APPLICATION OF A DIFFUSION MODEL TO THE SPREAD OF AN INVASIVE SPECIES: THE COYPU IN GREAT BRITAIN

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ABSTRACT

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A discrete diffusion model, based on that of Dobzhansky et al., is adapted for the spread of an invasive species through the cells of a grid. As a case-study, the model is parameterised to simulate the spread of the coypu, *Myocastor coypus* Molina, in East Anglia, Great Britain. The model parameters are K, the carrying capacity of the environment, D, diffusivity, and r, the population growth rate; these three parameters are estimated from published data that were collected in the field. In order to implement the model, a detection threshold, local diffusivity, an initial population size and an initial population focus had to be specified.

Experimental runs of the model are analysed to determine the relative importance of each of the parameters. The model, with a constant value of r, gave a good approximation to the observed coypu distribution. Contrary to expection, a model with variable values of r gave unsatisfactory results. A diffusion model such as this gives a 'front' to the spread of a species that is 'solid'; in reality some colonies exist ahead of the front and some areas behind the front remain uncolonized for a substantial period of time.

INTRODUCTION

The potential ecological impact that an animal species can have when it invades a new area means that it may be useful to have predictive models. Within the context of Great Britain one such invasive species, the coypu (*Myocastor coypus* Molina), makes a useful case study. The aim of this paper is to implement a predictive model for the spread of the coypu within Great Britain.

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Any model of an invasion must incorporate two basic components, the animal's movement and its reproduction. Movement, where individuals of the species disperse from their point of introduction, is analogous to the process of diffusion (Kendall, 1948). After developing a model which predicted a linear relationship between time and radial distance for a population expanding from a point source, Skellam (1951) demonstrated such a relationship for the spread of the muskrat (*Ondatra zibethica* L.) in Europe. He also demonstrated the analogy between his ecological model and models of random diffusion. Skellam's basic model is

$$\partial N/\partial t = rN + D \, \nabla^2 \tag{1}$$

where N is the number at a specific point in space, t is time, r is the population growth rate, ∇^2 is a density gradient in two dimensions (see below) and D is diffusivity. This represents population growth and dispersal at a single point in a continuous, two-dimensional plane. Growth is exponential and diffusion is proportional to the density gradient, which is expressed in the second term on the right of equation (1), where ∇^2 is

$$\nabla^2 = \partial^2/\partial x^2 + \partial^2/\partial y^2 \tag{2}$$

(x and y are the two axes of the plane). Thus, ∇^2 is a measure of the population density gradient in two dimensions and D is a constant of proportionality.

When applying Skellam's model it is convenient to constrain the full, continuous form of equation (1) by considering the environment as a series of discrete patches rather than as a continuous plane. Dobzhansky et al. (1979) and Long (1977) both employ such discrete diffusion models; in this study, the version used by Dobzhansky et al. (1979) in their study of the dispersal of *Drosophila* was chosen as it permits heterogeneous diffusivity values. The model has the same basic form as equation (1) except that the diffusivity term, ∇^2, is approximated. If the density of animals in square patch [i, j] is $N_{i,j}$, and the square has diffusivity $D_{i,j}$, then (assuming all patches are the same size)

$$\partial^2 N/\partial x^2 = \left(N_{i-1,j} - N_{i,j} \right) + \left(N_{i+1,j} - N_{i,j} \right)$$
$$= N_{i+1,j} + N_{i-1,j} - 2N_{i,j} \tag{3}$$

Similarly

$$\partial^2 N/\partial y^2 = N_{i,j+1} + N_{i,j-1} - 2N_{i,j} \tag{4}$$

Then

$$\nabla^2 = \partial^2 N/\partial x^2 + \partial^2 N/\partial y^2 \tag{5}$$

In practice, this approximation to the continuous form only holds if all diffusivities are the same. With a heterogeneous environment, if $D_{i,j}$ is the diffusivity associated with square $[i, \; j]$ and $N_{i,j}$ is the number of individuals present in the same square at time t, then (assuming no reproduction)

$$N_{i,j} = \tfrac{1}{4}\left(D_{i+1,j}N_{i+1,j} + D_{i-1,j}N_{i-1,j} + D_{i,j-1}N_{i,j-1} + D_{i,j+1}N_{i,j+1} \right)$$
$$- \left(1 - D_{i,j} \right)N_{i,j} \tag{6}$$

Diffusion is assumed to occur equally in each of the four cardinal directions, so the population of any square is the sum of a quarter of the animals diffusing from each of that square's neighbours, minus the animals diffusing from the square itself. Equation (6) assumes an infinite field. When it is implemented over a finite area, the calculation must be modified to take account of the edge of the grid.

