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Trapping for mink control and water vole survival: Identifying key criteria using a spatially explicit individual based model

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ABSTRACT

Introduced alien species are the second most important threat to global biodiversity after habitat loss. The American mink *Mustela vison* has been introduced to several countries and is threatening a number of native species worldwide. We developed a spatially explicit and individual based model as a planning tool to identify key criteria for the implementation of trapping campaigns as a way to control open American mink populations. We first predicted the minimum effort required to reduce populations of mink below a certain threshold and the best time of year in which to trap mink to minimise their numbers. We then employed this methodology to predict the best trapping strategy to ensure the long-term survival of the water vole *Arvicola terrestris*, one of the species most endangered by the spread of the mink in the UK. We also applied the mink and water vole population models to rationalise a set of observed data in an area of 50 × 30 km in the Upper Thames (UK). The model predicted that it is necessary to remove mink for at least 3 months every year and that a mixed strategy of trapping during the mating, late dispersal and winter seasons is best for keeping mink at low densities. Concentrating trapping during the late dispersal and winter seasons is instead best for ensuring the long-term survival of water voles. Targeting immigrating juvenile mink as well as reproductive adults is important. The model also showed that trapping efficiency might be an important factor to consider when choosing periods in which to trap.

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1. Introduction

Introduced vertebrate predators are an increasingly common, and often unwelcome, addition to native fauna, and they can have significant negative effects on native species (Mack et al., 2000). Whilst the problem is widespread, in Europe only a few control or eradication programs have been implemented probably due to the limited awareness of the public and the decision makers, the inadequacy of the legal frame-

work, and the scarcity of resources (Genovesi, 2005). Control and eradication campaigns may incur large costs in terms of animal welfare, human effort and funding (e.g. Gosling and Baker, 1989; Moore et al., 2003) and experience has shown that the success of such efforts varies widely, ranging from satisfactory to disappointing (Mack et al., 2000). Therefore, before undertaking such a campaign, a preliminary assessment of the likelihood of success and careful planning are vitally important. Indeed, a preliminary modelling exercise

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contributed crucially to the success of a coypu *Myocastor coypus* eradication campaign (Gosling and Baker, 1987), but there is, in general, a shortage of projects that employ this kind of approach for invasive species management. In this paper, we develop a modelling approach as a planning tool to evaluate the feasibility and to identify key issues determining the success of trapping as a way to control open populations of American mink *Mustela vison*.

The American mink is native of North America and is now established as an invasive species in South America, Europe, Russia and Asia (Dunstone, 1993). Several studies have demonstrated that mink can have serious impacts on native species, in particular ground-nesting birds (Craik, 1997; Nordström et al., 2003), rodents (Woodroffe et al., 1990; Banks et al., 2005), and mustelids of similar size (Maran et al., 1998; Sidorovich and Macdonald, 2001). In Europe, trapping campaigns have been or are being carried out to remove mink from certain areas, mostly islands (e.g. Macdonald et al., 2002b; Moore et al., 2003). Parts of the benefits of carrying out eradications on islands derive from the fact that immigration of mink from the mainland and hence re-establishment of populations is prevented or restricted (Nordström and Korpimäki, 2004). On the mainland, control or eradication campaigns require greater effort and a long-term commitment because immigration of mink from nearby areas can occur continuously (Sidorovich and Polozov, 2002). However, in spite of these problems there are cases when local control of mink on the mainland has been attempted to protect species and populations that are particularly endangered, such as in the case of the water vole *Arvicola terrestris* in Britain (Anon., 1995). Our work is aimed at developing a trapping strategy for locally controlling mink on the mainland in relatively small areas of less than 1000 km², where immigration is often an important factor in their population dynamics.

There are two main ways of reducing mink numbers, live-trapping and killing any American mink trapped or using lethal traps designed to kill instantly (Macdonald and Harrington, 2003). In the UK and most of Europe, mustelids and other animals of similar size are sympatric with mink hence live-trapping is more appropriate because it allows the selective removal of mink. With live-trapping, traps can be set on the ground, usually along water bodies, or on rafts floating on the water (Macdonald and Harrington, 2003; Reynolds et al., 2004). The use of floating rafts is relatively new, hence there are few data on the seasonal patterns of capture with this method. However, there are numerous data on the seasonal patterns of capture when using traps set on the ground. Our model is therefore based on the latter method of trapping.

To provide a framework for assessing the efficacy of mink trapping as a way to control mink, we developed a spatially explicit, stochastic, and individual-based model. The success of control programs is likely to be profoundly influenced by the life-history traits and space-use patterns of the target species (Conner et al., 1998) and spatially explicit and individual-based models allow ecologists to explore management scenarios in a spatial context by varying life history and management parameters. The analysis of the outputs of these models can help identify the most promising management approaches and thus design the most effective experiments so

that time and funding are used efficiently. We first worked with a system that incorporated a two-level interaction between trappers and mink to explore what is the minimum effort required to reduce populations of mink below a certain threshold, and to establish what is the best time of year in which to trap mink to minimise their numbers. In addition we investigated two further issues: (1) How does immigration from nearby areas affect the choice of the trapping periods? and (2) how does systematic trapping compare to occasional trapping? The optimal time of year for trapping can, however, depend on the life-history traits of the prey species that one wishes to protect, as well as those of the predator. We therefore introduced a third variable in the system in the form of a prey of mink, to investigate whether the best time of year in which to trap mink would change depending on the interaction between the life-history traits of mink and those of its prey. We choose water voles as a model prey. Agricultural changes in Britain in the last century have destroyed water vole habitat, and the arrival of the mink as a predator has further aggravated the situation to the point that water voles are now in danger of extinction having declined by 88% since the beginning of the XXth century (Woodroffe et al., 1990; Jefferies, 2003).

2. Methods

2.1. Model structure

The model consisted of two components: (1) a GIS that stored habitat and animal population information; and (2) an individual-based population dynamics module that simulated individual life histories and dispersal within the GIS-held landscape. The GIS stored and retrieved habitat information and we used Geographic Resources Analysis Support System (GRASS) for map output (Westervelt et al., 1990). The population dynamics module was written in the programming language C and integrated with the GIS component through a UNIX-shell environment.

