

**SCOTTISH  
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**RSM No 153**

**Predicting the outcome of a proposed re-  
introduction of the European beaver (*Castor fiber*)  
to Scotland**

**S Rushton<sup>1</sup>, A South<sup>1</sup> and D Macdonald<sup>2</sup>**

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## 1. INTRODUCTION

The beaver (*Castor fiber*) became extinct in Scotland in the 16th Century (Conroy & Kitchener, 1995). The causes of this extinction have been cited as hunting and habitat loss (Macdonald *et al.*, 1995). This decline was mirrored throughout Europe to the extent that, at the beginning of this century, there were only a few scattered populations. Since 1950 the species has been re-introduced into ten European countries (see Macdonald *et al.*, 1995). On the whole the re-introduction schemes have been successful and latterly there has been considerable interest in re-establishing the species in Scotland.

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

There have been several attempts to investigate the potential viability of re-introduced beaver populations. Nolet & Baveco (1996) developed a simulation model to analyse the viability of a re-introduced beaver population in the Netherlands. Their analysis concentrated on a single area of contiguous suitable habitat that they estimated could support a population of 190 beaver. They used data on survival and reproduction derived from the established source population in Germany and the translocated population in the Netherlands. The principal difference between the two populations was the lower natality rates in the translocated population. The model predicted a low probability of success when it was assumed that the low natality rates were a permanent result of poor habitat, and a high probability of persistence when it was assumed that natality rates would return to high levels for the offspring of the original founders. Macdonald *et al.* (1995) demonstrated how a population viability analysis could be applied to the beaver in Scotland. They simulated a single, randomly mixing population with a mean carrying capacity of 200-400 animals, with re-introductions of 10-100 animals with, and without, supplementary releases. A more realistic analysis of the potential spread of beaver, following re-introduction at three selected sites in Scotland, was undertaken by Macdonald *et al.* (1997). Populations were predicted to persist at the release sites but spread to new areas was predicted to be low.

The aim of this project is to evaluate the impacts of different release protocols on the viability of beaver populations in Scotland. We develop a stochastic simulation model for investigating the spread of beaver from release sites across the Scottish landscape, and analyse the sensitivity of the model to variation in its input parameters in order to identify those population parameters most likely to influence population success. We then use the model to investigate the potential responses of beaver populations to different release protocols over a range of life history parameters. The results are compared with those derived from the application of a commercial package for analysing population viability (VORTEX). The implications for schemes aimed at re-introducing beaver populations to Scotland are discussed.

## 2. TWO APPROACHES

Two modelling approaches were used to investigate the viability of introduced populations of beavers in Scotland. The first approach was based on a custom-built model that linked population dynamics and dispersal to a GIS system holding data on the spatial distribution of habitat suitable for occupation by beavers. This model was developed from a simple spatial dynamics model used in a previous research contract from Scottish Natural Heritage (Macdonald *et al.*, 1997), and was designed to investigate the spread of beaver populations in Scotland. Data describing the distribution of suitable habitats in Scotland were taken from the same source.

The second approach was based on the application of VORTEX (Lacy, 1993). The VORTEX analyses were designed to complement the custom-built model and to highlight the dependence of predictions on model structure. The analyses presented here are compared to a previous application of VORTEX to beaver population viability in Scotland (Macdonald *et al.*, 1995).

### 3. THE INTEGRATED GIS-POPULATION DYNAMICS MODEL

The initial model had two main components. First, a geographical information system (GIS) which stores environmental, habitat and animal population information. Second, an individual-based population dynamics module which simulates the life histories of individual beavers and their dispersal within the GIS-held landscape. The geographical information system used to store and retrieve habitat information and model output was GRASS (Westervelt *et al.*, 1990). The population dynamics sub-modules were written in the programming language C and integrated with the GIS component through a UNIX-shell environment. A flow diagram illustrating the links between the GIS and population dynamics modules is shown in Fig. 1.

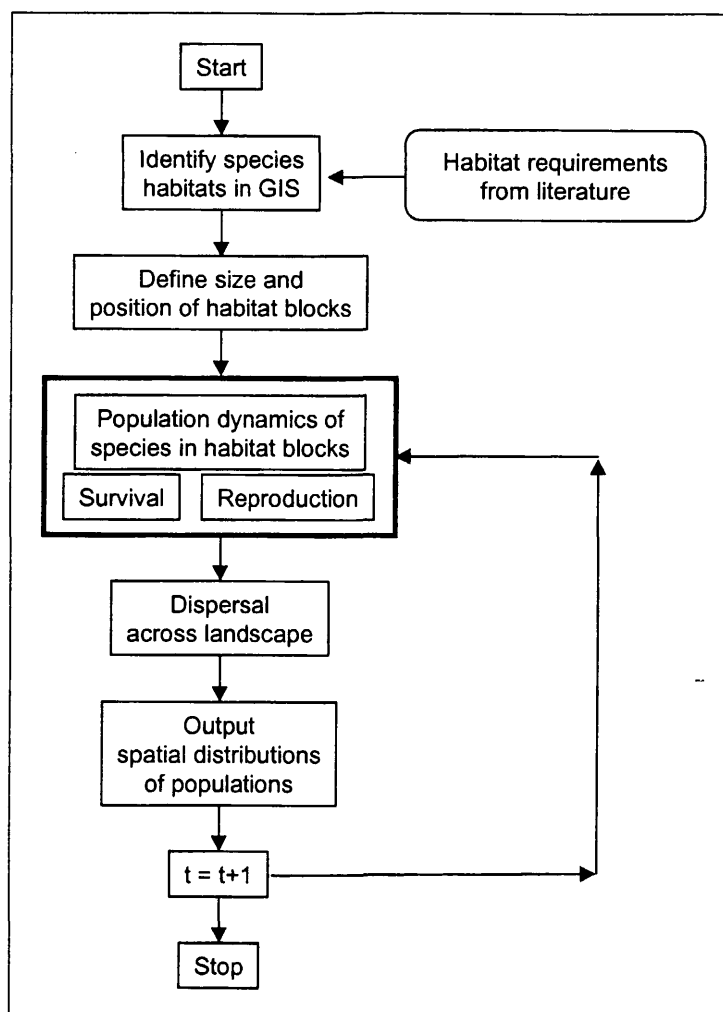


Figure 1. The integrated GIS and Spatial dynamics model for beaver populations

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

The land surface was partitioned into three: firstly, areas of habitat which could be used by beavers as home-ranges for foraging and breeding; secondly areas through which animals could move when dispersing, but which they could not exploit for home ranges; and finally areas which beavers were assumed not to enter. Identification of habitat suitable for occupation by beavers within the landscape was undertaken using the GIS module. Suitable habitats were defined on the basis of the distribution of deciduous woodland areas as recognised by categories of the land cover map for Scotland and a river network derived

from the 1:250,000 Bartholomew Digital map for Scotland. The size, composition and distribution of contiguous blocks of habitat were used to identify blocks of suitable habitat in which families/social groups of beavers could be found. The minimum area capable of supporting a population of each species was identified as contiguous blocks of woodland along river banks of greater than 3 km in length and blocks of marshland of greater than 10 hectares (ha). The carrying capacity of individual blocks of habitat was varied as a model input based on data from Nolet & Baveco (1996).

Dispersal habitats were assumed to be areas of non-montane land through which a river corridor or stream system ran. Areas of land through which beavers were assumed not to be able to create home ranges, or through which they could not disperse, were those without marshes, rivers or other water courses. Since the land surface of Scotland is extensively permeated by water courses the areas of non-dispersal, non-home range habitat were confined to mountainous areas.

### **3.2 Population dynamics and dispersal of beaver in landscapes**

Each block of suitable habitat within the landscape was modelled as having separate populations of families of beavers. Family groups were divided into four classes, adults capable of breeding (greater than 2 years of age); sub-adults (less than 2 years but greater than 1 year of age) and juveniles (1 year of age) and new young. Each group of families had their own dynamics which interacted through the processes 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 sub-adults from other habitat parcels and losses due to adult, sub-adult and juvenile mortality and emigration of sub-adults.

