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Reintroduction of the European beaver (*Castor fiber*) to Norfolk, U.K.: a preliminary modelling analysis

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Abstract

An existing spatial population model, developed to assess the reintroduction of the European beaver *Castor fiber* to Scotland, was applied to predict the likely result of reintroducing beavers to Norfolk, England. A habitat analysis was conducted using the Land Cover Map (classified satellite imagery developed by the Institute of Terrestrial Ecology) to predict the location of areas suitable for beavers. The model was used to simulate population processes within these areas and dispersal between them following a range of reintroduction scenarios. To represent uncertainty regarding the probable behaviour of beavers in Norfolk, the habitat analysis and model were applied using three sets of parameter values (high, medium and low) derived from the literature. It was predicted that Norfolk could support between 18 and 40 beaver families. Using high or medium parameter values, beaver populations were predicted to expand following reintroduction and spread to new areas. Using low parameter values populations were predicted to decrease, risk extinction and not colonize new areas. This analysis is a preliminary investigation into the likely fate of beavers in Norfolk. Checking the estimates of habitat availability in the field would enable greater confidence to be placed in these predictions.

Key words: *Castor fiber*, simulation model, GIS, population viability analysis, land cover map

INTRODUCTION

Bones of the European beaver *Castor fiber* found in East Anglia (the region including the county of Norfolk, U.K.) have been dated to around 2700 years before present (Corbet & Harris, 1991). Last records of beavers in Britain come from Wales (12th century) and Scotland (16th century) (Macdonald, Tattersall, Brown et al., 1995; Kitchener & Conroy, 1996) and their extinction has been attributed to over-hunting and habitat loss (Macdonald, Tattersall, Brown et al., 1995). Similar extinctions occurred across much of Europe and, despite recent recoveries of which many are the result of reintroductions (Nolet & Rosell, 1998), the European beaver is currently classified as vulnerable by the IUCN/SSC Rodent Specialist Group (Amori & Zima, 1993).

There has been considerable debate over the potential reintroduction of European beavers to Britain (see review in Macdonald, Tattersall, Brown et al., 1995) and the feasibility and desirability of a reintroduction to Scotland is currently being investigated by Scottish Natural Heritage (SNH, 1998). As well as returning a once important member of the native fauna, a reintroduction could increase the future viability of the species as a whole, particularly as there is the threat of replacement by alien Canadian beavers in parts of mainland Europe (Macdonald, Tattersall, Brown et al., 1995).

The county of Norfolk, England, is one area that could be suitable for beavers as it has a relatively high density of water courses and deciduous woodland, the two key habitat requirements of beavers (Nolet & Rossell, 1994). Current guidelines for reintroductions (IUCN, 1998) state that modelling should be used in the assessment of project feasibility. Such a modelling assessment has been applied to the recent reintroduction of beavers to the Netherlands (Nolet & Baveco, 1996) and to the proposed Scottish reintroduction (Macdonald, Tattersall, Rushton et al., 2000; South, Rushton & Macdonald, 2000). Here we apply the Scottish model to assess the likely fate of beavers if they were reintroduced to Norfolk.

METHODS

The model simulates the births and deaths of individual beavers within habitat patches and their dispersal...
between habitat patches (South et al., 2000). The model can be divided into two stages: (1) development of the habitat template; (2) simulation of population processes within the habitat template. In both of these stages there is uncertainty regarding the precise values that should be attributed to the parameters that make up the model (Table 1). This uncertainty arises from various sources. First, we cannot be sure that a species will behave as we expect, even if it has been intensively studied. Second, we cannot be sure how a species may behave in an area where it has not been studied. This latter source of uncertainty is a particular problem for reintroductions where species have been absent from an area for a long time.

To address these sources of uncertainty the model was run under 3 parameter scenarios: ‘high’, ‘medium’ and ‘low’, designed to represent the range of potential outcomes of reintroducing beavers to Norfolk. The ‘high’ scenario simulates a situation where the Norfolk habitat proves suitable for beavers and they do well, whilst the ‘low’ scenario simulates a situation where the habitat proves less suitable and beavers do relatively poorly. The parameter values used for each of these scenarios (see Table 1) were derived from field studies documented in the literature (see Nolet & Bavecó, 1996; South et al., 2000).