2.2. GIS: properties of the spatial component of the model

As a study area for our simulations we chose part of the Upper Thames catchment (UK) and its immediate surroundings (Ordnance Survey: N 230000 S 180000 E 456000 W 387000 – e.g. Fig. 8a for an outline of the study area) because a control operation was planned for this area and the model informed the planning of the control strategy. The total length of the rivers in the whole area was 1052 km. Of these, 127 km were selected for trapping in the model. A buffer of at least 15 km where the mink population was left undisturbed was left around the trapped area. The undisturbed population provided immigrants to the trapped area ensuring that the controlled population was open rather than closed.

2.2.1. Mink model

The land surface was partitioned into two categories: (1) areas of habitat that could be used by the mink for foraging, breeding and dispersing, namely rivers, streams and brooks and their immediate surroundings; (2) areas through which animals could move when dispersing but in which they could

not settle. We derived maps of river networks from the 1:250,000 Ordnance Survey map and used a spatial resolution of 1×1 km. This spatial resolution was chosen so that it was smaller than a mink home range, which is usually at least 2 km long (Dunstone and Birks, 1985), but large enough to be amenable to computation. Considering that mink have a territorial system characterised by intrasexual exclusivity and intersexual overlap (Powell, 1979), the spatial distribution of females was modelled independently from males, although males and females interacted through the process of mating. Home range length was considered to be fixed for females (3 km) and males (4 km) (Chanin, 1976; Yamaguchi, 2000) apart from the mating season when the home range of males was increased (Table 1 – ‘Mate search distance’) to simulate their roaming behaviour aimed at maximising their mating opportunities (Dunstone, 1993, p. 131; Yamaguchi et al., 2004). At this time of year males are also said to be ‘transient’.

2.2.2. Water vole model

The spatial component of the water vole model was also set at a resolution of 1×1 km. Because water voles have much smaller home ranges (90–300 m along the bank) each square of 1×1 km contained several voles. We assumed voles to occupy and disperse only along water bodies, as occurs in the UK. In the model, we assumed all habitats along rivers, streams, and brooks to be suitable. Predation of mink on water voles could occur if a water vole population coincided spatially with a 1×1 km square occupied by a mink.

2.3. IBM: dynamics of the model

2.3.1. Mink model

Change in population size was modelled in terms of gains, due to birth and immigration, and losses, due to death and emigration. The model was stage-structured so that discrete stages were recognised in the population (Caswell, 2001) and

simulated on a time step of 1 month. The life history processes of mortality, mating, breeding, and dispersal and the control were modelled at the level of the individual within different age classes (Fig. 1). Three age classes of mink were considered in the model: kits, juveniles, and adults (Dunstone, 1993). Kits were 1–3 months of age, during which time they were still associated with their mother. Juveniles were 4–6 months of age, during which time they were dispersing and acquiring territories. Adults were >7 months and they held territories. The ranges, mean values, and bibliographic sources of the parameters used in the model are listed in Table 1.

Mortality – Mortality was modelled on a monthly basis and could either be ‘natural’ or from trapping. For mortality originating by natural causes, we distinguished amongst different stages of the mink life cycle: (1) adults; (2) kits and juveniles; and (3) density-dependent mortality for dispersing juveniles. Dispersing juveniles incurred additional mortality if they could not find a territory where to settle, thereby adding a ceiling density-dependent component to mortality. Natural mortality of adults, kits, and juveniles was derived from estimates obtained from two feral American mink populations in Europe (Bonesi et al., 2006). These estimates were then transformed into monthly mortality using the formula provided by Krebs whereby survival on a standardised time basis (A_s) is calculated as (Krebs, 1999, p. 500):

$$A_s = O_s^{t_s/t_o}$$

where O_s is the observed survival rate, t_s is the standardised time interval, and t_o is the observed time interval. Mortality is then calculated as one minus survival.

Mortality due to control was defined as a probability of being trapped (trappability) that varied according to the age and sex of mink (see below). The probability of death for each individual was determined by sampling deviates from a uniform distribution in the range 0–1, with mortality occurring

Table 1 – Ranges and average values of life-history and control parameters used as model inputs and in the sensitivity analyses for mink based on studies in Europe and North America

Parameter	Range	Average scenario	Reference
<i>Life-history</i>			
Dispersal distance kits in August (km)	5–10	8	Bonesi pers.obs.
Dispersal distance kits in September (km)	5–15	14	Bonesi pers.obs.
Dispersal distance juveniles in October (km)	10–50	30	Mitchell (1961) and Gerell (1971)
Mate search distance (km)	5–20	14	Dunstone (1993)
Monthly adult mortality (proportion)	0.02–0.05	0.03	Bonesi et al. (2006)
Monthly kits and juveniles mortality (proportion)	0.12–0.26	0.19	Gerell (1971) and Bonesi et al. (2006)
Litter size	3–7	5	Gerell (1971)
<i>Control</i>			
Trappability	0.0–1.0	0.50	Gerell (1971), Ireland (1990), Smal (1991) and Yamaguchi (2000)
Trapping period ^a	1–5		
Trapping years ^b	1–5		

The dispersal distance is the maximum dispersal distance, individuals can settle in any area within that distance. Trappability is expressed here as the probability of trapping a mink in 1 month within its home range.

a Five separate control periods were considered: (1) January–March; (2) April–June; (3) August–October; (4) November and December; (5) January, October and November.

b There were five different control strategies with regarding to how many years trapping was carried on for: (1) trap for 3 years and then stop; (2) 1 year on and 5 years off; (3) 5 years on and 5 years off; (4) 3 years on and 3 years off; (5) trap all 20 years.