A discrete diffusion model with a boundary was employed by Dobzhansky et al. (1979). They found distinct differences in the diffusion rate of *Drosophila* with different habitat types; diffusion being faster in less favourable habitats. Using field data, they assigned different values for diffusivity to each habitat type and the model gave a good fit with observed results.

COYPU IN BRITAIN

The coypu is a large hystricomorph rodent which became established in parts of Britain, particularly East Anglia, about 1930 after individuals escaped from fur farms (Southern, 1964). Where it thrived, the coypu rapidly became a serious pest because of the damage it caused to crops, wild plants and drainage systems. As a result, coypu research and control programs were initiated in 1962.

The spread of the coypu in Britain has been well documented (Norris, 1967a, b; Gosling et al., 1979; Gosling and Baker, 1981; Gosling, 1985). The extent of these data make it possible to apply diffusion models to the spread of coypu in Britain. The large majority of distribution data available for the British flora and fauna are in the form of presence/absence maps based on the 10-km squares of the National Grid. Any model using such data could potentially be applied to a wide range of invasive species and thus would not be limited just to the coypu. There are, however, several limitations to the use of such gridded data. By definition they give no indication of the status of the population at a grid location, so that a presence could be the result of anything from a sighting of a single individual to a fully established population. Absences do not necessarily imply that a species is not present, only that the species has not been recorded. Also, the 10-km grid square is a
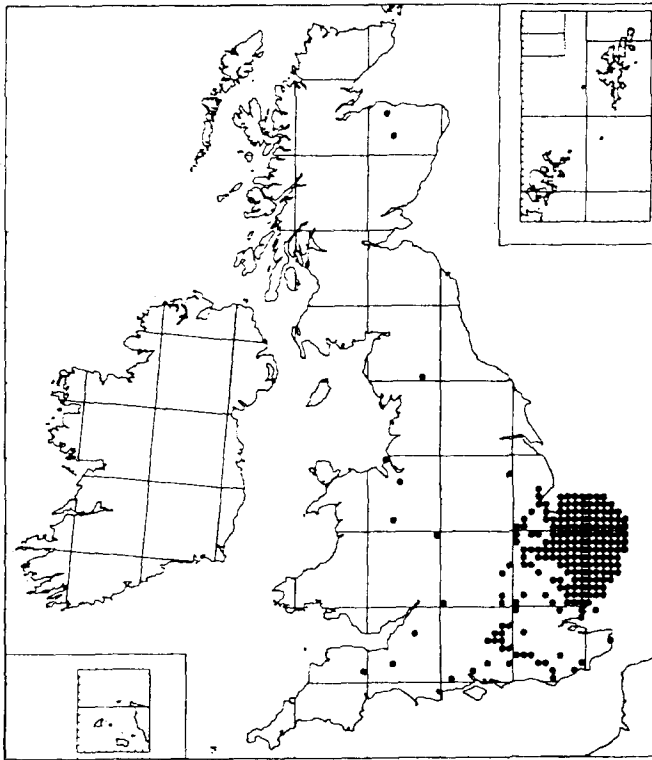
Fig. 1. Distribution of the coypu in the British Isles. The vertical and horizontal lines represent the 100-km lines of the British and Irish national grids. The presence of coypu within a 10 km national grid square is indicated by a circle. The map, which shows all records up to 1984, was prepared by the Biological Records Centre of the Institute of Terrestrial Ecology (from Usher, 1986).

relatively coarse unit in habitat terms. The distribution of coypu is shown in Fig. 1.