**Development of the habitat template**

The Institute of Terrestrial Ecology Land Cover map was used as the primary source of data for the creation of the habitat template. This is supplied at 25 m resolution and is derived from satellite data (Fuller, Groom et al., 1994). Each 25-m cell in the country was classified into 1 of 25 land cover classes. The land cover classes used here were deciduous woodland and inland water. As not all rivers appear at this scale, a river map provided by Bartholomew’s at a scale of 1:250000 was also used.

Beavers require deciduous woodland close to water. Fieldwork in the Netherlands has shown that territories occupied by a single beaver family (breeding pair with juveniles and sub-adults) contained a minimum of c. 2 km of wooded banks within a maximum of around 11 km of banks in total (based on 2–6 families over 4 years; Nolet & Rossell, 1994). Similar linear territory sizes of 3.1–6.5 km have also been recorded in Germany (Heidecke, 1986). The requirement for a minimum amount of linear habitat within a linear home range of limited size makes estimating areas of suitable habitat far from straightforward.

To estimate habitat availability, a map was first created containing all of the 25-m cells classified as deciduous woodland (Fig. 1) and then the cells that were within 25 m of a river or inland water were found. Each cell was assumed to represent 25 m of wooded banks, which would be true if the watercourse ran straight along one edge of the cell. The map was then divided up into 5-km squares. A 5-km square with a river running through the middle of it will contain c. 10 km of river banks, close to the maximum territory size for a beaver family. Therefore each 5 km square was classified as suitable or unsuitable based upon whether it was estimated to contain at least 2 km of wooded banks (40 × 25 m woodland cells within 25 m of water). In practice, the length of wooded and non-wooded banks will be underestimated where banks are not straight or there are tributaries and overestimated where banks run through only part of a 25-m cell or 5-km square. These inaccuracies should balance each other out at larger scales. Neighbouring 5-km squares classed as suitable by this method were then grouped together into the same habitat patch as beavers are likely to be able to move between them easily. The number of beaver families that could survive in each habitat patch was estimated by dividing the estimated length of wooded banks in the whole patch by the family habitat requirement parameter corresponding to either a high, medium or low habitat quality scenario (Table 2). Values for this parameter were derived from Nolet & Rossell (1994), see South et al. (2000) for further details.

A separate dispersal map was created by overlaying a 2-km grid and classifying all cells that contained a watercourse as suitable for dispersal because beavers disperse principally along rivers (Hartman, 1995).

### Table 1. Parameter values used in the simulations, under the high, medium and low scenarios

<table>
<thead>
<tr>
<th>Parameter</th>
<th>High</th>
<th>Medium</th>
<th>Low</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum dispersal distance (km)</td>
<td>120</td>
<td>80</td>
<td>40</td>
</tr>
<tr>
<td>Family habitat requirement (km)</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Mean litter size</td>
<td>4</td>
<td>2.5</td>
<td>1</td>
</tr>
<tr>
<td>Proportion of females breeding</td>
<td>0.7</td>
<td>0.5</td>
<td>0.31</td>
</tr>
<tr>
<td>Mortality probabilities</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>0.063</td>
<td>0.07</td>
<td>0.077</td>
</tr>
<tr>
<td>Sub-adult</td>
<td>0.063</td>
<td>0.07</td>
<td>0.077</td>
</tr>
<tr>
<td>Yearling</td>
<td>0.19</td>
<td>0.35</td>
<td>0.5</td>
</tr>
<tr>
<td>Juvenile</td>
<td>0.29</td>
<td>0.325</td>
<td>0.36</td>
</tr>
<tr>
<td>During dispersal</td>
<td>0.14</td>
<td>0.36</td>
<td>0.57</td>
</tr>
</tbody>
</table>

### Table 2. Predicted patch (see Fig. 2) carrying capacities (in number of beaver families), under the high, medium and low parameter scenarios