Reproduction in beavers was assumed to occur in one female in each family group and only in adult females of two years or older. The number of young produced in each litter in each family group was calculated by drawing deviates from a Poisson distribution with a mean number of animals per litter selected at run time. Mortality in adult beavers was assumed to occur after breeding. Mortality was estimated within each beaver family at the level of the individual. The likelihood of death for each individual was determined by sampling deviates from a uniform distribution in the range 0 to 1, with mortality occurring if the deviate was in the range of the average mortality for the relevant life stage. Thus for an adult mortality of 0.07% all deviates in the range 0 to 0.93 corresponded to an individual surviving, those from 0.93 to 1.0 corresponded to it dying. Mortality rates for each stage were based on data from Nolet & Baveco (1996).

Dispersal was modelled as a process occurring once a year. Only sub-adults that exceeded the carrying capacity of habitat parcels were allowed to disperse. Dispersal was modelled as a stochastic process. Dispersing animals interrogated the landscape, moving step-by-step through 2 km squares in the landscape if they contained suitable dispersal habitat. Animals stopped dispersal if they arrived at a dispersal square which contained one or more habitat blocks capable of supporting a breeding population. Animals moved on if the suitable habitat was already occupied by adults at carrying capacity. 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 squares through which dispersal was possible, the animal moved in the direction which was furthest from the preceding square occupied. Where there was more than one square equidistant from this point the square to move into was chosen at random. This pattern of dispersal gives a stronger directional component to dispersal than would a model of a random walk. If there were no suitable habitats available for occupation then dispersing animals were assumed to die.

### 3.3 Habitat data inputs for the model

Potential beaver release sites and dispersal habitats were the same as those identified in Macdonald *et al.* (1997). These data were in the form of National Grid co-ordinates for the geographical centre and total size of blocks of all woodland and marshland habitats of greater than 3 km length, adjacent to rivers in the 40,000 km<sup>2</sup> area comprising NH, NJ, NN and NO of the National Grid. A total of 94 sites was identified as being suitable for beavers by these criteria. The distribution of the 94 sites is shown in Fig. 2a. These 94 sites were used as potential release sites in the extended population viability model. The mean nearest neighbour distance for the 94 sites was 6.73 km (minimum distance 1.2 km; maximum distance 20.7 km; SD 4.58 km). The mean number of 200 m × 200 m blocks of habitat in the 94 sites was 26.3 (the minimum number of blocks was set at 15; maximum observed 158; SD 21.9 ). A histogram showing the size distribution of habitat parcels in terms of the numbers of beaver families they could support (following Nolet & Baveco, 1996) is shown in Fig. 2b. In excess of 70% of the habitat blocks were only capable of supporting one family of beavers and fewer than four blocks more than three families.

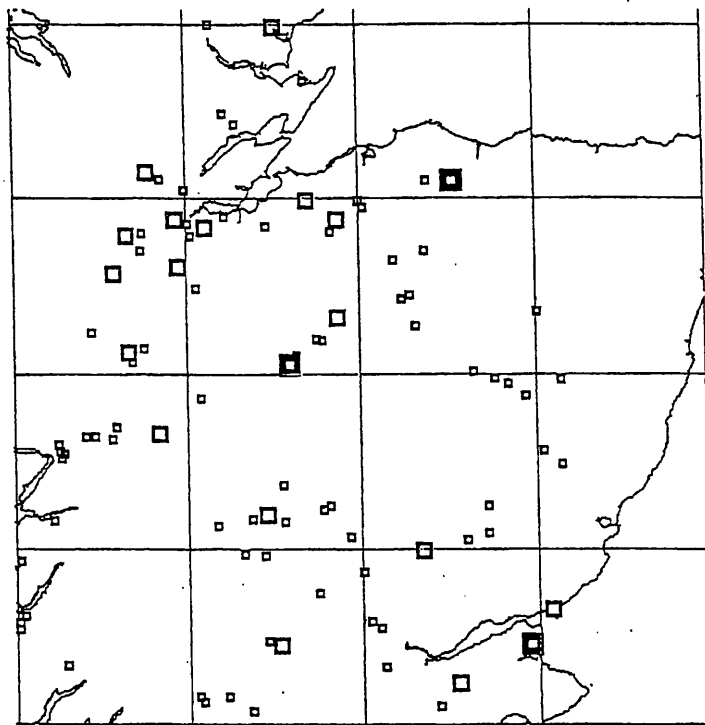


Figure 2a: Distribution of the 94 habitat patches predicted as being able to support at least one beaver family in the 100 km National Grid squares, NH, NJ, NN and NO in Scotland. Small squares = 1 family, medium squares = 2-3 families, large squares = 7-10 families. Grid = 50 km, south edge = 700,000, west edge = 2000,000.

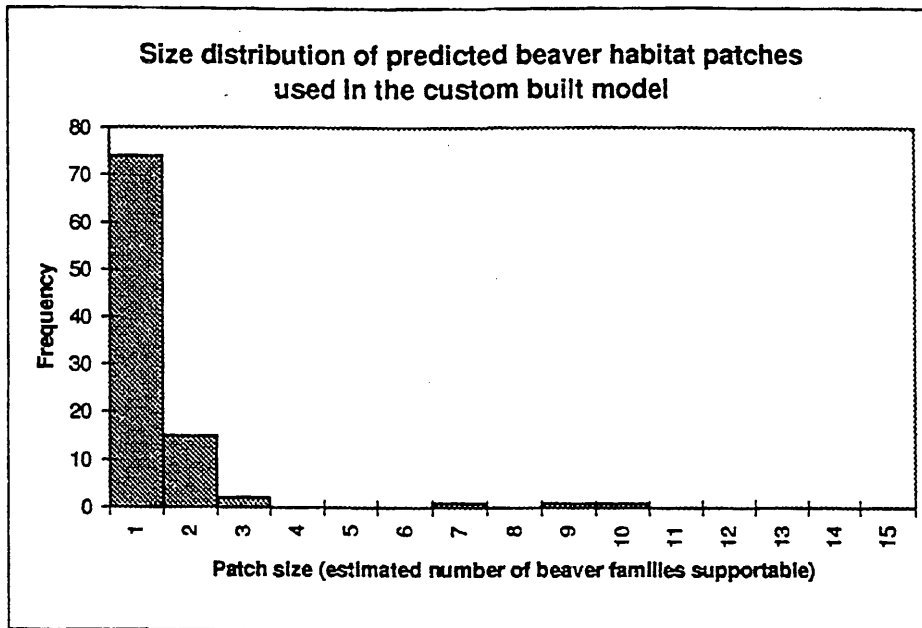


Figure 2b. Size distribution of predicted beaver habitat patches used in the custom built model.

### 3.4 Sensitivity Analysis

The sensitivity of the population dynamics model to input parameters was investigated by analysing the total population size and the persistence of populations of beavers over 30 years in Scotland 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 life history variables in the model. In this methodology, sample values of the input parameters are selected using a randomisation procedure subject to constraints on the extent of correlation of input variables that are imposed by the modeller.

Nine parameters were considered, namely

- i) maximum dispersal distance - the distance which beavers could disperse along the river corridor (the lower limit was 4 km and the upper 80 km);
- ii) minimum habitat requirement (an inverse measure of carrying capacity) - the number of 4 ha blocks of river habitat needed for a beaver family (the lower limit for linear stretches was set at 2 km and the upper at 3.6 km);
- iii) fecundity - the mean number of young per brood, with a lower limit of 1 and an upper limit of 3;
- iv) the proportion of females breeding each year with a lower limit of 50% and an upper limit of 70% (these values approximate field data for an established population in Germany (63%) and are higher than estimates obtained from the translocated population in the Netherlands (31%) (Nolet & Baveco, 1996));
- v) adult mortality per year, with a lower limit of 6.3% and an upper limit of 7.7%;
- vi) sub-adult mortality per year, with a lower limit of 6.3% and an upper limit of 7.7%;
- vii) yearling mortality, with a lower limit of 45% and an upper limit of 55%;
- viii) juvenile mortality per year, with a lower limit of 29% and an upper limit of 36%; and
- ix) dispersal mortality per year, with a lower limit of 40% and an upper limit of 80%. Data on all mortality parameters are sparse so the values used encompass the range recorded by Nolet & Baveco (1996). The ranges of the parameters considered in the sensitivity analysis are shown in Table 1.

In all cases there were insufficient data available to model the actual statistical distribution of each parameter. Furthermore, there were no data available to assess the extent to which each of the life history parameters were correlated with the others. A uniform distribution was assumed for each variable, with upper and lower limits around the average derived from the literature. Constraints on the extent of correlation allowed between each variable were set at a low level of 0.5. A total of 50 permutations of the input parameters was selected and the model was then run for 30 years, under one re-introduction scenario (a single release of 15 animals to each of eight randomly selected patches) for each permutation. At the end of each 30 year run, the number of patches occupied and the total population size of beavers present in the landscape were output. The impact of the individual life history parameters on model output were investigated using Generalised Linear Modelling with total population and number of populations as the dependent variables and the inputs as independent variables in regression. The analyses were undertaken in GLIM.