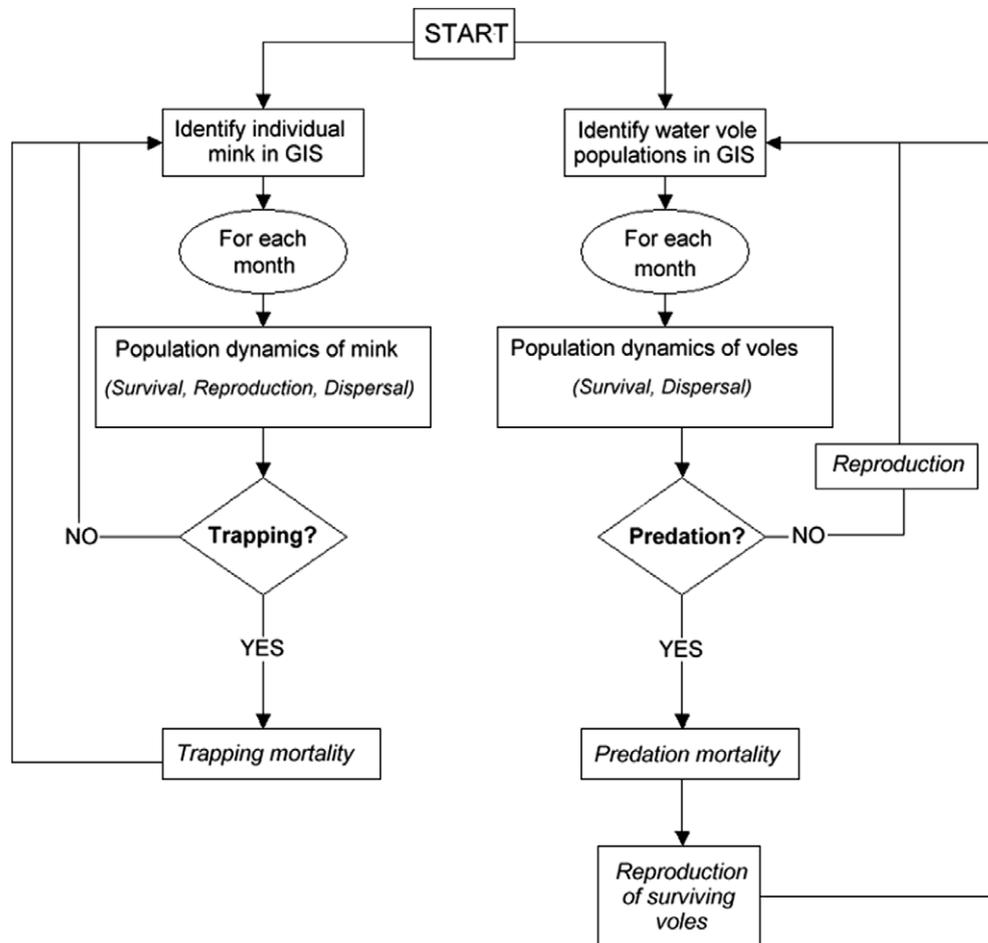


Fig. 1 – Flow chart of model structure.

if the deviate was greater than the value set for that specific simulation. This way of determining mortality introduced stochasticity in the model.

Reproduction – Mating was assumed to occur once a year in February and March and only for females ≥ 1 year (Birks, 1981; Yamaguchi, 2000). Kits were assumed to be born in May and to be associated with their mother until the end of July. If the female was trapped during this time, the kits were assumed to die as well. Females could mate only if there was a male within a certain distance of their home range.

Dispersal – Continuous portions of river-corridor free from other mink and hence suitable for establishing a territory were identified using a clustering algorithm (Hoshen and Kopelman, 1976). This algorithm classifies each suitable cell as belonging to a given cluster according to the classification of the neighbouring cells, if the latter are suitable themselves. Dispersing mink were assigned to clusters randomly provided that these were long enough to host a mink territory and were within the dispersal distance from the mother's home range (Table 1). Dispersal was modelled in juveniles as a process that saw individuals moving increasingly further away from their mother's home range. Juveniles were modelled as performing exploratory movements in August and September while acquisition of home ranges was considered to occur in October. During dispersal, mink could be trapped in an area

between the mother's home range and the location to which they dispersed.

We assigned juveniles to territories when these were found within a certain distance, L , from their starting point. Because mink travel along rivers rather than along straight lines, we assumed the relationship $R = \alpha L$ to hold between the linear distance L between two points and the distance travelled along rivers between them, R (Banavar et al., 2001). The parameter alpha is an "index of river sinuosity". If mink would travel in straight lines, then $\alpha = 1$, and $L = R$, but when mink follow rivers that bend and turn then α is greater than one. We calculated α for our particular case by simulating 20 random dispersals along the rivers in the control area and measuring L and R . We obtained a value of $\alpha \approx 2$, indicating that the average distance between two points on a river was twice as long when following the course of the river than the straight line connecting them.

2.3.2. Water vole model

In the water vole model mortality, reproduction, and dispersal were also modelled at the level of the individual. We considered two age classes: adults and young. Young were 1–3 months of age and were characterised by still being in their natal population and associated with their mother, whereas adults were ≥ 4 months of age and were characterised by

having dispersed and found a territory. The ranges and mean values of the parameters used in the model are listed in Table 2.

Mortality – Mortality occurred on a monthly basis and could be due either to ‘natural’ causes or to mink predation. We calculated monthly mortality rates using the formula by Krebs described above (Krebs, 1999, p. 500). For mortality due to natural causes, we distinguished amongst different stages of the water vole life cycle: (1) adult, (2) young, and (3) dispersal mortality. The latter occurred if an individual could not find a population where to settle within its maximum dispersal distance.

Mortality due to mink was applied as a predation rate acting on adults. Young voles were assumed to die of predation if their mother died. For use in the average scenarios, we estimated that a predation rate of 0.5 achieved a reduction of water vole populations by 90% within the span of 3 years. This rate of decline has been observed in empirical studies (Strachan et al., 1998; Barreto and Macdonald, 2000).

We varied the predation rate according to time of the year and sex of mink because studies on predation of mink on water voles showed that: (i) mink kill water voles relatively more in May–June (about 30%), followed by January–April and July–August (about 20%) and least in September–December (about 10%) (Strachan and Jefferies, 1996; Strachan et al., 1998); (ii) the main agents of water vole predation are female mink because they, unlike the males, can squeeze into the voles’ burrows (Strachan et al., 1998). Given the latter consideration, to differentiate male from female predation rate we reduced predation rate of male mink on water vole by 10%.

As in the case of mink, vole mortality was determined probabilistically.

Reproduction – We considered mating to be possible if there were at least two water voles in a 1×1 km square. Water voles could breed up to five times a year between April and September starting from the year after they were born (Corbet and Harris, 1991).

