the field were also more likely to be predicted to have them in the model than those areas that did not.

Partial correlation coefficients between the life-history input parameters and the two matching coefficients are shown in Table 3. Range requirement, mean number of broods and mean fecundity were the most important variables contributing to a high simple matching coefficient. The sign for the first variable was positive and the latter two were negative, suggesting that reduced reproductive success and increased home range requirement (effectively reduced carrying capacity) led to model predictions that closely matched the observed water vole distribution when assessed using this coefficient. In fact, range requirement, mean number of broods and mean fecundity were also the most significant contributors to goodness-of-fit between model outputs and the observed distribution of voles using the Czekanowski coefficient. In this case, however, the signs for the variables were opposite to those for the ana-

lysis with the simple matching coefficient. The difference was explained in terms of the contribution of not predicted: not observed habitat block counts in the former analysis, bearing in mind that a landscape with no water voles in it gave rise to a matching coefficient of 0.8.

#### THE EFFECTS OF MINK PREDATION AND HABITAT FRAGMENTATION ON THE VIABILITY OF WATER VOLE POPULATIONS

The effects on the occupation of habitats of including mink predation with the 100 sets of life-history parameters used in the sensitivity analysis are shown in Table 4. Partial correlation coefficients and associated *F*-values are shown. There were significant partial correlation coefficients for all variables except maximum dispersal distance and dispersal mortality for the analyses investigating the effects of the input variables on the predicted number of populations. The same was also true for the analyses considering the total population of animals, except that juvenile mortality was not significant. The presence of mink mortality was the second most significant variable in these analyses. Where mink predation was excluded, adult mortality was a significant factor.

In the absence of mink, the model predicted populations would go extinct in 20% of the life-history input scenarios. When mink predation was included this increased to 57% of scenarios.

The effects of habitat fragmentation on the viability of water vole populations with and without mink predation are shown in Fig. 1. The presence of mink predation generally doubled the probability that populations would go extinct at any one level of habitat fragmentation. Parameter estimates and deviance estimates of a generalized linear model relating number of extinctions to the number of habitat fragments and mink predation are shown in

**Table 3.** Partial correlation coefficients (*pr*) and associated *F*-values relating the predicted total number of habitat blocks occupied and total predicted water vole population along the River Windrush to the values of different life-history parameters used in each model run, with mink predation ( $n = 100$ )

Variable	Total number of habitat blocks		Total population	
	<i>pr</i>	<i>F</i>	<i>pr</i>	<i>F</i>
Maximum dispersal distance	0.14	1.88	0.12	1.38
Home range requirement	-0.48	27.41	-0.46	25.40
Fecundity	0.41	18.16	0.34	11.91
Broods	0.33	11.21	0.26	6.80
Adult mortality	-0.21	4.33	-0.23	5.30
Juvenile mortality	-0.21	4.10	-0.18	3.01
Mink mortality	-0.42	20.07	-0.38	15.64
Dispersal mortality	-0.09	0.85	0.10	0.98

Critical value of  $P < 0.05$  for  $F(1,93) = 3.95$ .



**Table 4.** Partial correlation coefficients (*pr*) and associated *F*-values relating the values of two arcsin-transformed matching coefficients comparing predicted and observed numbers of occupied habitat blocks along the River Windrush to the values of different life-history parameters used in each model run, with mink predation (*n* = 100)