Table 1. Values of life history and habitat parameters used in the GIS-population model for analysing population viability in Scotland.

Parameter	Lower value	Upper value
Maximum dispersal distance (km)	4.0	80.0
Minimum habitat requirement (km)	2.0	3.6
Fecundity	1.0	3.0
Proportion of females breeding	0.50	0.70
Adult mortality	0.063	0.077
Sub-adult mortality	0.063	0.077
Yearling mortality	0.44	0.55
Juvenile mortality	0.29	0.36
Dispersal mortality	0.40	0.80

### 3.5 Assessing the affects of size of introduced population, number of release sites and repeated annual releases on the viability of introduced beaver populations

The effects of initial release size and the number of release sites on the viability of populations of beavers were investigated by running the population viability model with a range of re-introduction sites and size of population released at each site. Sites were selected at random from the 94 predicted to be available in the 40,000 km<sup>2</sup> of the study area. Fifty permutations of randomly selected release site and initial population size at each site were used as model inputs. The model was then run repeatedly using the same 50 permutations of Life History Input (LHI) parameters used in the sensitivity analyses described above. The 50 LHI permutations used in this analysis were considered to be representative of the range that would be likely to occur in beaver populations in the field, and the number of times the population went extinct a measure of the potential population viability. The values for size of population released and number and identity of release sites were selected at random, so normal scores were used to assess the extent to which these data were normally distributed and amenable for analysis using Generalised Linear Modelling (GLM) approaches. The number of extinctions in each run of 50 life history permutations was used as a dependant variable in logistic regression to investigate the effects of variations in number of release sites and population release size on population viability.

The analysis was repeated with re-introductions of beaver populations at the same release sites for 5 years after the initial release for each set of LHI permutations in order to investigate the effects of introducing animals repeatedly over different years. The number of

extinctions in each run of 50 life history permutations with a yearly supplement of introduced beaver population was used as a dependant variable in logistic regression to investigate the effects of variations in number of release sites and population release size on population viability.

Three additional sets of 50 model runs were conducted in which 20 animals were introduced to one of the three largest patches identified in the habitat analysis.

## 4. APPLICATION OF VORTEX

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

Previous use of VORTEX to analyse the viability of the beaver in Scotland considered all animals as part of a single randomly mixing population (Macdonald *et al.*, 1995). The spatial structuring of populations is an important component of their viability, particularly in fragmented landscapes (e.g. Gilpin & Soulé, 1986). Here three VORTEX analyses were performed to outline how different representations of the spatial population structure determine viability predictions. The analyses are applied to the same area as the custom-built model, but as described below this area is represented differently. As a generic software package there are certain limitations in the ability of VORTEX to represent the social system of the beaver. Within these constraints the simulations presented here are tailored as closely as possible to the beaver and potentially important limitations are discussed.

### 4.1 Outline of the three sets of VORTEX runs

- 1) A single population, carrying capacity determined by summing the carrying capacities of all suitable habitat blocks in the 40,000 km<sup>2</sup> area comprising NH, NJ, NN, and NO of the National Grid.
- 2) A subdivided population, separate carrying capacities for spatially separated habitat blocks, dispersal between blocks dependant upon the straight line distance between them.
- 3) A single population, carrying capacity set to the same value as that for the largest sub-population in the subdivided population runs.

### 4.2 Setting parameter values

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

### **4.3 Representing beaver social structure**

It was not possible to represent explicitly the family structure of beavers (an adult bonded pair, kits yearlings and sub-adults) within VORTEX. Instead, carrying capacities were calculated by dividing the area of each of the 94 blocks of breeding habitat by the area estimated as necessary to support a single family group. The number of family groups was then multiplied by 5 (mean family group size) to obtain a carrying capacity estimate. This has the disadvantage that no constraints are placed upon the composition of family groups. This is likely to cause more errors in the sub-divided population runs and particularly in the small patches where by chance you could end up, for example, with families composed entirely of one sex or entirely of sub-adults.

### **4.4 Spatial structure in the three series of VORTEX runs**

#### *4.4.1 Single large population*

The habitat analysis (using the mean values from the custom-built model) predicted that the 94 habitat blocks could support 136 family groups, giving an estimated carrying capacity of 680 animals. Therefore the carrying capacity was set at 680 for the single large population runs. Runs were conducted with starting populations of 20 animals under high and low natality scenarios.

#### *4.4.2 Sub-divided population*

The current version of VORTEX (version 8.02 was used for this analysis) can handle a maximum of 50 sub-populations. As the habitat analysis identified 94 separate habitat patches that were potentially capable of supporting one or more beaver family, not all could be modelled as separate populations. To get around this problem, the distance between all patches was calculated so that patches close to each other could be amalgamated for input into VORTEX. It was found that if patches closer together than 9 km were amalgamated, the number of new patches was 46. The carrying capacities (in number of beaver families supportable) for the amalgamated patches were calculated by adding the carrying capacities of each of the constituent patches (thus this does not allow for a beaver family to live between more than one patch). Each amalgamated patch was assigned a centroid coordinate that was midway between the centroids of all of the constituent patches. Fig. 3a shows the spatial location of amalgamated patch centroids, and Fig. 3b shows the size distribution of the amalgamated patches. Subsequent use of the word 'patch' with regard to the VORTEX analyses, refers to these amalgamated patches.

Only sub-adults (2 year olds) were allowed to disperse (the same as in the custom-built model). Dispersal was modelled as only occurring once sub-populations reached carrying capacity (by setting the dispersal threshold ratio of population density divided by carrying capacity to 1).

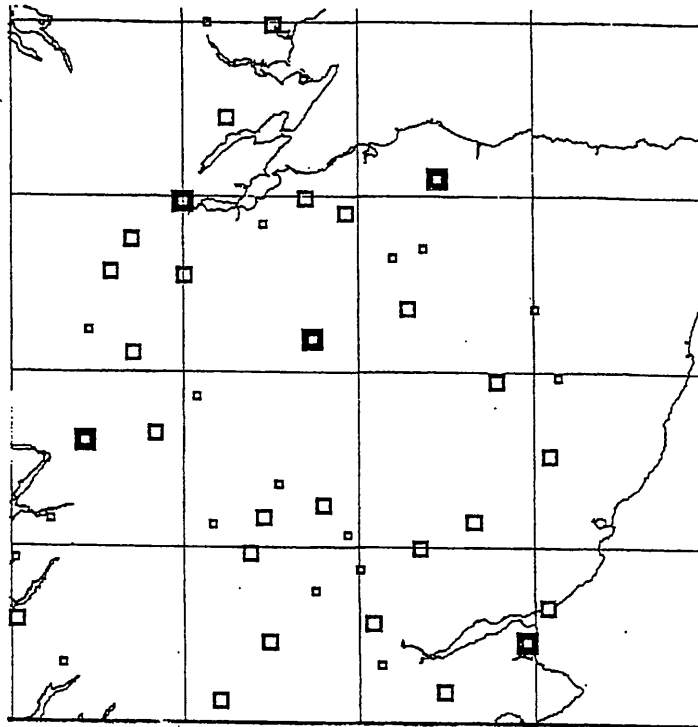


Figure 3a. Distribution of the centroids of the 46 amalgamated habitat patches used in the VORTEX analysis for the 100 km National Grid squares, NH, NJ, NN and NO in Scotland. (Habitat patches within 9 km amalgamated and their predicted carrying capacities summed.) Small squares = 1 family, medium squares = 2.5 families, large squares = 7-15 families. Grid = 50 km, south edge = 700,000, west edge = 200,000.