Dispersal – Because of high mortality, population turnover in water voles is high giving juveniles the opportunity to settle near or at their natal location, although they are known to be able to disperse longer distances up to 8 km (Stoddart, 1970; Aars et al., 2001; Telfer et al., 2003). In the model, we assumed an average dispersal distance for water

voles of 2 km (Euclidean distance) (cf. Telfer et al., 2003). We assumed voles to be dispersing in their third month of age. We used the same clustering algorithm as we did for mink to identify groups of river cells where water voles could disperse, but we did not allow them to disperse across land (Moorhouse, 2003).

2.3.3. Mink control sub-model

Trapping mortality was a risk for each individual mink if a trapper was present in one or more squares of 1×1 km that made up the mink’s home range. The probability of encountering and entering the traps set within 1 km of a mink’s home range was represented in the model by the ‘trappability parameter’ which is defined here as the probability that an individual mink would be killed within 1 km of its home range within 1 month. This parameter ranged between zero and one, where a value of zero meant that the mink would not be killed and a value of one meant that the mink would certainly be killed if a trapper was present.

Trappability is a function of both the trapper’s actions and the behaviour of mink. The list of possible trapper actions include variables such as the location of traps with respect to the river bank, how long traps are open, how many traps are set, and whether or not bait is used. Mink behaviour also affects the trappability parameter. With respect to behavioural factors, the following patterns have been observed:

- (1) During the mating season, adult males have a higher level of testosterone and therefore appear to be bolder and more prone to enter traps (Yamaguchi, 2000). At this time of year, males also are more active, i.e. spend a greater proportion of time out of the den, thereby increasing their chance to encounter traps (Dunstone, 1993).
- (2) During lactation and weaning, adult females may become more cautious (Smal, 1991), reduce their levels of activity and restrict their movements around the breeding den. During this season (April–June) females have a low probability of being trapped (Chanin, 1976; Birks, 1981).
- (3) Juveniles while dispersing have an inadequate knowledge of local terrain, they are possibly physically stressed because do not yet have a territory, and

Table 2 – Ranges and average values of life-history and predation parameters used as model inputs and in the sensitivity analyses for water voles

Parameter	Range	Average scenario	Reference
<i>Life-history</i>			
Maximum dispersal distance (km)	1–3	2	Stoddart (1970) and Telfer et al. (2003)
Monthly adult mortality (proportion)	0.04–0.11	0.07	Stoddart (1971)
Monthly young mortality (proportion)	0.16–0.41	0.28	Stoddart (1971)
Number of litters	1–5	3	Corbet and Harris (1991)
Litter size	2–7	6	Stoddart (1971) and Corbet and Harris (1991)
Carrying capacity (voles/km)	10–50	30	Macdonald and Strachan (1999)
<i>Predation</i>			
Monthly rate of predation	0.0–1.0	0.5	Strachan et al. (1998) and Barreto and Macdonald (2000)

The dispersal distance is the maximum dispersal distance, individuals can settle in any area within that distance.

therefore may not be well fed. For these reasons they may be more prone to enter traps (Smal, 1991), as they are easily re-captured (Gerell, 1971).

- (4) At all other times of year, the probability of trapping mink per unit area should be similar for both sexes and all ages.

We took into account the above observations and varied the likelihood of mink being trapped by increasing by 30% that of males during the mating season (January–March) and that of juveniles during dispersal (August–October), and by decreasing by 30% that of females during lactation and weaning (April–June). At all other times of year trappability was considered to be constant. These changes to the trappability parameter as a function of the mink yearly cycle were always applied.

In addition to trappability we considered two other parameters that defined the control strategy: how many years trapping was carried out and which periods within the year trapping was carried out (Table 1).

2.4. Model outputs

We performed simulations to follow the dynamics of the population of mink and water voles for 20 years and recorded the total number of individuals present in the trapped area each month. All simulations started with populations at full carrying capacity. In all analyses we excluded the first year because, up to the point until which trapping starts, the first year is not representative of a trapped mink population because it may include months in which the population has grown without the effects of trapping. As a response variable, we used the total number of individuals present standardised by the number of simulated months. This variable represents the average number of mink or water voles present in the trapped area each month, and we refer to this value as ‘monthly density’ of mink or ‘monthly density’ of water voles.

2.4.1. Sensitivity analysis

We studied how the parameters of the model influence the results by performing several simulations with different sets of parameters and then studying the relationship between the parameters and the response variable using logistic regression. 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 different variables in the model (see Rushton et al., 2000b for a description of the method). Since the distribution functions for the life-history parameters were not known with any level of detail and there were no data available to assess the extent to which each of the life history parameters was correlated with the others, a uniform distribution was therefore assumed for each variable with upper and lower limits derived from the literature (Tables 1 and 2), and all variables were assumed to vary independently of each other.

For the sensitivity analysis we carried out 500 simulations. We used the monthly density as response variables for both mink and water voles. We defined the response variable so

that it had a value of unity if the monthly density was greater than half the carrying capacity, and zero if it was less.

2.4.2. Low mink strategy

The first aim of this study was to identify the minimum effort in terms of time spent trapping that would keep mink densities below a threshold that we set arbitrarily at 20% of carrying capacity. We refer to this trapping strategy as the “low mink” strategy. We evaluated whether trapping needed to be carried out every single year and established the minimum number of months of trapping required in any 1 year. We then determined the best combination of months in which to carry out trapping by running each possible distinct combination of months 10 times and determining which one resulted in the lowest monthly density of mink averaged over the 10 simulations.

In addition to the best combination of months, we considered four other periods of trapping corresponding to homogeneous parts of the annual cycle of mink. We did this to study how different phases in the reproductive cycle of mink may respond to trapping, and to take into account the possibility that it may be easier to concentrate mink control effort once a year, rather than splitting it. Indeed there are additional costs involved in setting and then removing the traps, therefore it may be preferable to continue once started.

These fixed periods were divided as follows:

- January–March – mating season;
- April–June – gestation and weaning;
- August–October – dispersal of juveniles;
- November and December – winter when the territories are stable.