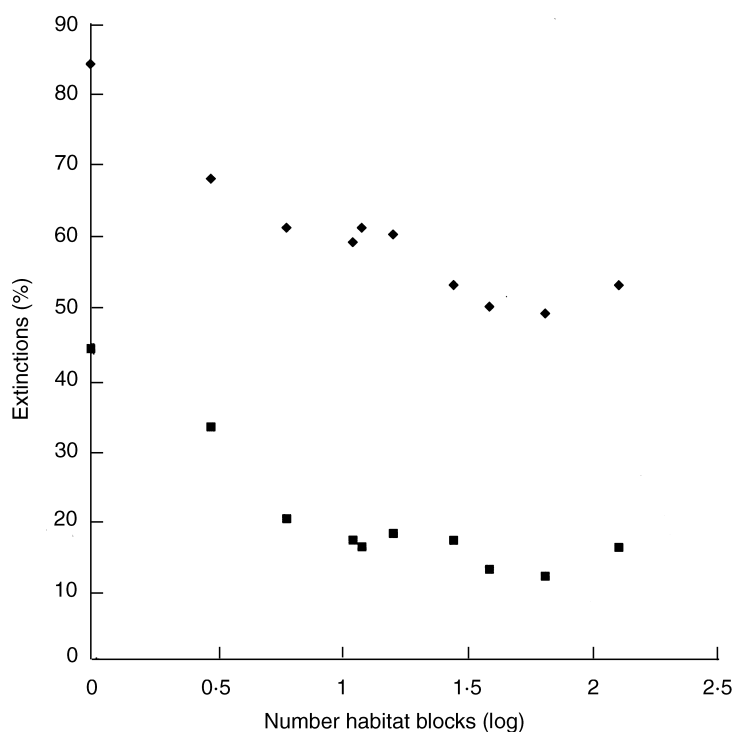
Coefficient	$(a + d)/(a + b + c + d)$		$2a/(2a + b + c)$	
	<i>pr</i>	<i>F</i> -value	<i>pr</i>	<i>F</i> -value
Maximum dispersal distance	-0.19	3.65	0.10	0.95
Home range requirement	0.74	113.26	-0.78	145.96
Mean fecundity	-0.44	22.76	0.53	36.08
Mean broods	-0.58	46.73	0.67	76.46
Adult mortality	0.22	4.66	-0.22	4.86
Juvenile mortality	0.32	10.81	-0.38	16.03
Dispersal mortality	0.04	0.16	0.07	0.43

Critical value of  $P < 0.05$  for  $F(1,93) = 3.95$ .

Table 5. There was a significant negative relationship between the number of model runs in which vole populations went extinct and the number of habitat fragments present and mink predation. A model including an interaction term (level of fragmentation  $\times$  mink predation) did not increase the deviance explained, suggesting that mink predation and habitat fragmentation did not interact in determining population extinction.

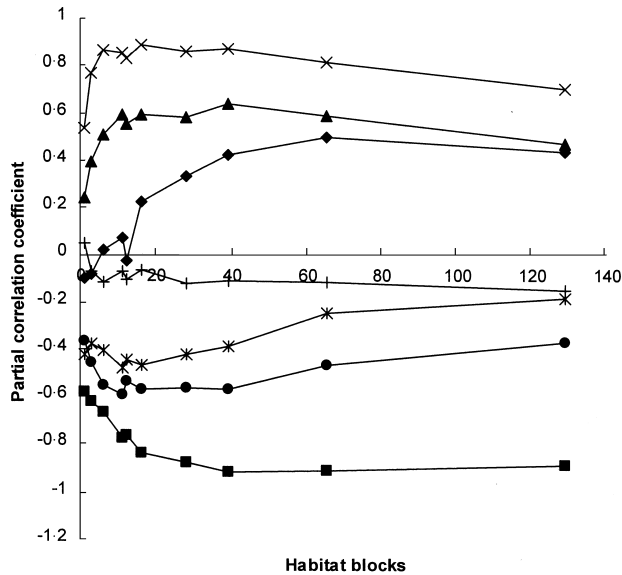
Changes in the values of partial correlation coefficients measuring the contribution of individual life-history and habitat variables (but without mink pre-

dation) to the number of populations predicted by the model in relation to changes in the number of habitat blocks available in the landscape are shown in Fig. 2. Data for the equivalent analysis including mink predation are shown in Fig. 3. These plots show the contribution of each life-history variable to the output of the model at each level of habitat fragmentation. Considering the analysis where there was no mink predation, for all variables except dispersal mortality the partial correlation coefficients increased with increased number of habitats, reached a peak and then gradually declined. The

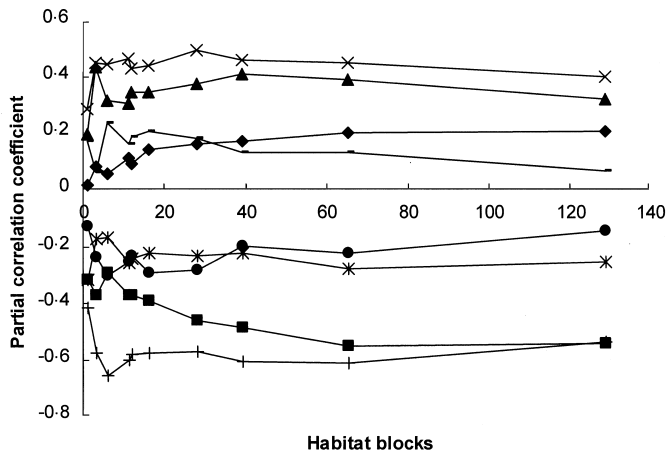
**Fig. 1.** Change in the proportion of extinctions predicted by the model when run with different levels of habitat fragmentation. Diamonds show the predicted number of extinctions in the presence of mink predation; filled squares show the predicted extinctions in the absence of mink predation.