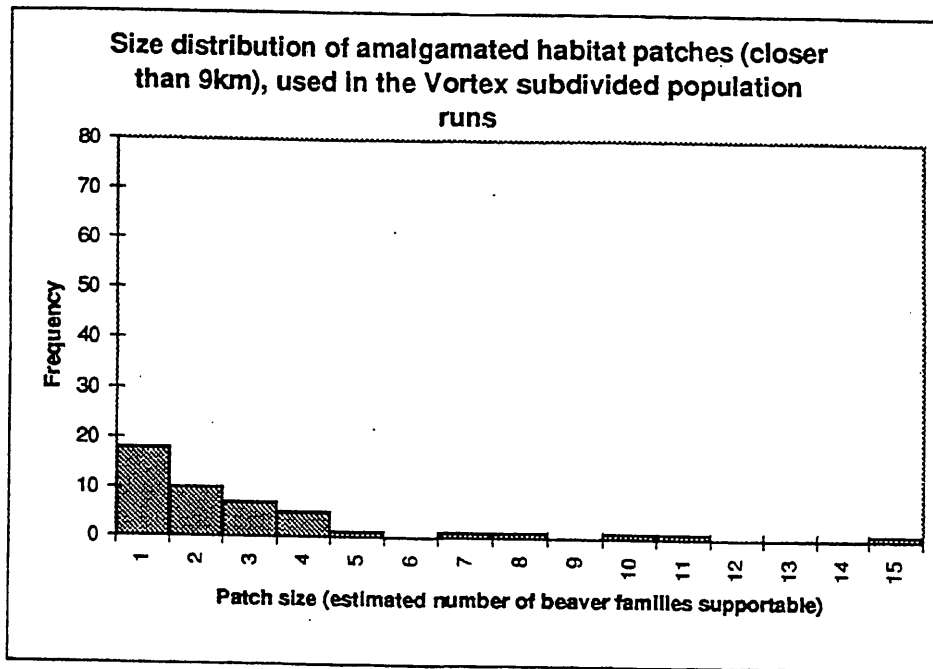


Figure 3b. Size distribution of amalgamated habitat patches (closer than 9 km), used in the VORTEX subdivided population runs.

VORTEX uses a dispersal matrix to define dispersal between patches. The values within this matrix define the probability of dispersal from each patch to every other patch. The dispersal matrix was derived by first calculating the distance between each of the patches. Then, for each patch the identity and number of patches that were within the defined maximum dispersal distance were calculated. A maximum dispersal distance of 50 km was used in this analysis. In the final step a dispersal probability was calculated for each patch as  $1/(\text{number of patches within dispersal range})$ , and this value was used as the probability of dispersal from the patch to each other reachable patch. Thus animals were assumed to have an equal probability of dispersing to all reachable patches, providing they were below carrying capacity. Within VORTEX a patch within the dispersal distance is chosen randomly and if this is already at carrying capacity another is chosen, this process is repeated up to ten times and if a patch below carrying capacity is still not found the animal dies. This combination of the dispersal threshold and the dispersal probabilities used mean that, once a population reaches carrying capacity, all 'excess' sub-adults disperse to one of the patches within the maximum dispersal distance (or die if they do not locate one that is below carrying capacity). Dispersal mortality was set at 60% (values of 40% to 80% were used in the custom built model).

Runs were conducted under high and low natality scenarios, for 20 animals introduced between the four largest patches (i.e. five animals in each patch), and with all patches close to carrying capacity. Additional runs were conducted under the high natality scenario for 20 animals introduced to the largest patch, and for 20 animals introduced between four of the smallest patches.

#### *4.4.3 Single sub-population*

A single population was simulated with a carrying capacity equivalent to that of the largest amalgamated patch in the subdivided population analysis (75 animals). Runs were conducted under high and low natality scenarios with a starting population of 20 animals.

## 5. RESULTS

### 5.1 Integrated GIS-population dynamics model

#### 5.1.1 Sensitivity Analysis

Parameter estimates describing the effects of variations in individual life history inputs to the model on the model outputs of total beaver population and the number of beaver populations are shown in Table 2. The most obvious feature is that only two variables appear to have any significant effect on model output. These were the minimum habitat requirement and the fecundity. Of these, the most important was the minimum habitat requirement, which was negatively correlated with both model outputs.

Table 2: Parameter estimates, standard errors and approximate t values (one-sided test) for GLMs relating the number and total population sizes of released beaver populations after 30 years for one release scenario under 50 different life history parameter scenarios.

Variable estimate	Total population size			Number of populations		
	Parameter	s.e.	t	Parameter	s.e.	t
Constant	5.188	1.179	4.40	3.302	3.415	0.97
Dispersal distance	-0.006	0.006	1.00	-0.001	0.019	0.05
Min. habitat required	-0.322	0.035	9.20***	-0.285	0.101	2.82***
Mean fecundity	-0.304	0.046	7.39***	0.235	0.134	1.75*
Females breeding	0.589	0.567	1.03	0.289	1.657	0.17
Adult mortality	-7.805	9.716	0.83	-2.976	28.00	0.11
Yearling mortality	-0.112	1.122	0.09	-0.215	3.257	0.06
Sub-adult mortality	-0.650	9.343	0.06	-2.245	26.87	0.08
Juvenile mortality	-1.559	1.870	0.63	-2.434	5.434	0.44
Dispersal mortality	0.252	0.317	0.79	0.103	0.919	0.11
Deviance explained		193			14	
Residual deviance		23			9	
Null deviance		216			23	

\* P<0.05; \*\*\* P<0.005

#### 5.1.2 The effects of size of introduced population, the number of release sites and repeated annual releases on the viability of introduced beaver populations

There were 50 permutations of size of the introduced population and number of release sites. Correlations of the normal scores for the number of animals released with the number of release sites were 0.993 and 0.991 respectively, providing no evidence to suggest that the distribution of either parameter was not normal. The results of GLMs relating the probability of extinction to variation in the number of populations released and the size of release population is shown in Table 3a. All models were significant, with the size of population released and the number of animals in each release population explaining 38% of the total deviance in the predicted extinctions.

The number of populations released was more important in determining extinction than was the size of population released, explaining 23% and 13% of the deviance in GLMs with each parameter assessed individually. This suggests that the number of release sites may be a

more critical factor determining the success of a re-introduction scheme than the number of animals actually released. The results of GLMs relating the probability of extinction to variation in the number of populations released and the size of release population when animals were released repeatedly for 5 years are shown in Table 3b. All models were significant and the amount of variation explained was similar to that in the non-repeat release model runs at 32%. As with the non-repeat release models, the number of populations released was more important in determining extinction than was the size of population released, explaining 19% and only 2% of the deviance in GLMs with each parameter assessed individually.

Table 3a. Parameter estimates and standard errors relating the probability of extinction after 30 years generated by the custom built model, following a single release.

Fifty different life history parameter scenarios were run for each of 50 release scenarios.

	Parameter estimate		s.e.
constant	2.903		0.141
number of populations	-0.2900		0.017
size of released population	-0.1162		0.0085

	Both parameters	Number of populations	Size of populations
Deviance explained	516	317	180
Residual deviance	842	1041	1178
Deviance of null	1358	1358	1358

Table 3b. Parameter estimates and standard errors relating the probability of extinction after 30 years generated by the custom built model, following repeated releases every year for five years. Fifty different life history parameter scenarios were run for each of 50 release scenarios.

	Parameter estimate		s.e.
constant	2.288		0.176
number of populations	-0.3510		0.020
size of released population	-0.0996		0.0086

	Both parameters	Number of populations	Size of populations
Deviance explained	377	231	30
Residual deviance	805	951	1152
Deviance of null	1182	1182	1182

### 5.1.3 Predicting the likelihood of extinction for introduced populations of beaver under random patch choice

The parameter estimates for the GLMs, relating extinction probability to the size and number of re-introduced populations, were used to evaluate the likelihood of success of re-introduction schemes. Dr M Cole (SNH, pers. comm.) suggested that a population of 20 animals was the current practical limit to the number of animals that could be collected annually for use in any release scheme. Predicted likelihoods of population persistence in

the 40,000 km<sup>2</sup> of the study area for schemes based on releasing a total of 20 animals are shown in Table 4. Also shown are estimates for release populations of 50 and 100 animals. For all permutations of 20 total animals released the likelihood of extinction after 30 years was predicted to be in the range 76-62%. The probability of extinction was predicted to be much lower in the repeat release scenario in the range 64-38%. The lowest extinction probabilities were predicted for scenarios with the highest number of populations rather than the greatest number of animals. For an annual release population of 100 animals, the likelihood of extinction after 30 years declined to 23% for a single release and 9% if beaver were released repeatedly over 5 years.

Table 4. Predicted probabilities of extinction after 30 years generated by the custom built population dynamics and dispersal model. Different sized populations of beaver released at different numbers of randomly chosen sites in Scotland.