Environmental heterogeneity was incorporated into the model in two ways, as diffusivity and as carrying capacity, both of which are related to the habitat content of each of the 10-km grid squares. Carrying capacity is a reflection of the extent of suitable habitat within a grid square. Diffusivity should be larger in unfavourable habitats as individuals will have to move further to find suitable locations (as confirmed experimentally in *Drosophila* by Dobzhansky et al., 1979) although the muskrat in Europe may have moved faster in favourable habitats (M.H. Williamson, University of York, personal communication). For both elements of environmental heterogeneity, mean species-specific values for the parameters were estimated, and these were then adjusted by local coefficients associated with each grid square.

Population growth used the logistic model rather than the exponential model. At the colonising front of a population there will be little difference between the two models as coypus will not be present at large enough densities for the logistic population regulation to come into effect. Where the population is already established, the logistic model is the more realistic of the two. In addition, Skellam's (1951) basic diffusion model was also modified by the inclusion of threshold values. These ensured that a process could not occur in a grid square until a minimum number of animals was present. For example, a threshold of 2 would ensure that breeding could not occur within a grid square until at least two animals were present within it. Similar thresholds were introduced to control diffusion from a square, detection in a square and presence in a square.

APPLICATION OF THE MODEL

Parameterization for the species

The coypu population has never attained a natural equilibrium level in Britain. This means that estimation of many of the population parameters is fairly speculative. To an extent, however, this is compensated for both by the accuracy of the retrospective population estimates which the intensity of a trapping campaign permitted (Gosling et al., 1979) and by the volume of data resulting from the campaign.

In estimating the population growth rate, r, the drawbacks of the trapping data become apparent. The population growth rate can be regarded as the difference between birth rate and death rate. In Britain, except in hard winters, the only significant cause of coypu death is trapping (L.M. Gosling, Coypu Research Laboratory, Ministry of Agriculture, Fisheries and Food personal communication, 1986), and thus death rate is strongly correlated ($P < 0.01$) with trapping effort. As the latter has not been constant, it is difficult to assign a single, realistic value to r. Two approaches are possible; one adopts a variable value of r and the other uses a single value consistent with the animal's biology.

For the former approach, population estimates were read from the graph in Gosling (1985) and transformed to natural logarithms. This results in a graph where three distinct phases are apparent (Fig. 2); a rise over the period 1970–74, a 5-year period when the population remained reasonably constant, and then a sharp decline. Fitting three separate regression lines to these stages produced significant regressions ($P < 0.05$) for the first and third stages and an insignificant fit ($P < 0.1$) for the intermediate stage. These slopes can be taken as the population growth rates, being 0.52, -0.12, and -0.56 respectively. Calculating a mean of these, with weighting for the
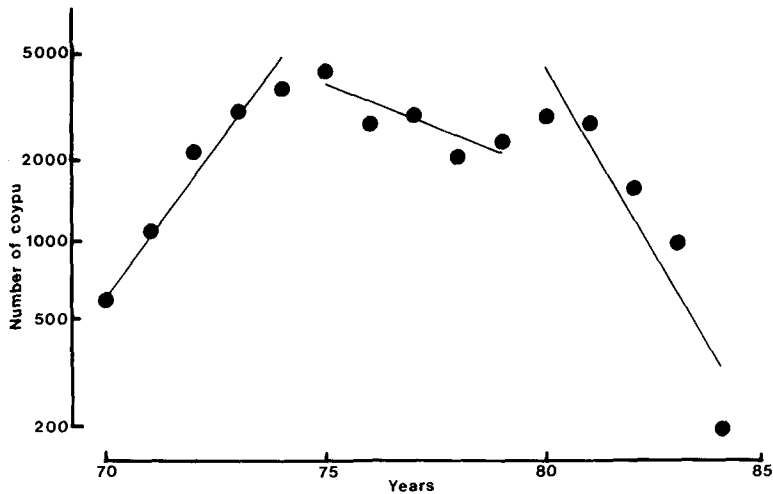
Fig. 2. Numbers of coypu in East Anglia, plotted on a logarithmic scale, from 1970 to 1984, showing fitted regression lines. The data are from Gosling (1985).

length of each stage, gives a value of -0.02 for r. Clearly this mean value does not represent the population over the entire period, so to model the expanding population a value of 0.52 would be more appropriate.