<table>
<thead>
<tr>
<th>Patch identification and location</th>
<th>No. of families supportable in each patch under the three parameter scenarios</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High</td>
</tr>
<tr>
<td>1 Glaven and North</td>
<td>3</td>
</tr>
<tr>
<td>Bure</td>
<td></td>
</tr>
<tr>
<td>2 Scarrow Beck</td>
<td>1</td>
</tr>
<tr>
<td>3 Wensum</td>
<td>8</td>
</tr>
<tr>
<td>4 Bure and Ant</td>
<td>22</td>
</tr>
<tr>
<td>5 Yare</td>
<td>4</td>
</tr>
<tr>
<td>6 Tiffey</td>
<td>1</td>
</tr>
<tr>
<td>7 Fritton</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>40</td>
</tr>
</tbody>
</table>
Simulation of population processes

The population model runs on a yearly time step. Within each year individuals give birth and die subject to the probabilities in Table 1. If the habitat patch they occupy reaches saturation (Table 2), they disperse. Dispersal was simulated by moving individual dispersers cell by cell through the 2-km dispersal grid until either they reached a habitat patch below saturation, in which case they were made to settle there, or they exceeded the maximum dispersal distance (Table 1), in which case they were killed off (South et al., 2000).

Four reintroduction scenarios were simulated, all with equal numbers of males and females: (a) 16 adults to patch 4; (b) 16 adults equally divided between patches 4 and 3; (c) 8 adults to patch 4; (d) 8 adults equally divided between patches 4 and 3 (for patch identities see Table 2). Patches 4 and 3 were chosen for the simulated releases as the habitat analysis predicted that they could support the largest number of beavers. For each combination of the 3 parameter scenarios and 4 release scenarios, 100 replicate runs of 30 years were conducted. The probability of population persistence for each scenario was calculated as the number of runs in which the population persists divided by the total number of runs. The population model was written in C and integrated with the GIS package GRASS (Wester-velt et al., 1990) using UNIX scripts.

RESULTS

The habitat analysis predicted that between 40 and 18 beaver families could be supported in Norfolk, dependent upon which habitat quality scenario was used (Table 2). In all three scenarios, the region encompassing the rivers Bure and Ant and much of the Norfolk Broads (Fig. 2, patch 4) was predicted to make up over half of the suitable habitat in Norfolk. Under the high habitat quality scenario, six other patches were predicted to be able to support at least one beaver family, whereas under the medium and low scenarios only three others were predicted to contain sufficient habitat.

Predictions of the population model were dependent upon the parameter scenario used (high, medium or low), and less on the release scenario (Figs 3 & 4). In all scenarios there was a slight decrease in the mean number of adults in the first 3 years following release, and, unsurprisingly, releases of 16 animals always re-
sulted in higher mean population sizes than releases of 8 individuals (Fig. 3). The high parameter scenario predicted increases in mean population size, reaching the estimated carrying capacity of the whole area by year 30 (Fig. 3a). The population increased faster when individuals were released in a single patch than when the same number of individuals was split between two patches. Population growth was slower using the medium parameter scenario. In contrast to the pattern observed when using the high parameter scenario, releasing eight animals at two patches resulted in higher population growth than for the release of 16 animals at one patch (Fig. 3b). Mean population size decreased for all release scenarios when the low parameter scenario was used. Division of releases between patches resulted in a faster population decline than when the same number of animals was released at a single patch (Fig. 3c).

Under the high parameter scenario beavers spread to, and had a high probability of persistence in, all patches predicted to be able to support more than one family (Fig. 4). Probability of persistence in the Glaven, Wensum, Bure and Yare was 1 for all reintroduction scenarios except the release of four animals to each of two patches when probabilities of persistence were between 0.97 and 0.99 for the four patches and 0.99 for the whole population (Fig. 4d). The same reintroduction scenario was also the only one to result in an overall probability of persistence of <1 under the medium parameter scenario (Fig. 4d). The release of eight animals to the Bure and Wensum resulted in a higher probability of persistence in the Wensum, Yare and Glaven than when 16 animals were released in the Bure alone (Fig. 4a, b). Use of the low parameter values resulted in overall probabilities of persistence of <1 in all reintroduction scenarios. No additional patches were colonized except in a single replicate of the reintroduction scenario in which eight animals were released in two patches (Fig. 4b).