**Table 5.** Parameter estimates and logistic regression relating the proportion of times populations went extinct in 100 model runs against the number of habitat fragments in the landscape and the presence (or absence) of mink predation ( $n = 20$ )

Variable	Estimate	SE	<i>t</i>	<i>P</i>
Constant	0.6183	0.0744	8.30	0.0001
Number of habitat blocks	−0.0065	0.0013	−4.68	0.0001
Mink predation	−1.8498	0.1052	−17.58	0.0001



**Fig. 2.** Change in partial correlation coefficients for life-history input variables against the predicted number of populations at different levels of habitat fragmentation. Model run without mink predation. Crosses, the number of broods per female; circles, juvenile mortality; stars, adult mortality; pluses, dispersal mortality; squares, minimum habitat requirement; diamonds, maximum dispersal movement; triangles, female fecundity.



**Fig. 3.** Change in partial correlation coefficients for life-history input variables against the predicted number of populations at different levels of habitat fragmentation. Model run with mink predation. Crosses, number of broods per female; circles, juvenile mortality; stars, adult mortality; pluses, mortality due to mink; squares, minimum habitat requirement; diamonds, maximum dispersal movement; triangles, female fecundity; – dispersal mortality.

**Table 6.** Logistic regression of predicted extinction of extant water vole populations on the River Windrush against values of different life-history parameters used in each model run, without mink predation ( $n = 100$ )

Variable	Estimate	SE	<i>t</i>
Constant	12.470	4.217	2.92
Maximum dispersal distance	-0.154	0.178	0.86 NS
Home range requirement	-1.372	0.304	4.51
Fecundity	0.839	0.440	1.90
Broods	2.247	0.594	3.78
Adult mortality	-8.139	3.761	2.16
Juvenile mortality	-10.400	3.810	2.72
Dispersal mortality	-0.886	1.681	0.52 NS
Deviance for null model	138		
Decline in deviance due to model	93		
Residual deviance	45		

Critical value of *t* at 93 d.f., 1.66.

change in the coefficients with increased number of habitat blocks was not uniform across all variables, with values for the maximum dispersal distance variable increasing more slowly than brood number, minimum home range requirement and fecundity. The results suggest that: (i) at high levels of habitat fragmentation the effects of the modelled life-history parameters on the number of populations predicted to be present were less significant, suggesting that stochastic effects involved with individual mortality and reproductive success were more important; (ii) the impacts of the individual life-history variables varied with the level of fragmentation.

In the presence of mink predation the results were similar except in so far as all partial correlation coefficients were lower, suggesting that the impact of any one variable was reduced. Furthermore, there was considerably more fluctuation in the apparent significance of individual variables at high levels of fragmentation. The effects of minimum home range requirement on the model output also reached their greatest at a much more reduced level of fragmentation (60+ habitat blocks compared with 40 blocks)

in the presence of mink predation than when it was absent.

#### THE VIABILITY OF THE EXTANT WATER VOLE POPULATIONS IN THE WINDRUSH IN RELATION TO LIFE-HISTORY PARAMETERS AND MINK PREDATION

Water vole populations were predicted to go extinct in 52% of life-history input scenarios run without mink predation and in 72% of scenarios in the presence of mink predation, suggesting that mink may have considerable impact on the viability of extant populations of water voles on the river. Parameter estimates from generalized linear models relating the probability of extinction of the extant populations of water vole to variations in each of the life-history parameters in the absence of mink predation are shown in Table 6. Results of similar analyses in the presence of predation are shown in Table 7. The most obvious feature of the results is that the probability of extinction was significantly related to all of the input parameters with the exception of the

**Table 7.** Logistic regression of predicted extinction of extant water vole populations on the River Windrush against values of different life-history parameters used in each model run, with mink predation (extinction = 1; persistence = 0;  $n = 100$ )