The linear relationship that Skellam (1951) derived between time and radial distance for the spread of muskrat in Europe also has direct relevance to the coypu in Britain. The slope of this relationship, the expansion rate of the population, is a function of both r and the diffusivity. It can be seen from Fig. 3 that the coypu's range was significantly reduced by the hard winter of 1962/63, after which recolonisation occurred but at a reduced rate. This latter stage gives an expansion rate of 3.8 km/year. With all other parameter values set at their default values (Table 1), the model was run a number of times varying the values of D_{max} so that the resulting expansion rates could be calculated. Since a value of 3.9 km/year was obtained using a value for D_{max} of 0.5, this was adopted as the default value.

This value of D_{max}, when multiplied by the mean value for the local diffusivities (0.248, see below), gives an overall diffusing proportion of 0.124. This represents a time interval of a quarter of a year as four iterations of the diffusion process were run per time interval. This suggests that, on average, approximately one-eight of the population of a grid square will leave that square over the course of three months. Initially, this seemed large, but as diffusion is also occurring in the reverse direction, the net effect is reduced. The young adult males constitute the most mobile proportion of the population (S.J. Baker, personal communication, 1986), and as the truncated age distribution which results from trapping means that they will represent a
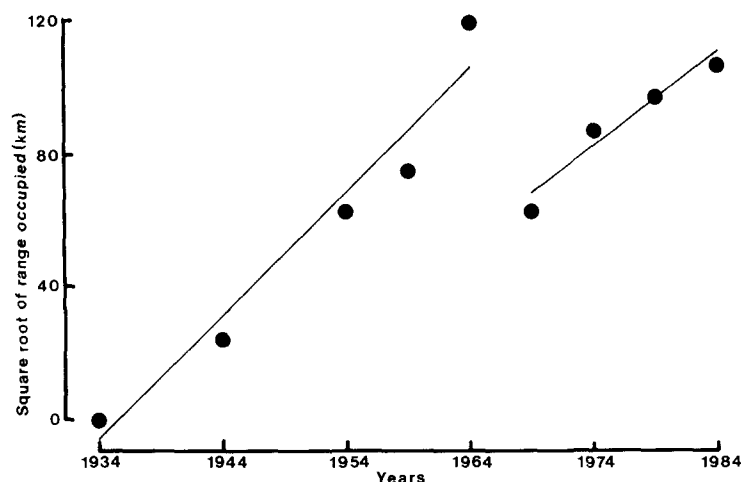
Fig. 3. Range expansion of the coypu from 1934 to 1984, showing fitted regression lines for the two periods before and after the extremely cold 1962/63 winter.

large proportion of the population, the one-eighth value does not seem inconsistent with coypu ecology.

The maximum number present in any one square is the carrying capacity of that square. K_{max}, the overall, species-specific value required for the model, is that population which a 10-km square of ideal coypu habitat could support. This figure cannot be calculated directly as accurate censuses are not available for the early 1960's when the coypu was most numerous in Britain. Instead, an estimate was made by making assumptions about the population of late 1975 when there were about 19000 males and females

TABLE 1

Default values of the parameters used in the coypu simulation model

Parameter	Value
K, carrying capacity	3000 animals per 10-km grid square
D, see equation (1)	0.5
r, see equation (1)	0.52 (fixed)
	0.52, −0.12, 0.56 (time dependent)
Detection threshold	4 animals
Local diffusivities	0.248 (mean)
Initial population	50 animals per grid square in 6 squares
Initial population foci	National Grid squares TG3010, TG4010, TG3000, TG4000, TM3090, TM4090 (indicated in Fig. 4)
Run length	20 years

(Gosling et al., 1979). At this size, L.M. Gosling (personal communication, 1986) observed that density-dependent effects were beginning to become apparent in the population, suggesting that the population was at about 65% of the carrying capacity. Assuming an even distribution over the territory occupied, an estimate of K was approximately 21 animals per km^2 and thus $K_{max} \approx 2100$ animals per grid square. The calculation was repeated excluding all peripheral grid squares where densities would be expected to be lower. This resulted in an estimate for K_{max} of 2730. 3000 was adopted as the default value for K_{max}, since it is better to increase the estimate and thus slightly reduce any density dependent effects.