2.4.3. Water vole protection strategy

The second aim of this study was to investigate whether the best time of year in which to trap mink changes when the goal is to obtain viable water vole populations rather than to minimise mink numbers. We refer to this strategy as the “water vole protection” strategy. In this case, the desired mink density was not set as an arbitrary threshold at the start like in the low mink strategy, but emerged as a function of the long-term survival of the water voles. To identify the water vole protection strategy, we kept the life history parameters of both water voles and mink fixed to mean values, and the predation rate of mink on water voles fixed at 0.5 as discussed above, while we varied the control parameters. Similar to identifying the low mink strategy, we first identified the best combination of months to trap mink in order to achieve maximum density of adult water voles in the trapping area. Then we examined this period together with trapping during the four different phases in the reproductive cycle of mink to see how these affected the densities of water voles.

2.4.4. Effect of mink immigration on the control period

We assessed the effect of mink immigration from adjacent non-trapped areas in relation to the different trapping periods. We kept the life history parameters of mink fixed to mean values, the trappability parameter fixed to 0.5 and

trapping occurring all years, while varying the maximum dispersal distances and trapping periods.

2.4.5. Comparing systematic vs. occasional trapping

We compared the effect of systematic trapping, where a whole area is trapped according to a well-defined strategy, vs. occasional trapping, where trapping is spatially fragmented and where different trapping strategies are adopted in different sections. The first case mimics a strategy that could be adopted by an institution interested in controlling mink employing co-ordinated professionals to carry out trapping. The second case represents situations where trapping is carried out by individual trappers or landowners, according to their own trapping strategy. To represent occasional trapping we selected 52 km of the 127 km trapped systematically. These 52 km were split into 19 sections between 1 and 6 km long, each representing a different trapper. Each trapper was assigned to one of five control strategies in which control periods and control years were varied. We then performed 10 simulations of 20 years for systematic and occasional trapping and compared the resulting monthly densities of mink. To compare the two trapping regimes, we standardised the monthly densities of mink obtained with each by the effort measured in terms of how many km of rivers were trapped, by the number of months and by the number of years during which trapping was carried out. We kept the life history parameters of mink fixed to mean values and the trappability parameter fixed to 0.7 while still incorporating seasonal variation in trappability.

2.5. Application of the model

The spatially explicit individual based models developed in this work were applied by predicting the distributions of mink and water voles in the Upper Thames for which detailed observations have been published (Barreto, 1998; Barreto et al., 1998; Strachan et al., 1998). The observed data were grouped in 5×5 km squares of the National Grid. Maps at equivalent spatial resolution were created by scaling up the model output from 1 to 5 km resolution using the GRASS GIS. The published data recorded mink and water voles in 1975 and in 1995. The 1975 data were used to set the initial conditions. At this time mink were at an early stage of colonisation while water voles were widely distributed (Barreto, 1998; Barreto et al., 1998; Strachan et al., 1998). The models were evaluated using mean life-history parameters for both mink and water voles. A probability density map for each species was obtained from averaging 100 simulated maps. This probability density map was then transformed into a presence/absence map by setting a 50% threshold above which a square was considered to be positive. Maps of observed distribution of mink and water vole in 1995 and maps generated by the model for year 20 were compared and the output classified in a confusion matrix that cross-tabulates the observed and predicted presence/absence patterns (Fielding and Bell, 1997). We used two measures of classification accuracy:

- (1) Correct classification rate = $(a + d)/N$,
- (2) Kappa = $\frac{[(a + d) - ((a + c)(a + b) + (b + d)(c + d))/N]}{[N - ((a + c)(a + b) + (b + d)(c + d))/N]}$,

where N is the total number of 5×5 km squares; a is the total number of 5×5 km squares observed and predicted to be occupied; b is the total number of 5×5 km squares observed to be empty but predicted to be occupied; c is the total number of 5×5 km squares observed to be occupied but predicted to be empty; and d is the total number of 5×5 km squares observed and predicted to be empty.

While the correct classification rate measures the proportion of squares where there is agreement between the predicted and observed distributions, the coefficient Kappa is a better measure of agreement because it makes full use of the information contained in the confusion matrix (Fielding and Bell, 1997).

3. Results

3.1. Sensitivity analysis

3.1.1. Mink model

Sensitivity analysis revealed that the most important parameters in determining the monthly density of mink in the controlled area were adult mortality, kit mortality, litter size, juvenile dispersal distance in October, and the three control parameters of trappability, trapping periods, and trapping years (Table 3). In the logistic regression relating the set of parameters with the abundance of mink, the comparison of the constant-only model with the full model showed a highly significant probability value, indicating that the predictors, as a set, reliably predicted whether mink were above or below half of the carrying capacity ($G = 334$, $df = 16$, $p < 0.0001$). Although there is evidence that the parameter of dispersal distance was not zero, the odds ratio was very close to one indicating that a 1 km increase in the dispersal distance minimally affects whether mink are above or below half of the carrying capacity. The model was able to predict correctly whether mink were above or below half of the carrying capacity 97% of the simulations.

3.1.2. Water vole model

In the presence of mink predation, the distribution of the monthly density of voles was skewed toward zero. Therefore, we re-defined the binary variable as unity if the monthly density was above the mode (mode = 30 voles) and zero otherwise. All the model parameters were important in determining whether water voles were above or below the defined threshold, except for dispersal distance (Table 4). The three parameters that were most important were adult mortality, young mortality and mink predation. The comparison of the constant-only model with the full model, showed a highly significant probability value, indicating that the predictors, as a set, reliably predicted water vole presence in both models (With predation: $G = 561$, $df = 7$, $p < 0.0001$). The model was able to predict correctly 99% of the simulations.