Variable	Estimate	SE	<i>t</i>
Constant	35.820	17.080	2.09
Maximum dispersal distance	-0.948	0.530	1.78
Home range requirement	-2.517	1.183	2.12
Fecundity	1.044	0.880	1.18
Broods	5.647	2.911	1.93
Adult mortality	-18.070	9.286	1.94
Juvenile mortality	-28.560	16.640	1.71
Dispersal mortality	1.020	4.241	0.24 NS
Mink predation	-32.110	14.760	2.17
Deviance for null model	118		
Decline in deviance due to model	102		
Residual deviance	16		

Critical value of *t* at 92 d.f., 1.66.

maximum dispersal distance and the dispersal mortality in the absence of mink predation. The most significant variables were the number of broods and minimum home range requirement, to which the probability of extinction was negatively and positively related, respectively. When mink predation was included in the model, the level of mink predation and the minimum home range requirement were the most significant predictors of extinction. Consideration of the input parameters for the 100 model runs showed that the population of water voles on the Windrush would go extinct under all scenarios if mink predation rate was greater than 30% per annum, irrespective of the values of the life-history parameters used.

## Discussion

Most, if not all, recent fieldwork on the distribution of the water vole in the UK has shown that the species is in decline. If the present trends persist it is unlikely that the water vole will occur on many British river systems in 20 years without some form of intervention from humans. There is a requirement for basic models that can be used to explain the response of the water vole to its environment, its predators and to conservation management strategies before conservation intervention becomes feasible. While it seems likely that associative approaches are inadequate, the alternative stochastic population modelling approach adopted here is not without shortcomings. The use of individual-based spatial modelling approaches in conservation has been a subject of some dispute (Bart 1995). Wennergren, Ruckelhaus & Kareiva (1995) concluded that such models were of limited value in tactical conservation. One of the most important reasons for this is that these models attempt to link landscape-scale processes to behavioural processes that are poorly understood (Lima & Zollner 1996). Behavioural processes permeate virtually every component of individual-based models, from the initial definition of what comprises a habitat to how animals disperse through the landscape, so any individual-based model must first be assessed in terms of how these processes are modelled.

The behavioural factor that is likely to have the most impact on the output of individual-based models is the way in which dispersal is modelled. Lima & Zollner (1996) classified different methods for modelling dispersal in terms of an information continuum, along which different models can be grouped on the basis of how the modelled animal is assumed to 'perceive' its landscape. These range from those where animal movement is random through to those where the animal has cognitive powers and learning. Each of these extremes makes different assumptions about how animals move, often without any empirical information. In this

study we assumed that animals moved away from their birth range through a dispersal corridor (the river) in units of 200 m until they found sufficient habitat blocks of 25 m length to remain, and blocks were only occupied if there was space available within the habitat patch as a whole. Animals were constrained to move away from squares that they had visited immediately prior to the move they were making, and which they had rejected, unless there was nowhere else to go. This makes the assumption that water voles could not detect suitable habitat except where it was within a range of 200 m; it also assumes that they were capable of recognizing where they had already been over the short-term. Are these 'plausible behaviours', and are they realistic? Water vole home ranges are typically between 75 and 300 m, so 200 m is probably within the trivial daily range of an individual and as such it might be expected that water voles would find available habitat if they entered a 200 × 200 m block of land with suitable habitat. Water voles also mark their home ranges with scent-marked latrines (Stoddart 1971) so olfaction, and hence past experience of the landscape, plays a major role in habitat use, as has been suggested for other rodents (Kozakiewicz & Szacki 1995). While there may be grounds, therefore, for believing that individual water voles can detect where they have been before, the directionality imposed on water vole movement in the model may have been unrealistic. The difficulties of observing behavioural processes of this type have been cited as important factors limiting individual-based models (Conroy *et al.* 1995). While there is little information available on the dispersal behaviour of water voles, it is easy to assess the consequences of adopting an imposed directionality in dispersal relative to the extreme plausible behaviours of complete random movement in, or complete knowledge of, the landscape. In the former behaviour, each step would be independent of previous steps, animals would eventually return to their starting points and their net movement from the starting point would be zero if they did not find a suitable site (Berg 1993). If we assume that there is a finite limit to the distance that animals can disperse, then random movement would lead to lower population sizes and a greater rate of population extinction in the landscape. With perfect knowledge, in contrast, the converse would be the case because all animals capable of reaching an available habitat would do so, subject to the constraints of the maximum distance that water voles could disperse. The responses of populations to an imposed directionality in dispersal lies between these extremes, because of the form of landscape through which the animals have to disperse. Animals can only disperse in one of two directions, up or down the river, so, whilst the initial 'choice of direction' may be random, with an imposed directionality the chance of individual animals actually finding a suit-

able habitat will depend on the maximum distance that they can disperse. Thus, the model developed here is likely to have used a more realistic representation of dispersal than either of the other behaviours discussed above.