Number of populations	Size of population	Extinction Probability	
		Single release	Repeated releases over 5 years
2	10	0.76	0.64
4	5	0.76	0.59
5	4	0.72	0.53
7	3	0.62	0.38
10	5	0.35	0.15
5	10	0.57	0.38
10	10	0.23	0.09

#### 5.1.4 *Predicting the likelihood of extinction for populations introduced to the three largest patches*

For the three sets of runs in which 20 animals were introduced to one of the three largest patches, predictions of population persistence to 30 years were all 100%. These persistence probabilities are much higher than those generated by the random patch choice scenarios.

#### 5.1.5 *Predicting change in patch occupation and total population size*

Of all the runs in which the number of animals and patches were chosen randomly, in only a very small percentage was there an increase in the number of patches occupied after 30 years (2.4% for the single release runs and 3.8% for the multiple release runs) (Table 5). For the runs in which 20 animals were introduced to one of the three largest patches, the percentage of runs that resulted in an increase in the number of patches occupied was higher, but still relatively low at 12.7%. For all three scenarios the mean increase in patch occupation, for those runs that did increase, was less than 3 patches (Table 5). Thus, for all of the custom built model runs, there was little increase in patch occupation. For each of the three sets of runs (single release, multiple release and release to the large patches), the mean total population of beavers after 30 years was less than 20 and less than the total number released (Table 6).

Table 5. Predicted change in patch occupation over 30 years generated by the custom built population dynamics and dispersal model.

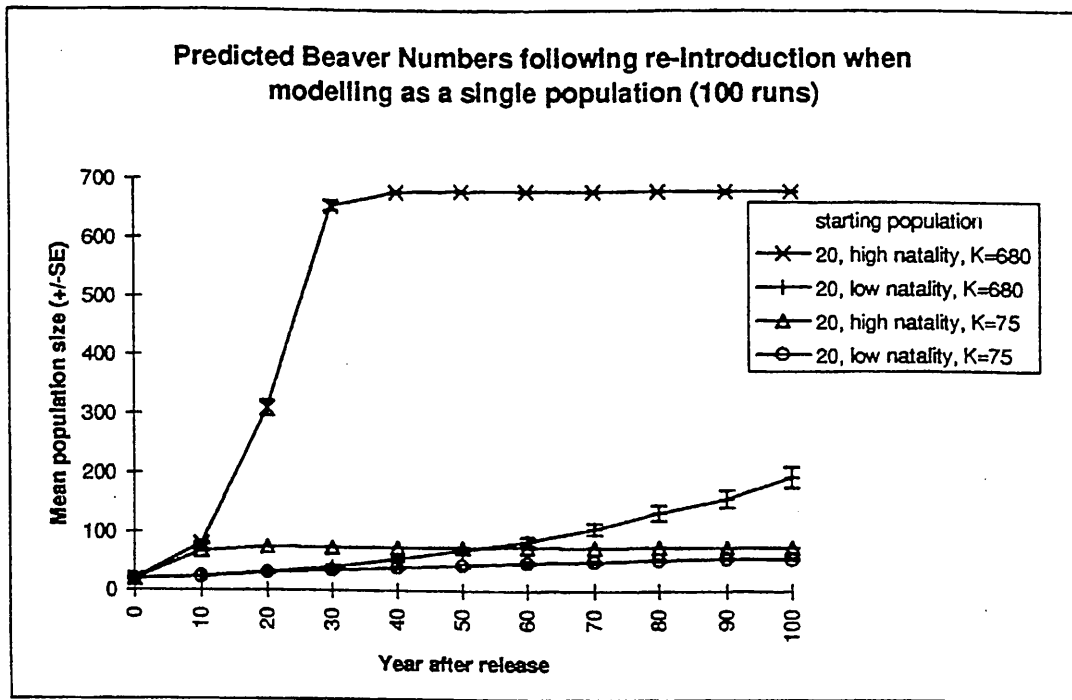
Model scenario (total number of runs)	No. of runs in which patch occupation increases	Max. patch occupation increase	Mean increase across runs in which patch occupation increases
Single release of 1-20 animals in 1-10 patches (n = 2500)	60 (2.4%)	4	1.55
Repeated releases over 5 years of 1-20 animals in 1-10 patches (n = 2500)	95 (3.8%)	11	2.59
Single release of 20 animals in one of the 3 largest patches (n = 150)	19 (12.7%)	3	2.32

Table 6. Comparing predicted population size after 30 years in different model runs of beaver re-introduction to Scotland (all with high natality values based on an established German population rather than a translocated Dutch population (Nolet & Baveco, 1996).

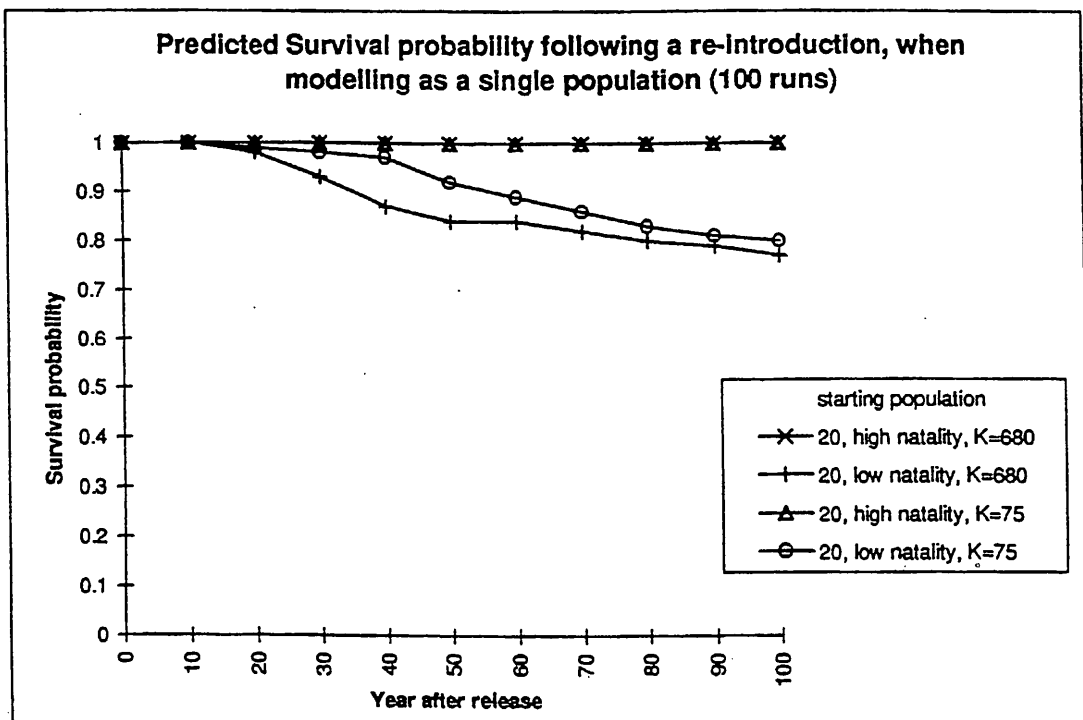
Model scenario (no. of runs)	Mean population size (year 30)	Mean number of animals released	Mean change in population size (year 30)
Custom built model Single release of 1-20 animals in 1-10 patches (n=2500)	5	48	-43
Custom built model Repeated releases over 5 years of 1-20 animals in 1-10 patches (n=2500)	12	297	-285
Custom built model Single release of 20 animals in one of the 3 largest patches (n=150)	18	20	-2
VORTEX, subdivided population. Single release of 5 animals in each of 4 small patches (n=100)	2	20	-18
VORTEX, subdivided population. Single release of 20 animals in the largest amalgamated patch (n=100)	146	20	126
VORTEX, single population. (K= 680). Single release of 20 animals (n=100)	654	20	634

## 5.2 Results of VORTEX PVA analyses

When the whole area was represented as a single randomly mixing population, mean population size increased under both natality scenarios (Fig. 4a). Population sizes increased very rapidly under the high natality scenario, and reached carrying capacity within 50 years. Probability of population persistence over 100 years was 100% when natality was high and 77% when natality was low (Fig. 4b). Simulations of a single population with a carrying capacity of 75 resulted in almost identical persistence rate predictions (Fig. 4b) and population sizes increasing towards carrying capacity (Fig. 4a).