3.2. Model predictions

3.2.1. Low mink strategy

Carrying capacity of mink in the control area of 127 km of river habitat was about 85 mink (0.70 mink/km), therefore a

Table 3 – Results of the sensitivity analysis for mink

Predictor	Coefficient	SE	Z	p	Odds ratio	95% CI Lower	95% CI Upper
Constant	15.90	3.62	4.40	0.00			
Dispersal distance October	0.18	0.04	4.56	0.00	1.20	1.11	1.29
Mate search distance	0.20	0.10	2.00	0.05	1.22	1.00	1.48
Litter size	2.51	0.32	7.71	0.00	12.24	6.48	23.15
Kit mortality	-99.48	15.42	-6.45	0.00	0.00	0.00	0.00
Adult mortality	-237.90	44.02	-5.40	0.00	0.00	0.00	0.00
Dispersal distance August	0.23	0.28	0.85	0.40	1.26	0.74	2.17
Dispersal distance September	-0.10	0.15	-0.71	0.48	0.90	0.67	1.20
Trappability	-3.85	0.88	-4.39	0.00	0.02	0.00	0.12
<i>Periods of trapping</i>							
April–June	1.60	0.61	2.61	0.01	4.96	1.49	16.52
August–October	-2.35	0.77	-3.04	0.00	0.10	0.02	0.43
November–December	-0.01	0.60	-0.02	0.99	0.99	0.31	3.21
January, October, and November	-1.82	0.67	-2.70	0.01	0.16	0.04	0.61
<i>Years of trapping</i>							
Strategy 2 ^a	-1.19	0.58	-2.04	0.04	0.30	0.10	0.95
Strategy 3	-3.73	0.72	-5.17	0.00	0.02	0.01	0.10
Strategy 4	-4.97	0.88	-5.62	0.00	0.01	0.00	0.04
Strategy 5	-5.89	0.98	-6.01	0.00	0.00	0.00	0.02

The analysis was carried out by means of logistic regression where the response variable was whether mink in the control area were below or above half of the carrying capacity, and the explanatory variables were all the life history and control parameters. There were 97 cases in which mink were above half of the carrying capacity and 403 cases in which they were below.

a See Table 1 for a definition of the strategies.

Table 4 – Results of the sensitivity analysis for the water voles

Predictor	Coefficient	SE	Z	p	Odds ratio	95% CI Lower	95% CI Upper
Constant	3.20	1.78	1.80	0.07			
Adult mortality	-56.66	12.00	-4.72	0.00	0.00	0.00	0.00
Kit mortality	-8.69	3.20	-2.71	0.01	0.00	0.00	0.09
Number of litters	0.93	0.20	4.58	0.00	2.54	1.71	3.79
Litter size	0.70	0.16	4.46	0.00	2.01	1.48	2.74
Carrying capacity	0.35	0.05	7.02	0.00	1.42	1.29	1.57
Dispersal distance	0.29	0.45	0.63	0.53	1.33	0.55	3.23
Mink predation	-26.63	3.50	-7.62	0.00	0.00	0.00	0.00

The analysis was carried out by means of logistic regression where the response variable was whether water voles in the control area were below or above the mode and the explanatory variables were all the life history and the predation parameters.

reduction of mink by 80% was achieved when the monthly density was below 17 mink (0.13 mink/km). By varying the three control parameters while keeping the life history ones fixed, we found that monthly densities of mink below the threshold of 20% of carrying capacity (17 mink), which was arbitrarily set as a successful suppression, were obtained only by trapping in all years. For this reason we decided to keep trapping fixed to all years and perform the simulations by varying only the trappability parameter and the number of months in which trapping was carried out.

In order to achieve a reduction of mink densities by 80% at average life history parameters values, it was necessary to trap for at least 3 months (range = 9–62 mink present, n = 220 combinations of 3 months). When trapping for only 2 months, there were cases in which densities were above the threshold even when using the best combination of months (range = 16–67 mink present, n = 66 combinations of 2 months). When trapping for only 1 month, the monthly

densities of mink were always above the threshold (range = 38–73 mink present, n = 12 months). In the analysis of the combinations of 3 months in relation to reductions of mink numbers, combinations of months between October and March, including the mating, late dispersal, and winter seasons led to the highest reductions of mink densities. In particular, the best combination of 3 months included the months of January, October, and November. Unsuccessful control involved combinations that included months of the central part of the year, from April to September, including the gestation-weaning and early dispersal seasons.

When comparing the continuous trapping periods of 3 months corresponding to phases of the reproductive cycle of mink, all periods, except for April–July, were able to achieve the desired reduction of mink densities of 80%, but trapping using the best combination of 3 months (January, October and November) was more profitable than any of the continuous trapping periods (Fig. 2). As trappability increased the

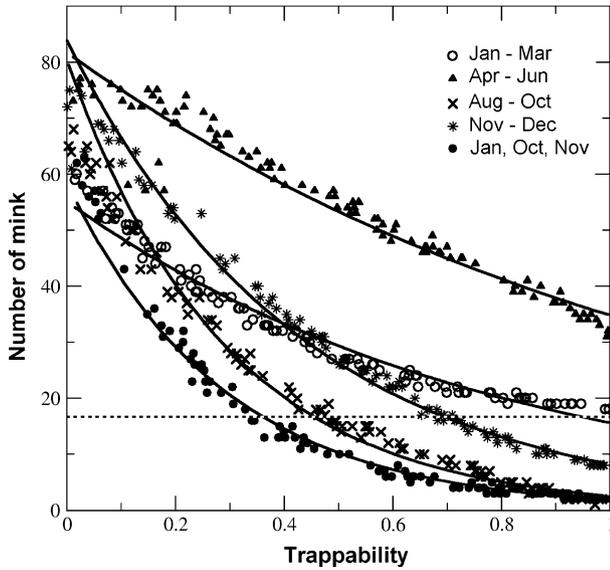


Fig. 2 – Predicted number of mink in relation to their trappability and the periods in which they were trapped. The dotted line identifies the threshold below which we considered a strategy to be successful having achieved 80% reduction of mink densities. Exponential curves $y = a_1 e^{-a_2 x}$ were fitted to each of the different periods of trapping in order to better visualise the relationships between the different data sets.

predicted number of mink did not decrease in the same fashion for all the five periods considered (Fig. 2) and although trapping using the best combination of 3 months always resulted in the lowest density of mink, independent of trappability levels, this was not true for the other periods. In this way, periods of trapping that worked best at low trappability were not necessarily the best ones at high trappability.