A basic assumption of all spatially explicit models is that the home range requirements of the species can be identified, so that the position of the resources required by the species can be defined in space. This assumes that landscape attributes perceived by humans can be directly translated into those perceived by the species under investigation. In the case of the water vole we assumed that only marshland and rough grassland adjacent to rivers were suitable habitats and that these were of equal quality. The use of two very broad categories of habitat was crude and undoubtedly overestimated the availability of habitat for the water vole. The categories within the ITE land cover map are wide because they are based on satellite imagery. It is likely that the marsh category of this data set encompassed habitats not used by water vole. Thus vegetation dominated by *Phragmites australis* Cav. and that dominated by *Phalaris arundinacea*, L. are both classified as marsh, but the former species is favoured by the water vole and the latter is not (Woodall 1993). Conversely, restricting habitats to two types may have also led to an underestimation of available habitat because some habitats that may have been suitable were excluded from being habitats at all. Habitat selection is known to vary with sex in the water vole (Woodall 1993), with males being less selective than females. There is also evidence that other rodent species may make behavioural adaptations to differences in habitat quality (Wegner & Merriam 1990) and the disposition (levels of fragmentation) of the habitat blocks (Kozakiewicz & Szacki 1995), either increasing their home ranges in poor quality habitat or utilizing novel ones. None of these phenomena was modelled. While it is likely that there were errors of both overestimation and underestimation of available habitat in this study, it is also likely that the errors arising from overestimation of available habitat were greatest because both the habitat discrimination and the scale of resolution of the ITE land cover map were coarse relative to the scale of space use by the water vole. Thus it is likely that the model overestimated what habitat was available in the landscape.

Process-based models are usually judged by the results of the validation exercises undertaken. The results of the validation analyses showed that the fit between model predictions and the observed distribution was good for most runs. The simple matching coefficient provided poor discrimination between model runs because the landscape was dominated by areas with no water voles and zero predicted: zero observed counts were high. Similar results were noted by Rushton *et al.* (1997) in a modelling study

of grey squirrel and red squirrel distributions. The analysis based on the Czekanowski coefficient was more informative, in that it showed that the best fit of the model to the observed distribution occurred when home range requirement was low and reproductive output high. Under these circumstances the maximum match between predicted and observed numbers of populations was 46%. While the analyses indicated that the model predicted a higher proportion of blocks would be occupied in areas where water voles were observed than where they were not, it is clear that there was some overprediction.

Given these constraints what do the results of the study tell us about the dynamics of the water vole? Both the model predictions and the field observations indicated that water vole populations along the river were highly fragmented, with populations existing in small groups that were separated. Past studies have shown that water vole populations are clumped (Woodall 1993) and highly fragmented (Lawton & Woodroffe 1991). Habitat fragmentation might be expected to have impacts on water vole populations because the species has a comparatively low dispersal ability (Stoddart 1970) and, as such, its ability to reach isolated habitat blocks may be restricted. Indeed, Lawton & Woodroffe (1991) concluded that in their study area 30% of suitable sites were not occupied because of isolation and predation by mink. Theoretical studies have shown that dispersal success is an important factor determining patch occupancy (Fahrig & Paloheimo 1988; Doak, Marion & Kareiva 1992) and empirical studies have also implicated dispersal as a factor determining habitat occupancy in other small mammal species (Bright, Mitchell & Morris 1993). Andren (1994) even suggested that there was a threshold proportion of between 10% and 30% cover in the landscape that would lead to suitable habitats remaining unoccupied because they were too far apart.