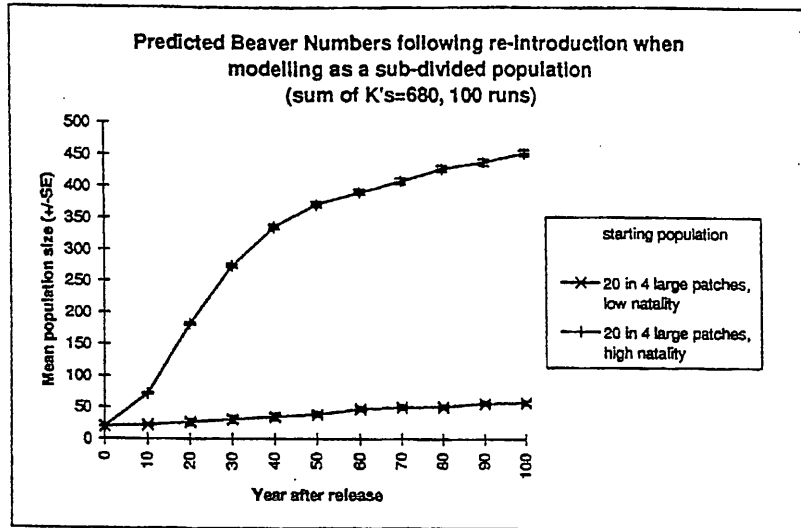
(a) Predicted beaver numbers following re-introduction when modelling as a single population (100 runs).



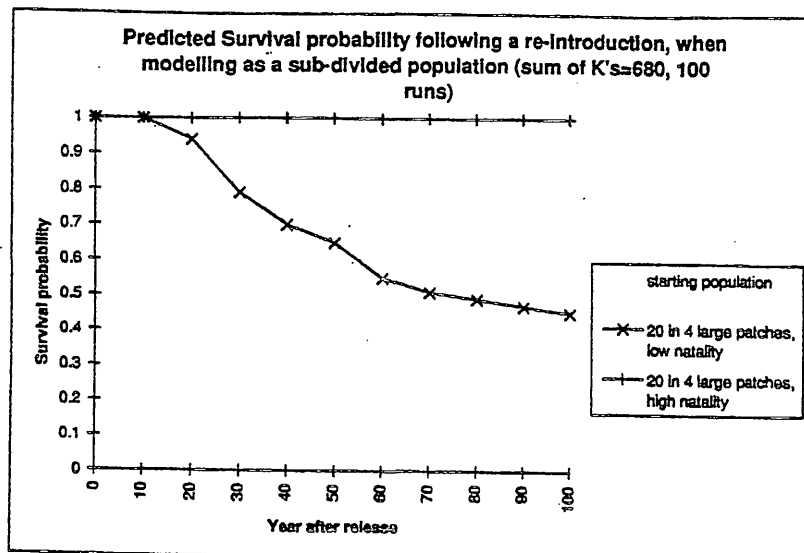
(b) Predicted Survival probability following a re-introduction, when modelling as a single population (100 runs).

Figure 4. VORTEX PVA analysis of single population

When the whole area was represented as a sub-divided population the predictions were generally less optimistic. Fig. 5a shows that when 20 animals were introduced to four large patches, the population increased slowly under a low nataly scenario and rapidly under the high nataly scenario, although in both cases these increases were slower than when considering a single population of equivalent size. Persistence remained at 100% for the high nataly runs, but declined to 79% and 45% at 30 and 100 years respectively for the low nataly runs (Fig. 5b). When they were started close to carrying capacity, populations declined initially under both nataly scenarios, but levelled out at around 580 animals under the high nataly scenarios and continued to decline slowly, reaching around 220 animals at year 100 under the low nataly scenarios (Fig. 6a). In both cases persistence remained at 100% (Fig. 6b).

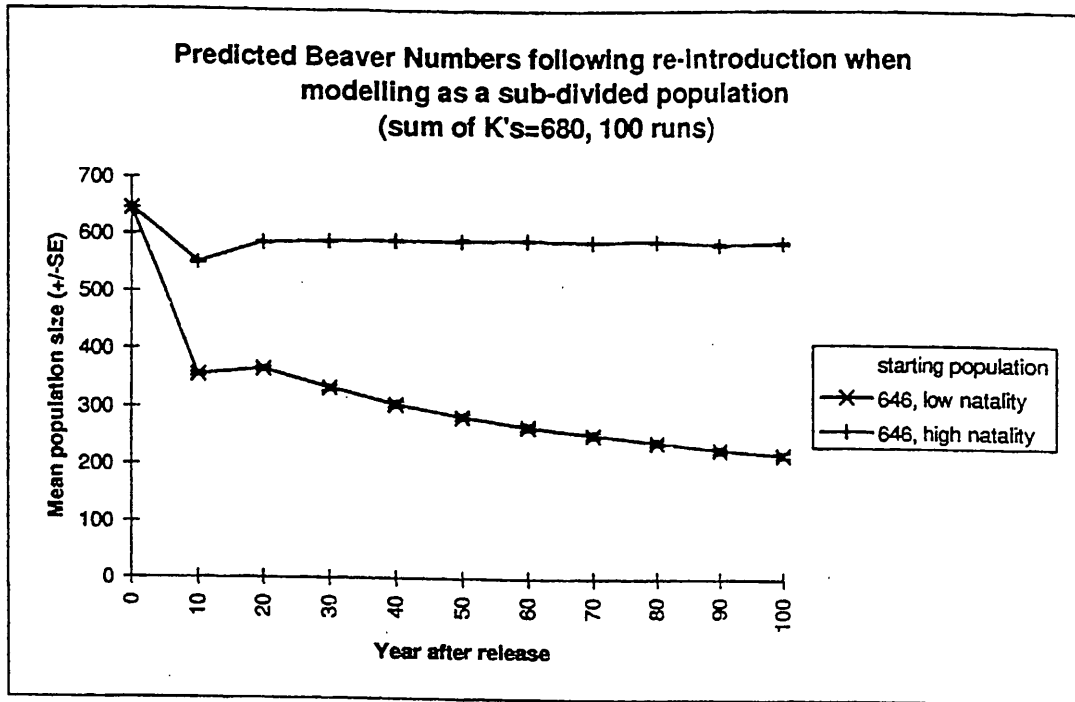


(a) Predicted beaver number following re-introduction when modelling as a sub-divided population (sum of block carrying capacities = 680, 100 runs)

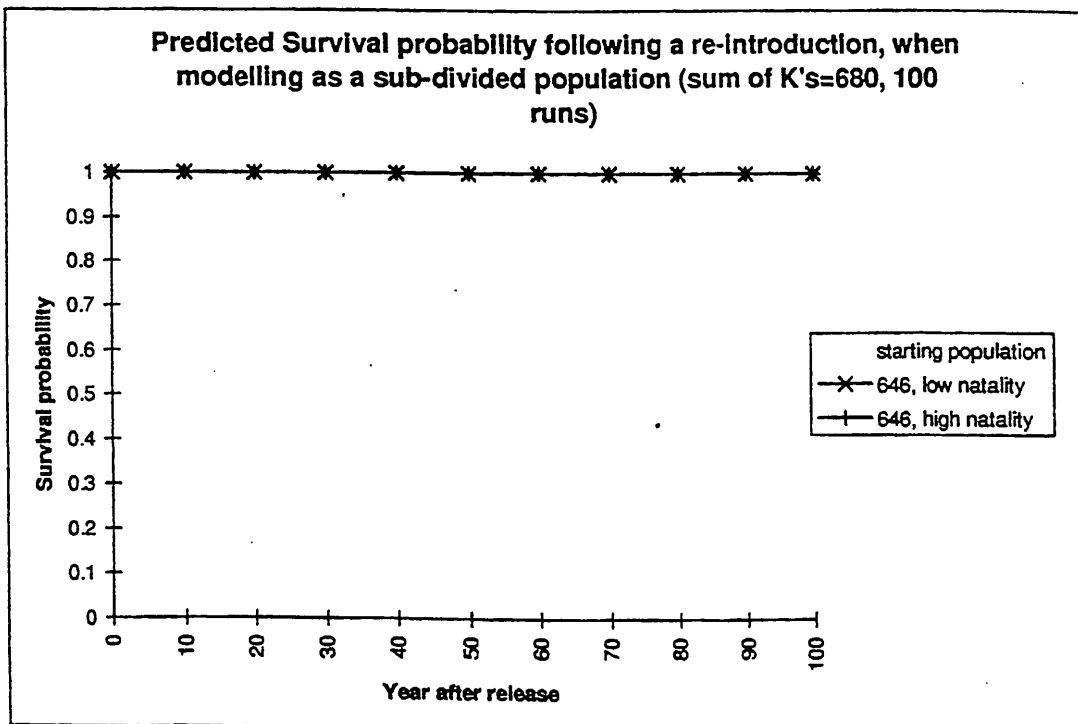


(b) Predicted survival probability following a re-introduction, when modelling as a sub-divided population (sum of block carrying capacities = 680, 100 runs).