Different control periods produced different levels of variation in terms of mink densities across the year (Fig. 3). In particular, if control occurs between August and October the monthly densities of mink appear to be rather constantly reduced, with coefficient of variation (CV) = 34%, $n = 12$. If

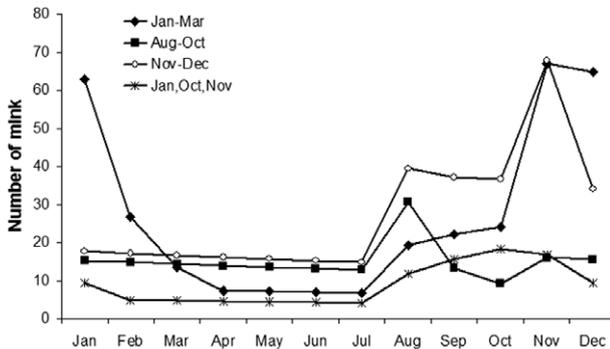


Fig. 3 – Number of mink in the control area throughout the year as a function of the trapping period. Kits, young mink up to 3 months of age, are not included in the calculations while juveniles are. The densities are calculated at the start of each month. Trappability was kept fixed at 0.5.

control occurs in any of the other four periods then variability is higher, with CV = 87% ($n = 12$) during January to March, CV = 38% ($n = 12$) during April to June, CV = 59% ($n = 12$) during November and December, and CV = 60% ($n = 12$) during January, October and November.

In conclusion, the model suggests that the best strategy involves controlling mink every year for 3 months, and at least during the mating, late juvenile dispersal and winter seasons.

3.2.2. Water vole protection strategy

By varying the three control parameters while keeping life history and predation fixed, we found that water vole populations survived after 20 years in only 97 out of 500 cases, whereas in all other cases they went extinct. In the majority of cases (76%) in which water voles survived, the trapping strategy was one by which mink were trapped every year. For this reason we decided to keep trapping fixed to all years and perform the simulations by varying only the trappability and the monthly periods of trapping. To maximise the number of water voles the best months for trapping were October, November and December. However, this strategy was only marginally better than trapping in January, October and November, which are the best 3 months of control to reduce mink densities by 80% (January, October, November = 2658 voles on average; October, November, December = 2721 voles on average; t -test = 1.7, $df = 9$, $p = 0.06$, one tail). As for the low mink strategy, the slopes of the function that link mink trappability to the number of water voles in the different periods, vary (Fig. 4). At low water vole densities trapping mink between August and October was as efficient as trapping between October and December (Fig. 4). Trapping mink only between April and June always led to water vole extinction.

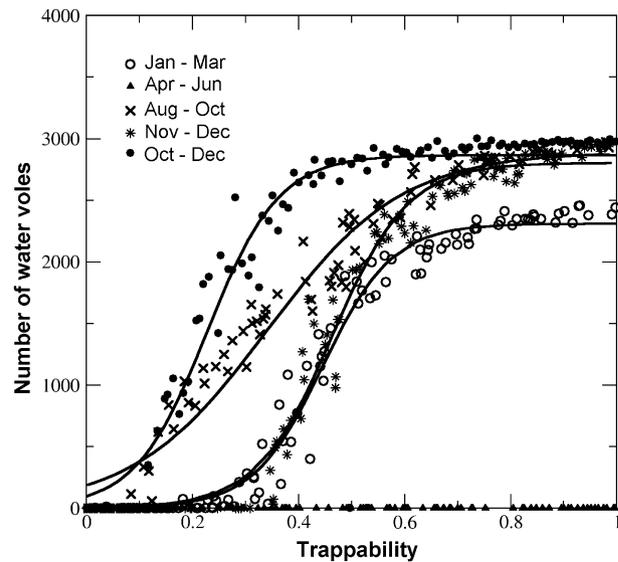


Fig. 4 – Predicted viability of water vole populations in relation to mink control parameters (trappability and the periods in which mink were trapped). The data represent the monthly average of adult water voles across 19 years of the simulation excluding the first year. Logistic curves $y = \frac{a_1}{1 + e^{(a_2(a_3 - x))}}$ were fitted to each of the different periods of trapping in order to better visualise the relationships between the different data sets.

The relationship between the number of water voles and the trappability of mink increased according to a logistic function (Fig. 4). This result suggests the existence of an effective threshold in the number of mink above which water voles are not able to survive. We found that when plotting the number of female mink against the number of water voles, a threshold emerged that was independent of the trapping strategy centred at around about 20 female mink in the control area or about 0.15 female mink/km (Fig. 5a). A threshold also was apparent when plotting the number of male mink against water voles, but this threshold was more dependent on the trapping strategy (Fig. 5b).

These results suggest the optimal strategy for maintaining viable populations of water voles is to trap mink during their late juvenile dispersal and winter seasons.

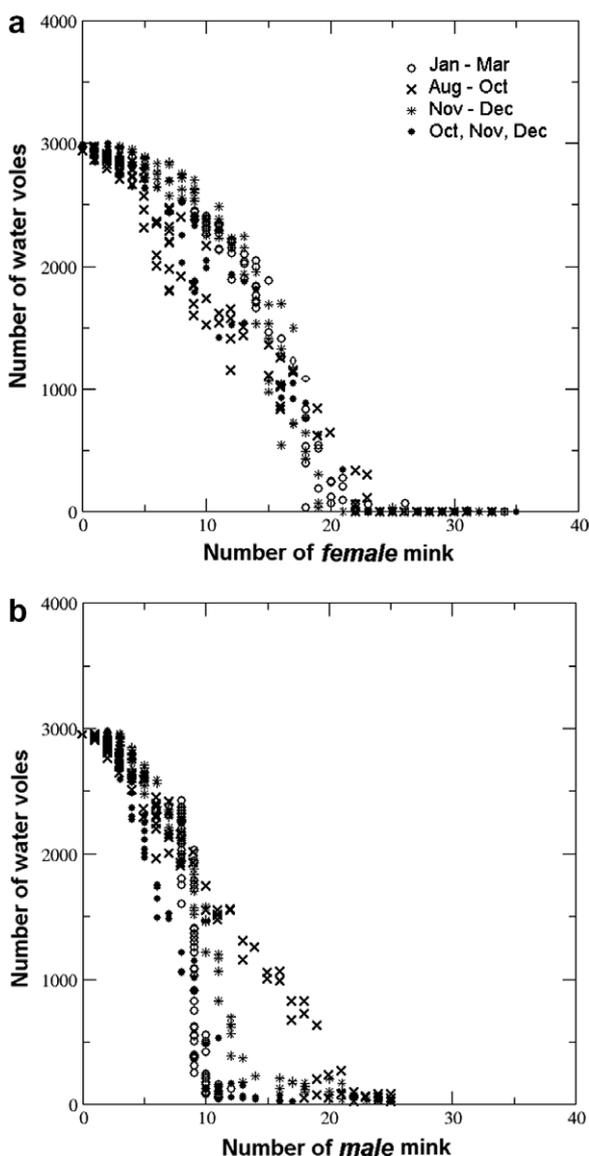


Fig. 5 – Number of water voles in the control area after 20 years against the monthly densities of female (a) and male (b) mink averaged over 19 years for different trapping periods. Different densities of mink were obtained by varying the control parameter of trappability between 0 and 1.