The results suggest that the persistence of populations in the landscape was influenced by different demographic variables as the habitat fragmentation was changed in the model. At the lowest level of fragmentation, population persistence was most strongly linked to the home range requirement variable and the number of litters. In this case the populations were close enough in space and dispersal so easy that the individual populations effectively functioned as one 'patchy population' (Harrison 1994). Increased fragmentation initially caused an increase in the significance of all life-history variables. This suggests that populations in the landscape were gradually becoming isolated, shifting more from an almost contiguous population with dynamics dominated by one variable, home range requirement, to a metapopulation structure where other variables, such as dispersal ability, became individually more significant, through to the extreme case where small

populations existed in complete isolation. At very high levels of fragmentation, variations in the life-history inputs to the model had less significant impacts than at lower levels. This is quite easily interpreted as an increased impact of stochastic processes in the model. The model demonstrates the impact of 'demographic stochasticity' associated with small and isolated populations (Shaffer 1981; Harrison 1991). More interestingly, the results suggest that the impacts of the different life-history parameters on population persistence in the landscape depended on the level of fragmentation. The level of fragmentation at which each demographic variable reached its peak significance in determining the number of populations in the landscape was different. Adult and juvenile mortality rates were most significant at high levels of fragmentation, where the number of suitable habitat units was less than 20% of the total, while dispersal ability was most significant at a fragmentation level of 50%. Eberhard (1991) showed that the threshold population size at which demographic stochasticity becomes significant in determining population persistence is dependent on the life-history traits of the species. These results go further, in that they suggest that the importance of demographic parameters in determining population persistence will depend on the level of fragmentation. They also suggest that identifying life-history parameters that are crucial to the viability of water vole populations can only be undertaken in the context of the landscape in which the populations are found.

What are the implications of these results for the practical conservation of the water vole? The water vole is a good example of the declining-population paradigm in conservation (Caughley 1994). The causes of decline have been identified as predation and habitat loss/degradation (HMSO 1995); the next step in this paradigm is to remove or neutralize the agents of decline. Mink are generalists, they do not specialize on water vole, but, because they search their foraging areas systematically (Gerrell 1970), they are capable of eradicating water vole populations very rapidly (Strachan *et al.* 1998). Thus eradicating mink would be a logical step in conserving water voles, and the results presented here suggest that reducing mink predation would increase the viability of water vole populations on this river at all levels of habitat fragmentation. While the need for research on the logistics of mink control has been stressed (HMSO 1995), control is unlikely to be practical at the landscape scale as it would be costly and difficult to achieve. Mink are highly mobile and are likely to recolonize areas from which they have been removed (Dunstone 1993). This effectively leaves habitat management as the only practical option for conservation.

Is habitat management a viable option for the River Windrush? Water vole populations in 1996

were highly fragmented, with the separation between each greater than the maximum recorded dispersal distance recorded by Stoddart (1970) and Leuze (1980). This means that localized extinction cannot be avoided by rescue effects (recolonization events) from adjacent populations. Furthermore, the results of the modelling suggest that with fewer than 20 populations in this landscape, populations are probably at a level where their persistence may become subject to 'demographic stochasticity'. Analysis of the persistence of the extant populations suggested that in more than half of the potential life-history scenarios modelled water voles would go extinct. This would indicate that the future of the water vole populations on the River Windrush looks bleak without human intervention. The results of the artificial landscape manipulation analyses suggest that increasing habitat availability would decrease the likelihood that water vole populations become extinct, but to reduce the chance of extinction to below 10% would require increasing the number of available blocks of habitat along the 20.1-km of river by 20 times (Fig. 1). Management at this scale would be very costly and probably impractical. Thus, the River Windrush populations may already be 'living dead' (Hanski, Moilanen & Gyllenberg 1996) in the sense that extinction is inevitable (and this is likely to be the case irrespective of any future predation by mink).

While extinction of the River Windrush water vole populations is probably inevitable, there may be more hope for populations of water voles in other river systems where there is scope for radical riparian management. Barreto, Macdonald & Strachan (1998a) postulated the 'tightrope hypothesis', which states that the extreme linearization of riparian habitats, like those on the Windrush, makes water vole populations vulnerable to mink predation. They argued that there is an interaction between mink predation and habitat such that predation on water voles might be lower if the habitat is sufficiently large and non-linear. The authors cite examples of water vole populations co-existing with mink in areas where the habitat is non-linear, not fragmented and where there are suitable refugia from mink predation. In effect the authors suggest that predation efficiency is a function of shape and size of the habitat. The current model, while generic in the sense that it can be applied in any riparian landscape, does not include a habitat:predation interaction, but actually assumes they are independent of each other. Quantifying this relationship through field research and extending the model further to include it would provide a landscape management tool for investigating water vole population viability in relation to the size, shape and disposition of habitats in other landscapes. This would be particularly valuable in riparian systems where there is scope for managing habitats around the river as well

as immediately alongside it. This combination of field research and population modelling might not only provide useful insights into the role of habitat structure in determining population persistence, but might also provide some hope for reversing the trend towards extinction that faces the water vole in the UK.