DISCUSSION

The predictions made here are, as in all modelling exercises, dependent upon the simplifications that are a necessary part of the modelling process. We will discuss these briefly here as they are covered in more detail elsewhere, with respect to the analysis of the proposed reintroduction of beavers to Scotland (South et al., 2000).
The habitat analysis assumed that any sites with sufficient deciduous woodland close to water would be suitable for beaver. In reality there will be other factors that may make sites unsuitable, such as highly fluctuating flow regimes or a lack of soft substrates for burrowing (Gurnell, 1997), and this may restrict the amount of habitat actually available for beavers in Norfolk. In addition, the distribution of woodland in this study was estimated from classified satellite data, which has associated errors and has been estimated to be between 79% and 84% accurate (Fuller, Wyatt & Barr, 1998). In a more comprehensive study it would be necessary to assess the accuracy of the habitat analysis in the field (Macdonald, Tattersall, Rushton et al., 2000). Another potentially important factor could be the large human population of Norfolk. This may reduce the numbers of beaver that could be supported, although elsewhere in Europe beavers are found in farmland and quiet urban areas (Macdonald, Tattersall, Brown et al., 1995).

The population model predicted small decreases in the number of adults in the first few years following release, in all scenarios. This occurs as the offspring of the released individuals take 3 years from birth to reach maturity. The range of reintroduction scenarios simulated here made relatively little difference to model predictions, certainly much less than the effect of uncertainty in model parameter values. Nevertheless, patterns can be seen in the results of the different reintroduction scenarios. Under most combinations of reintroduction and parameter scenario, releasing a group of animals to a single patch resulted in higher population sizes and probability of persistence than splitting the same release size between two patches. This occurs as the smaller populations are more vulnerable to demographic stochasticity. In smaller populations there is a greater chance that all individuals may die in 1 year, or that sex ratios may become skewed, reducing breeding rates (Gilpin & Soulé, 1986). However, under the medium parameter scenario with a release size of 16 animals, population growth was higher when animals were released in two patches rather than just one (Fig. 3b). In this particular situation the negative effects of demographic stochasticity were counteracted by the positive effect of individuals being spread more widely across the landscape increasing the probability of new patches being colonized. The colonization of new patches temporarily reduces density-dependent constraints and allows more rapid population growth.

The results of the population model suggest that beaver populations would persist and expand following reintroduction, providing that beavers exhibited life-history parameters at least equivalent to those used in the medium parameter scenario (midway between the highest and lowest estimates derived from the literature). Environmental variation or the chance of locally catastrophic events, such as flooding or pollution incidents, were not accounted for as we did not have any data on which to base parameter estimates. These parameters can have a considerable impact on the predictions of population models (Beissinger & Westphal, 1998) and probably have a considerable influence on the success or failure of a reintroduction attempt, particularly in the early stages when populations are small. Where our model predicts a probability of persistence of 1, this should be considered in the context of what is included in the model. In the real, stochastic, world a reintroduction will always have a chance of failure.

There is considerable uncertainty associated with the reintroduction of a species to an area from which it has been absent for hundreds of years. As a preliminary assessment, this analysis suggests that providing beavers in Norfolk were to fare at least as well as the average of previously published studies they would probably persist. However, population sizes are likely to remain relatively small, at least in the initial years following a release, making them vulnerable to chance events. Based

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**Fig. 3.** Predicted population growth of beavers in Norfolk following initial release. Mean number of adults from 100 replicate runs (± se). Parameter value scenario: (a) high; (b) medium; (c) low. For each release size (eight and 16 animals): solid line, release of all animals in the Bure; dotted line, release split equally between the Bure and the Wensum.
on these results, we suggest that a reintroduction of beavers to Norfolk is feasible; whether or not it would be desirable requires similar careful consideration.

Acknowledgements

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REFERENCES