Detectability of coypus is a function of both the number present in a grid square and the effort of looking for them. This is demonstrated by the apparent increase in the coypu's range which coincided with the start of trapping. Thus, the detection threshold of an area is a function of the trapping intensity. With the current reduced numbers of the coypu population, efficient siting of trapping effort has become more important, so the animal's range has been divided into core, buffer and peripheral zones, with trapping effort being apportioned accordingly. Thus a single individual is far more likely to be detected in the two core zones of the Norfolk Broads and the Suffolk grazing marshes than in the large peripheral areas to the west of East Anglia. Allowing for this limitation, and for access problems encountered in some areas (e.g. on Ministry of Defence land), a threshold of four individuals was selected.

A value of 1 is possible for the breeding threshold as some movement of pregnant females does occur (Norris, 1967a). However, as males tend to be more mobile than females (S.J. Baker and L.M. Gosling, personal communication, 1986) it seems likely that the first arrivals in an uncolonised area would be male. Allowing for this and for viability and maturity, it seems reasonable to assume that breeding cannot occur in a square until 5 or more individuals are present in it.

A diffusion threshold of 0, similar to Skellam's model, was used because L.M. Gosling (personal communication) suggested that movement occurs at all densities. The presence threshold of 1 was used to prevent fractional numbers of animals appearing in the model's output.

Parameterization to area

The environment of East Anglia was represented by estimating local diffusivities and carrying capacities for each of the 10 km grid squares of the area. The relationship between carrying capacity and habitat extent is one of direct proportionality, but the relationship between extent and diffusivity is less straightforward. Diffusivity is higher in less favourable environments

(Skellam, 1951; Dobzhansky et al., 1979), so if extent is taken as a measure of habitat favourability, then diffusivity is inversely proportional to extent. However, diffusivity will be higher if the available habitat is distributed between a number of discrete patches rather than concentrated in a single area, so local diffusivity was regarded as proportional to the number of patches divided by the extent of habitat.

Suitable coypu habitats are freshwater margins and both coastal and freshwater marshes. The extent of these habitats was estimated from the Ordnance Survey 1:50000 maps of East Anglia. For each 10-km grid square, extent was taken as the number of 1-km grid squares which contained two or more small water bodies or one or more large water body. The number of patches of wetland habitat in each 10-km square was recorded; areas were counted as discrete if they were separated by at least 2 km of non-wetland habitat.

Simulation starting conditions

The map detail incorporated into the model for the simulation runs was a schematic representation of East Anglia. The area used was 150 km (15 grid squares) wide, 200 km long and stretches from Skegness in the north to Greater London in the south, and from Peterborough in the west to the East Coast (Fig. 4). The model was initialized with a population of 300 animals distributed evenly over six grid squares of the Norfolk Broads area. This was intended to represent the coypu population after the 1962/63 winter; this period was chosen both because the population re-spread after the hard winter and because most of the parameter values were estimated from the data collected in the 1970's and 1980's, during the post 1962/63 spread in range.

RESULTS

To simulate the spread of the coypu, two series of runs of the model were performed; one with r fixed and one with r varied to match actual changes in the post 1963 mortality rates. Runs were also made varying the parameter values in relation to each other in order to investigate the sensitivity of the model to changes in each parameter.