Figure 5. VORTEX PVA analysis of sub-divided population



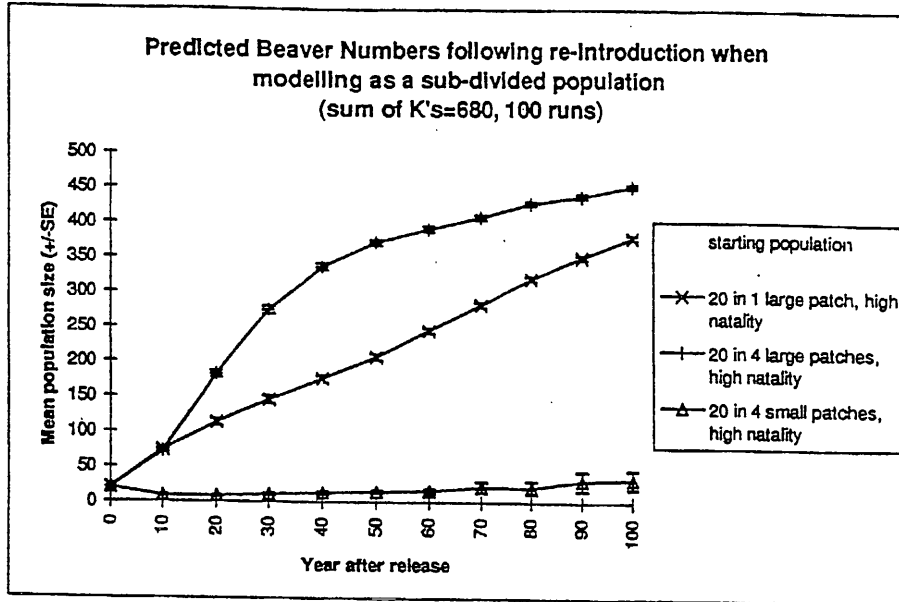
(a) Predicted beaver numbers following introduction when modelling as a sub-divided population (sum of block carrying capacities = 680, 100 runs).



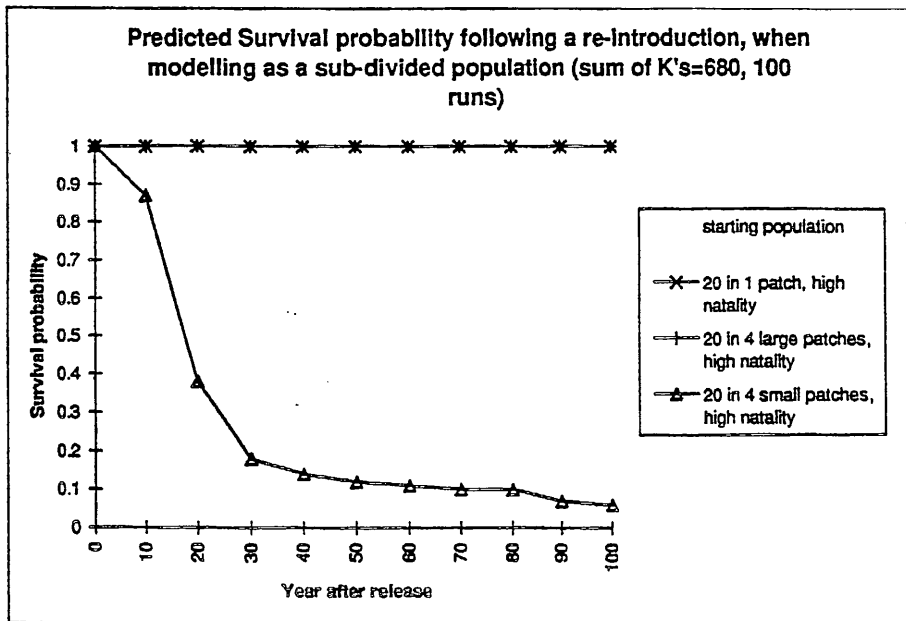
(b) Predicted survival probability following a re-introduction, when modelling as a sub-divided population (sum of block carrying capacities = 680, 100 runs)

Figure 6. VORTEX PVA analysis of sub-divided population, with introductions just below carrying capacity

Fig. 7 compares the results of three different release scenarios, each of 20 animals, modelling as a subdivided population using high natalty parameters. Rate of population increase was highest when five animals were introduced to each of four large patches (reaching around 270 animals by year 30 and 440 by year 100) and lowest when five animals were introduced to each of four small patches (not reaching 50 animals by year 100) (Fig. 7a). Population persistence remained at 100% under both large patch scenarios but declined to 18% and 6% by years 30 and 100 respectively, under the small patch scenario (Fig. 7b).



(a) Predicted beaver numbers following re-introduction, when modelling as a sub-divided population (sum of block carrying capacities = 680, 100 runs).



(b) Predicted survival probability following a re-introduction, when modelling as a sub-divided population (sum of block carrying capacities = 680, 100 runs).

Figure 7. Comparison of three release scenarios

### 5.3 Results summary: comparing predictions of the different approaches

Table 7 shows the population persistence predictions made by the different modelling scenarios for an initial introduction of 20 animals using high natality parameters. The table shows predicted population size and change from a selection of the different model runs. The one thing that is immediately noticeable about the results of the different scenarios and approaches is the diversity in their predictions of population size and persistence. It is possible to split the predictions of the different modelling approaches and scenarios into four broad categories.

a) **Prediction of high persistence and large population increase**

All of the VORTEX high natality runs, with the exception of those simulating re-introduction to the small patches.

b) **Prediction of high persistence and low or negative population change**

The custom built model runs simulating re-introduction to the large patches.

c) **Prediction of medium persistence and low or negative population change**

VORTEX, low natality runs. Custom built model runs simulating large, repeated releases to multiple randomly chosen patches.

d) **Prediction of low persistence and population decline**

Custom built model runs simulating single releases to randomly chosen patches (and those simulating small repeated releases). VORTEX, high natality runs simulating re-introduction to small patches.

Table 7. Comparing predictions of population persistence in different model runs of beaver re-introduction to Scotland (all with starting populations of 20 animals and high natality values based on an established German population rather than a translocated Dutch population (Nolet & Baveco, 1996).

<b>Model run (all with a release size of 20 animals)</b>	<b>Persistence probability after 30 years (%)</b>	<b>Persistence probability after 100 years (%)</b>
Custom built model GLM derived from releases in randomly chosen patches.	24-28	-
Custom built model Releases in 1 large patch	100	-
VORTEX, subdivided population Releases in 4 small patches	18	6
VORTEX, subdivided population Release in 1 large patch or 4 large patches.	100	100
VORTEX, single population K=75 or 680.	100	100

## 6. DISCUSSION

The most obvious way to investigate whether or not a species is capable of surviving in a landscape following introduction is to release the animal and monitor changes in the population afterwards. In the past, introductions of non-native species have followed this *ad hoc* approach and particular difficulties have been encountered as the species impacts directly on the native fauna and on human economic activity. In contrast, *re-introduction* of once native species is considered desirable ecologically, because it may enhance the conservation of the species globally and is often seen as a step in remedying any ecosystem degradation that followed on from the original extinction. Whilst there are ecological and conservation arguments for species re-introduction, it is clearly illogical to undertake it without some consideration of 1) how the species will respond in the 'new' landscape in which it finds itself; 2) whether or not the re-introduction is practicable; and 3) some assessment of the likely success of the release scheme. The only practical method for investigating re-introduction schemes prior to translocating the animals is through the use of techniques which simulate population behaviour mathematically, i.e. through modelling.