### Acknowledgements

We would like to thank S. Telford, University of Aberdeen, for commenting on the manuscript. The field work component of this project was funded by the Environment Agency (GB). OS data were made available under the Digimap scheme.

### References

- Akcakaya, H.R., McCarthy, M.A. & Pearce, J.L. (1995) Linking landscape data with population viability analysis: management options for the helmeted honey eater. *Biological Conservation*, **73**, 169–176.
- Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitats: a review. *Oikos*, **71**, 335–366.
- Barreto, G.R., Macdonald, D.W. & Strachan, R. (1998a) The tightrope hypothesis: an explanation for plummeting water vole numbers in the Thames catchment. *UK Flood Plains* (eds R.G. Bailey & P.V. Jose), pp. 311–327. Sherwood Westbury Academic & Scientific Publications, Otley, UK.
- Barreto, G.R., Rushton, S.P., Strachan, R. & Macdonald, D.W. (1998b) The role of habitat and mink predation in determining the status and distribution of water voles in England. *Animal Conservation*, **1**, 129–137.
- Bart, J. (1995) Acceptance criteria for using individual-based models to make management decisions. *Ecological Applications*, **5**, 411–420.
- Berg, H.C. (1993) *Random Walks in Biology*. Princeton University Press, Princeton, N.J.
- Bright, P.W., Mitchell, P. & Morris, P.A. (1993) Dormouse distribution: survey techniques, insular ecology and selection of sites for conservation. *Journal of Applied Ecology*, **31**, 313–329.
- Caswell, H. (1989) *Matrix Population Models*. Sinauer, Sunderland, MA.
- Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215–214.
- Conroy, M.J., Cohen, Y., James, F.C., Matsinnos, Y. & Maurier, B.A. (1995) Parameter estimation, reliability and model improvement for spatially explicit models of animal populations. *Ecological Applications*, **5**, 17–19.
- Corbet, G.B. & Harris, S. (1993) *Handbook of British Mammals*, 3rd edn. Blackwell Science, Oxford, UK.
- Doak, D.F., Marion, P.C. & Kareiva, P.M. (1992) Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theoretical Population Biology*, **41**, 315–336.
- Dunstone, N. (1993) *The Mink*. T. & A.D. Poyser, London, UK.
- Eberhard, T. (1991) Colonisation in metapopulations: a review of theory and observations. *Biological Journal of the Linnean Society*, **42**, 105–121.
- Fahrig, L. & Paloheimo, J. (1988) Effect of spatial arrangement of habitat patches on local population size. *Ecology*, **69**, 468–475.
- Ferreras, P. & Macdonald, D.W. (1999) The impact of American mink *Mustela vison* on water birds in the upper Thames. *Journal of Applied Ecology*, **36**, 701–708.
- Francis, B., Green, M. & Payne, C. (1993) *The GLIM System Release 4 Manual*. Oxford University Press, Oxford, UK.
- Fuller, R.M., Groom, G.B. & Jones, A.R. (1994) The land cover map of Great Britain: an automated classification of Landsat Thematic Mapper data. *Photogrammetric Engineering and Remote Sensing*, **60**, 553–562.
- Gerrell, R. (1970) Home ranges and movements of mink in Sweden. *Oikos*, **8**, 83–109.
- Hanski, I., Moilanen, A. & Gyllenberg, M. (1996) Minimum viable population size. *American Naturalist*, **147**, 527–541.
- Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, **42**, 73–88.
- Harrison, S. (1994) Metapopulations and conservation. *Large-Scale Ecology and Conservation Biology* (eds P.J. Edward, R.M. May & N.R. Webb), pp. 111–129. Blackwell Science, Oxford, UK.
- HMSO (1995) *Biodiversity: The UK Steering Group Report. Volume 2. Action Plans*. HMSO, London, UK.
- Jefferies, D.J., Morris, P.A. & Mulleneux, J.E. (1989) An enquiry into the changing status of the water vole *Arvicola terrestris*. *Mammal Review*, **19**, 111–131.
- Kareiva, P. & Wennergren, U. (1995) Connecting landscape patterns to ecosystem and population processes. *Nature*, **373**, 299–302.
- Kozakiewicz, M. & Szacki, J. (1995) Movements of small mammals in a landscape: patch restriction or nomadism. *Landscape Approaches in Mammal Ecology and Conservation* (ed. W.D. Lidicker), pp. 78–93. University of Minnesota Press, Minneapolis, MN.
- Lawton, J.H. & Woodroffe, G.L. (1991) Habitat and the distribution of water voles: why are there gaps in a species' range? *Journal of Animal Ecology*, **60**, 79–91.
- Leuze, C.C.K. (1980) The application of radio tracking and its effect on the behavioural ecology of the water vole *Arvicola terrestris* (Lacepede). *The Handbook of Biotelemetry and Radio-Tracking* (eds C.J. Amlaner & D.W. Macdonald), pp. 361–366. Pergamon, Oxford, UK.
- Lima, S.L. & Zollner, P.A. (1996) Towards a behavioural ecology of ecological landscapes. *Trends in Research in Ecology and Evolution*, **11**, 131–135.
- Liu, J., Dunning, J.B. & Pulliam, H.R. (1995) Population effects of a forest management plan on Bachman's sparrow (*Aimophila aestivalis*): linking a spatial explicit model with GIS. *Conservation Biology*, **9**, 62–75.
- McCarthy, M.A. & Burgman, M.A. (1995) Sensitivity analysis for models of population viability. *Biological Conservation*, **73**, 93–100.
- Macdonald, D.W., Mace, G. & Rushton, S.P. (1997) *Proposals for Future Monitoring of British Mammals*. Department of the Environment Transport and Regions, London, UK.
- Parry, M.L., Hossell, J.E. & Wright, L.J. (1992) Land use in the United Kingdom. *Land Use Change: Cause and Consequences* (ed. M.C. Whitby), pp. 7–15. ITE Symposium No. 27. NERC, HMSO, London, UK.
- Rushton, S.P., Lurz, P.W., Fuller, R. & Garson, P.J. (1997) Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and