The parameter values used were the default values (Table 1). The results of two simulations, with fixed and variable r values, are illustrated in Fig. 4, together with the coypu's actual distribution. Comparing the actual distribution (Fig. 4b) with the simulated distribution with constant r (Fig. 4c), it can be seen that the two are quite similar; both feature a population 'front' which extends from just south of The Wash to the east coast near Ipswich.
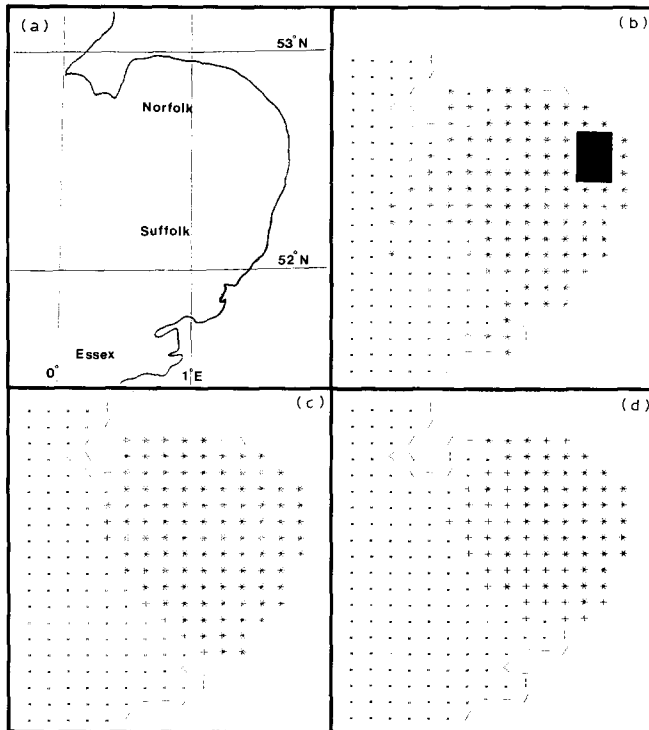
Fig. 4. Distribution in 1984. (a) A sketch map showing the geographical location of East Anglia; note that the computer-drawn maps (b–d) are distorted. (b) The actual distribution, adapted from Usher (1986). (c) The simulated distribution with constant r (0.52), and (d) the simulated distribution with r variable. On these maps dots indicate no coypu, lines the coastline. In (b), * indicates that at least one coypu was recorded. The initial population foci (Table 1) are shown solidly marked. In (c) and (d), * indicates detectable populations (i.e. more than 4 animals), and + indicates animals present but not detectable (i.e. 1–3 animals).

The actual distribution, however, is less homogeneous, with isolated colonies existing beyond the front, particularly along the coast: also, some squares inside the front apparently remained uncolonised (or else coypus were unrecorded in these squares). With variable r (Fig. 4d), the results are not as satisfactory; the population front has receded, leaving some isolated detectable colonies. Investigation revealed that colonies were predicted to remain in grid squares which had large local carrying capacities and low diffusivities, as the extent of suitable habitat ensured that coypus remained in appreciable numbers.

    In both the actual and simulated distribution maps, gaps in the distribution are apparent in grid squares on the north Norfolk coast. In the simulations these gaps result from there being no potential coypu habitat on the map of the area, and presumably this also accounts for the actual

absence of coypus. Both squares were allotted a carrying capacity of zero, and although animals entered these squares by diffusion during the early stages of the simulation, the population crashed when it reached the breeding threshold and it did not become re-established.

To investigate the sensitivity of the model to the parameters, a number of experimental runs were made. The parameter values were varied systematically and the overall range expansion rates were analysed by analysis of variance. The effects of each parameter were thus investigated relative to the other relevant parameters. The main effects of the principle dispersal and reproductive parameters, r, K_{max} and D_{max}, were all significant ($P < 0.05$), as were the interactions between r and D_{max} and between r and K_{max}. As the model is deterministic, there was no three-way interaction and thus the interaction between D_{max} and K_{max} was the only non-significant term in the analysis of variance. The largest proportion of the total variation (81.5%) was associated with variation in r, whilst a further 17.5% of the variation was associated with D_{max}. Despite its significance, K_{max} was relatively unimportant. This was confirmed by setting K_{max} to a large value, to remove any density dependence in breeding, which resulted in minimal change in the overall expansion rate. The relative unimportance of K_{max} results from the densities present at the colonising front being too low for density dependence to affect the population. The carrying capacity also proved to be of little importance when the effects of heterogeneity of local D and K values were tested by comparison with a homogeneous environment with the same overall mean values (the diffusivity effect was significant, $P < 0.05$, but the K effect was not significant).