The objective of all modelling is to summarise systems such that their behaviour can be explained with the minimum of complexity and the minimum number of driving variables. This included all factors important in determining system behaviour and excluded those which are not. The objective of Population Viability Analysis (PVA) is "the quantitative evaluation of all factors and their interactions that act on populations and contribute to their risks of short- and long-term decline or extinction." (Boyce, 1992). In systems as complex as those concerned with population dynamics there are inevitably many potential routes for modelling. This is particularly the case in PVA where there are many packages available commercially. The models underlying these packages each make different assumptions about population processes that can have considerable influences on the outcome of analyses (Lindenmayer *et al.*, 1995). The choice of what is important and included and unimportant and excluded processes depends on what the authors of each package deemed important (Lindenmayer *et al.*, 1995). The conclusions based on any PVA must therefore be considered in the light of the underlying modelling assumptions.

The analysis of the viability of a re-introduced population is subtly different to that needed for an established species, in that there is an increased emphasis on the role of spatial population processes. In a population re-introduction scheme, the number of populations to be re-introduced and the number of organisms released is inevitably small for practical reasons. Thus, the modeller is interested not only in the long-term viability of the population in the proposed re-introduction sites, but crucially in the ability of the organism to disperse to and colonise new sites. Whilst it may be desirable to incorporate models of dispersal into spatial population dynamics to make these models more realistic, it is not clear how this should be achieved. Dispersal is a behavioural process and providing accurate mathematical descriptions of the processes that initiate, undertake and complete dispersal is difficult. Indeed, the inability to model behaviour realistically is seen as a critical factor determining the value of individual-based modelling (Lima & Zollner, 1996) and the value of such models for conservation management generally (Conroy *et al.*, 1995).

The predictions of persistence and population spread varied considerably between the different approaches and scenarios presented here. The low natality VORTEX runs predicted medium persistence and low population spread. The high natality VORTEX runs predicted high persistence and large population increases, except when animals were introduced to small patches alone, in which case low persistence and population decline were predicted. The custom built model runs (also using high natality parameters) generally predicted low persistence and population decline, except when animals were introduced to

the larger patches, in which case persistence was high but the population was not predicted to increase. The difference between the VORTEX and custom-built model predictions was illustrated most clearly by the runs that simulated a single release of 20 animals to one of the largest patches; the VORTEX runs predicted a mean population of 146 animals after 30 years, whereas the mean population size predicted by the custom built model was just 18.

The difference between the predictions of the low and high mortality VORTEX runs (based on data from an established beaver population in Germany and a translocated population in the Netherlands respectively) is consistent with the predictions made by Nolet & Baveco (1996). Their model predicted a 20% probability of persistence over 100 years under a low natality scenario and a 100% probability of persistence under a high natality scenario. This suggests that the likelihood of success of a beaver re-introduction to Scotland will be dependant on natality rates exceeding those measured by Nolet & Baveco (1996) in the Netherlands.

The difference in predicted persistence between introductions to small and large patches was consistent across both modelling approaches. Releases to large patches generally ended in predicted persistence, releases to small patches (and these include most of the random patch choice runs as the majority of patches are small) generally ended in predicted extinction. Small patches are more vulnerable to demographic stochasticity and therefore have a lower probability of persistence in isolation. In addition, small patches have a lower potential to produce dispersers, and thus are less likely to be the source for the colonisation of other patches. This predicts that beavers would have a higher probability of persistence and spread in Scotland if releases were targeted at the larger potential release sites.

The difference between the mostly optimistic VORTEX predictions and the mostly pessimistic predictions made by the custom built model is most likely a result of their different representation of the dispersal process. In the custom built model the dispersal process was represented explicitly. Individual animals were simulated as moving through areas suitable for dispersal until either an area suitable for occupation was found, in which case the animal settled there, or the maximum dispersal distance was exceeded, in which case the animal died. The movement algorithm had a directional component but was largely stochastic and assumed the animals had no knowledge of the location of patches suitable for occupation. In contrast, in the VORTEX runs, the representation of the dispersal route was not explicit. Instead, individuals had an equal probability of dispersing to any available patches within the pre-defined straight line dispersal distance. The principal difference between these representations of dispersal was that in the custom built model, individual dispersers might not find a patch even if there was one within the dispersal distance. Both representations of dispersal have little more to support them than a 'standard of plausibility' (Lima & Zollner, 1996). Whether or not the beaver spreads across Scotland will depend on the dispersal behaviour of the species in the Scottish landscape and to what extent it resembles either of these representations.

The predictions generated by these model runs should be considered in the light of the simplifications and uncertainties that were a part of the modelling process. The outputs of both models are dependant on the habitat data used as the spatial template for modelling. It was assumed that any sites with deciduous woodland adjacent to rivers or consisting of large blocks of marshland were suitable habitats for beaver. This is a gross simplification of the habitat requirements of beaver and there is a number of other factors that could determine how much habitat was actually available. Firstly, it is clear that other characteristics besides vegetation - particularly the flow characteristics of the river and soil type - are important determinants of habitat suitability (see reviews in Gurnell, 1997 and Macdonald, *et al.*, 1995). Rivers with highly fluctuating flow regimes are unlikely to be suitable for beavers. Beavers also prefer to have access to sites where they can create

occupation by beaver from those identified using vegetation alone. Conversely, it was assumed that beaver families needed contiguous blocks of habitat. It is not clear to what extent beavers can use highly fragmented habitats along the river. If they were capable of using this then many areas of fragmented habitat along the river systems would become suitable. The relative importance of these factors is difficult to assess in the absence of data from a Scottish, wild-living population of the species.

In both modelling approaches dispersal was set to occur only when a population reached carrying capacity. The assumption that dispersal is density-dependent in beavers has to be true ultimately, but the beaver is a social animal. Thus it is likely that the dispersal response to increased population pressure is plastic and not driven by a simple threshold effect. Pre-saturation dispersal could increase the likelihood of the colonisation of new patches but would also increase the overall impact of dispersal mortality on the total population in any one year. In addition, neither approach considered social factors in the choice of settlement patches by dispersers. It seems plausible that individuals (males particularly) are more likely to settle in patches in which other beavers are already present. In the models presented here single animals will have settled in unoccupied patches and been unable to breed. In the field this is less likely to occur and, hence, populations could remain more tightly packed and persistence and spread could be higher.

Another aspect of beaver social behaviour, namely the formation of family groups in which only one female breeds, could not be represented in the VORTEX runs although it was included in the custom built model. The VORTEX runs might be expected to be overly optimistic as they potentially allow more than one female within a family group to breed. However the VORTEX runs are also potentially overly pessimistic as the carrying capacity of small patches could be reached with all males or all females. This would stop other migrants from settling and therefore breeding within the patch would be stopped. The custom built model could be modified to represent dispersal in the same way as the VORTEX runs, to establish how this inability to represent family structure might bias the VORTEX predictions.

It must be stressed that the model runs presented here take no account of local events that could cause catastrophic mortality, for example extreme flooding or pollution incidents. The threat of such events would, dependant upon their frequency, reduce the probability of persistence of isolated populations, but should have little effect on the persistence of a large, widely distributed metapopulation.

Finally, as beaver life history data are not yet available for Scotland, all of the model predictions should be treated with some caution. This analysis predicts the likely outcome of a beaver re-introduction to Scotland based on current knowledge of beaver biology elsewhere. Should a re-introduction programme go ahead, monitoring of beaver biology in the early stages would provide data to allow these predictions to be verified and subsequently refined.

## **7. CONCLUSIONS**

1. A beaver re-introduction to Scotland would be very unlikely to succeed if natality rates remained as low as those recorded shortly after translocation into the Netherlands (Nolet & Baveco, 1996).
2. A re-introduction programme based on releasing animals in the larger habitat patches is more likely to be successful than one in which release patches are chosen irrespective of size.
3. Beavers would be likely to persist at the larger release sites if i) they achieved natality rates equivalent to those of established populations in Germany, and ii) populations experienced no catastrophic events.
4. The dispersal behaviour of beavers, following release in the fragmented Scottish landscape, will determine whether the species will remain in small populations vulnerable to chance extinctions and catastrophic events, or whether it will spread from release sites to form a large, interacting 'meta-population' relatively invulnerable to local catastrophes.

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## SCOTTISH NATURAL HERITAGE

Scottish Natural Heritage is an independent body established by Parliament in 1992, responsible to the Secretary of State for Scotland.

Our task is to secure the conservation and enhancement of Scotland's unique and precious natural heritage - the wildlife, the habitats, the landscapes and the seascapes - which has evolved through the long partnership between people and nature.

We advise on policies and promote projects that aim to improve the natural heritage and support its sustainable use.

Our aim is to help people to enjoy Scotland's natural heritage responsibly, understand it more fully and use it wisely so that it can be sustained for future generations.