- population dynamics approach. *Journal of Applied Ecology*, **34**, 1137–1154.
- Rushton, S.P., Lurz, P.W.W., Mitchell-Jones, A. & South, A.B. (1999) Modelling the distribution of red squirrels on the Isle of Wight. *Animal Conservation*, **2**, 111–120.
- Shaffer (1981) Minimum population sizes for species conservation. *Bioscience*, **31**, 131–134.
- Strachan, R. & Jefferies, D.J. (1993) *The Water Vole Arvicola terrestris in Britain 1989–1990: Its Distribution and Changing Status*. The Vincent Wildlife Trust, London, UK.
- Strachan, C., Jefferies, D.J., Barretot, G.R., Macdonald, D.W. & Strachan, R. (1998) The rapid impact of resident American mink on water voles: case studies in lowland England. *Symposium of the Zoological Society of London*, **71**, 339–357.
- Stoddart, D.M. (1970) Individual range, dispersion and dispersal in a population of water voles *Arvicola terrestris*. *Journal of Animal Ecology*, **39**, 403–425.
- Stoddart, D.M. (1971) Breeding and survival in a population of water voles. *Journal of Animal Ecology*, **40**, 487–494.
- Vose, D. (1996) *Quantitative Risk Analysis. A Guide to Monte Carlo Simulation Modelling*. Wiley, Chichester, UK.
- Wegner, J. & Merriam, G. (1990) Use of spatial elements in a farmland mosaic by a woodland rodent. *Biological Conservation*, **54**, 263–276.
- Wennergren, U., Ruckelhaus, M. & Kareiva, P. (1995) The promise and limitations of spatial models in conservation biology. *Oikos*, **74**, 349–356.
- Westervelt, J.M., Shapiro, M., Goran, W. & Gerdes, D. (1990) *Geographic Resource Analysis Support System, Version 4.0. User's Reference Manual*. USACERL ADP Report N-87/22. Champaign, Illinois.
- Woodall, P.F. (1993) Dispersion and habitat preferences of the water vole (*Arvicola terrestris*) on the River Thames. *Zeitschrift Fur Säugetierkunde*, **58**, 160–172.
- Woodroffe, G.L., Lawton, J.H. & Davidson, W.L. (1990) The impact of feral mink on water voles *Arvicola terrestris* in the North Yorkshire Moors National Park (England, UK). *Biological Conservation*, **51**, 49–62.

Received 6 March 1999; revision received 27 January 2000