In addition to r and K, breeding in the model is also influenced by the minimum density required for breeding to occur in a grid square. The importance of this breeding threshold was investigated relative to r. Although the expansion rate significantly decreased with increasing breeding threshold, it was of relatively little importance when compared to r which in this test accounted for 93.8% of the total sum of squares. In a similar investigation, the detection threshold was only just significant ($P = 0.05$) and r accounted for the majority of the variation (98.4%).

The diffusion threshold was investigated relative to both D_{max} and K_{max}. The expansion rate increased with increasing K_{max} and D_{max}, but decreased with an increasing diffusion threshold. The analysis of variance indicated that both the diffusion threshold and D_{max} were significant ($P < 0.05$), as was their interaction, but that, as before, carrying capacity had little effect on the expansion rate.

The influence of the initial values of the model was investigated by a three-way analysis of variance. The results indicated that the position of a site of introduction was important, largely because proximity to the coast-

line restricted range expansion. The initial density, as expected, was also important as a large initial density enabled breeding colonies to be established in neighbouring squares more rapidly.

Overall, these statistical analyses suggest that the diffusivity, the population growth rate and the diffusion threshold need to be estimated with the most accuracy. The starting conditions also have some influence on the final behaviour of the model, but this is chiefly attributable to the starting site, the position of which is often known for an introduced species.

DISCUSSION

Modelling of invasive species reflects aspects of both an epidemic and an endemic phase. Mollison (1986) included in the former a species' ability to invade, its competitive ability to succeed initially, and, if successful, its rate and manner of spread, whilst the latter included the species' competitiveness, ability to persist and, if successful, the level and pattern of persistence. Whilst the model explored in this paper is primarily concerned with the epidemic aspects of the coypu's invasion, the use of negative values of r (due to trapping pressure) explores aspects of the species' persistence.

The fact that the simulation, with r varied to resemble the three phases in Fig. 2, did not produce a satisfactory distribution map can probably be attributed to the population control measures. A single value of r does not take into account the differential death rates, due to varying intensities of trapping, in different parts of the range. Most trapping occurred in areas where the coypu was already well established, in the central area of its range, and hence the rate of range expansion was only minimally affected. Indeed, as the peripheral trapping actually extended the *perceived* range of the animal, it is perhaps not surprising that the simulation with constant r produced the more realistic distribution.

One of the differences between the simulated and actual distributions was the form of the population 'front'. The existence of colonies beyond the population front suggests, as might be expected, that random diffusion (a physical process) is not an entirely appropriate model for the manner in which coypus disperse (a biological process, with an element of stochasticity). Being a wetland animal, coypus will tend to stay within close proximity to water so that movement will tend to be restricted to corridors along rivers and through marshes. This is particularly apparent in Essex where the animals seem to have colonised the estuarine marshes through linear movement along the coast. The patchiness behind the population front may either be a detectability effect or a genuine effect attributable to colonies going extinct locally. It does not appear to be an environmental effect, since, apart from the Norfolk coast squares, there appear to be no squares inside the

occupied area which remained consistently uncolonised throughout the full time sequence of the distribution maps.

The nearest that the simulations came to generating such patchiness either side of the population front was in the simulation run when r became negative. The resultant distribution showed a few isolated colonies left as the population front receded. This does, however, pose questions concerning detectability; the population was approaching the detection threshold from above rather than below, suggesting that the species would seem to disappear suddenly when it reached this critical density. The detection threshold may be a less satisfactory concept when the population is declining, as there will be a good a priori reason for suspecting the presence of the species, which may not be the case when the species first appears in a new area.

Overall, the model gives a reasonable representation of the spread of the coypu. The model's chief limitation appears to be the representation of trapping pressure through a single overall value of population growth rate, r. Other parameter values seem satisfactory. The statistical analyses indicated that the next most important parameters were diffusivity and the diffusion threshold, and that these seem to have been estimated reasonably. As both of these were estimated virtually independently of the volume of coypu research data available, this suggests that the model could be of use for other invasive species where there is limited background research. This leaves the problem of estimating r. Accurate population estimation is only possible with destructive sampling, yet such sampling limits the utility of the estimate of the population growth rate. As it seems likely that these models would only be used for pest species, where sampling would be destructive, the problems of estimation may not be unique to the coypu.

Although the model has proved reasonably applicable to the coypu, the problem of generalization still remains. A feature of this discrete model is the division of a geographical area into many 10 km grid squares. Working with such a large unit of area has created problems of sensitivity; for example, random diffusion does not provide a good representation of dispersal which may be influenced by local barriers and corridors. This problem is particularly apparent with the coypu as its wetland habitat is often linear; it may be less of a problem with a species such as *Rhododendron ponticum*, a plant of woodland and, sometimes, open or disturbed areas with acidic soils (Usher, 1986).

In the parameterization, the chief problem was to estimate the diffusivity. Although Skellam's (1951) continuous diffusion model allowed this parameter to be estimated from the slope of the range expansion on a graph, such estimates are not entirely applicable for the discrete model where the expansion tends to be in a series of jumps from grid square to grid square. Unless the problem of the relationship between discrete and continuous

forms of the diffusivity can be resolved, it will remain necessary to estimate diffusivity empirically, although the nature of the presence/absence data does permit a range expansion graph to be plotted. There is a further problem in that the diffusivity may vary in time. Usher (1986) indicated that the rate of spread of an invasive species may be slow to begin with, and then increase greatly after a lengthy establishment phase. This feature of increasing diffusivity with time is also discussed by Williamson and Brown (1986).

The distribution data played quite a minor role in the overall parameterization (estimation of maximum carrying capacity and diffusivity). The research on the coypu meant that it was relatively easy to estimate values for most of the parameters; such research is not available for many other invasive species. The difficulty in assigning values to the various thresholds in the coypu simulation suggests that research effort directed at a population which was in the initial stages of establishing itself would be very useful. Such research would also have practical application since appropriate control measures would be most effective in the early stages of population establishment (Usher, in press).

The limited geographical range of the coypu in Britain also eased the parameterization of the model, as this has facilitated research and made the estimation of the local diffusivities and carrying capacities simpler. Models of other invasive species, such as grey squirrel (*Sciurus carolinensis*) or mink (*Mustela vison*), could be problematical as the larger geographical range would exaggerage inaccuracies in the model's predictions. This problem could be resolved by modelling smaller, more manageable areas, each of which is investigated separately, or by concentrating on the colonizing front of the population.

For a novel invasive species, such as the recent establishment and spread of *Crassula helmsii* in Britain (Dawson and Warman, 1987), the model would have to use parameters derived from the species' native geographical range. As these could differ from the new range, the extrapolation would be a speculative process. However, the apparent success of the model in this study, despite the speculation involved in much of the parameterization, suggests that the modelling of such a situation may be feasible.

An assessment of the utility of the model can be gained by considering how well it has fulfilled the aim of making the prediction. In practice, such a model would be used to estimate both where the invasive species would reach and when it would reach each area. Of the two simulations in Fig. 4, the one with varying values of r could only be employed retrospectively, and thus for practical prediction the model with constant r would have been used. The latter predicted the coypus' range reasonably well, and so the model could be considered to be successful. Such a model might also be used to predict the effect of proposed control measures; if these involved trap-

ping, shooting, etc., then the death rate of the population would increase, thus decreasing r. If control modified the habitat, then the value of K would be reduced.

Mollison (1986) is optimistic about the use of models, indicating that models for the sub-processes of the invasion process have been successful. The model presented here was also successful in predicting the geographical and temporal spread of the coypu. However, the simulation with variable r suggests that the model may not adequately represent a situation where management is reducing either r or K. Models, although acceptable for aspects of biological invasions, may need continued development and refinement if they are to predict the effects of management. This kind of management prediction is stressed by Holdgate (1986), and is essential if answers are to be found to the question asked by Williamson and Brown (1986): "How should management systems be developed to best advantage...?".

ACKNOWLEDGMENTS

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