3.2.3. Effect of mink immigration on the control period

At low levels of immigration, using any of the four successful trapping periods (i.e. excluding trapping between April and June) yielded approximately similar levels of suppression of the mink population (Fig. 6). At high levels of immigration the two strategies that involved trapping during the juvenile dispersal season (August–October) and in January, October and November, were by far more successful than trapping in the winter or mating seasons. Trapping between April and June seemed to be particularly sensitive to immigration levels, with relatively low levels of mink densities at low immigration rapidly increasing to high mink densities as immigration pressure increased.

3.2.4. Comparing systematic vs. occasional trapping

Monthly densities of mink (corrected by the effort) were reduced significantly more with systematic than with occasional trapping (t-test two tails: 2.12, df = 16, $p < 0.001$). The mean monthly density of mink with occasional trapping was 18 mink (SD = 6), while that of systematic trapping was 10 mink (SD = 3). These results suggest that, for the same effort, adopting a systematic strategy achieved better results than adopting occasional mixed strategies. If we ignore the effort, and re-calculate mink densities in the control area with the occasional strategy, then the mean monthly density of mink is 56 mink (SD = 20), which is not a substantial reduction when compared to a carrying capacity of the area of about 85 mink.

3.3. Application of the model

The direct use of the water vole mean life history parameters did not lead to a good match between observed and predicted

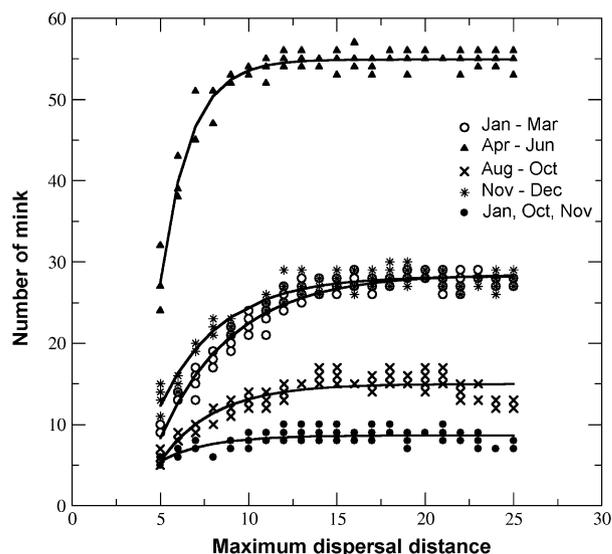


Fig. 6 – Number of mink in the control area as a function of immigrant pressure in relation to the trapping period adopted. Immigrant pressure is expressed as the dispersal distance divided by two to take into account the sinuosity of rivers (see methods). Exponential curves $y = a_1(1 - e^{-a_2(x-a_3)})$ were fitted to each of the different periods of trapping in order to better visualise the difference between data sets.

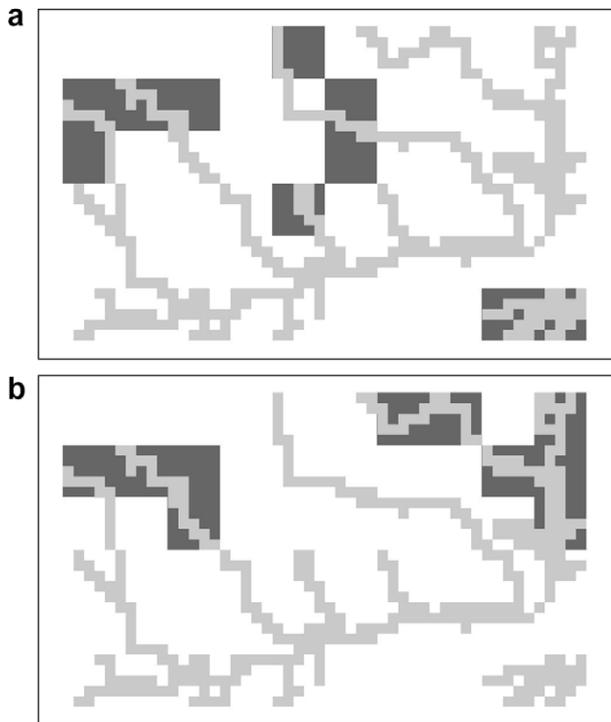


Fig. 7 – Maps of the observed (a) and predicted (b) distribution of water voles in the Upper Thames in 1995. The grey squares represent the observed distribution in 1995. All 5 km squares were occupied by water voles in 1975.

distributions of water voles (correct classification rate of 29% and a Kappa coefficient of -0.040). In this case, the confusion matrix indicated that with these parameters water voles tended to survive more than expected and indeed the increase of the adult and young mortalities to values in the upper ranges reported for these parameters (respectively to 0.11 and 0.41, see Table 2) lead to a better fit (correct classification rate = 66%, Kappa coefficient = 0.007). The low value of the Kappa coefficient in this latter case results from the fact that only one of the three areas in which water voles were observed, was predicted to be populated (Fig. 7a and b). By contrast, the use of the mink mean life history parameters provided a good correlation (correct classification rate of 73% and a Kappa coefficient of 0.461) between the observed and the predicted distributions of mink in 1995 in the Upper Thames (Barreto, 1998; Barreto et al., 1998; Strachan et al., 1998). Both the observed and predicted distributions located mink in the eastern area and along the main stretch of the river Thames (Fig. 8a and b). All the mortality values above are expressed as monthly mortality values.

4. Discussion

4.1. Model results

The model suggests that it is possible to suppress mink to very low densities if trapping is sustained for at least 3 months per year and carried out every year. This result is dependent not only on the values of life-history parameters

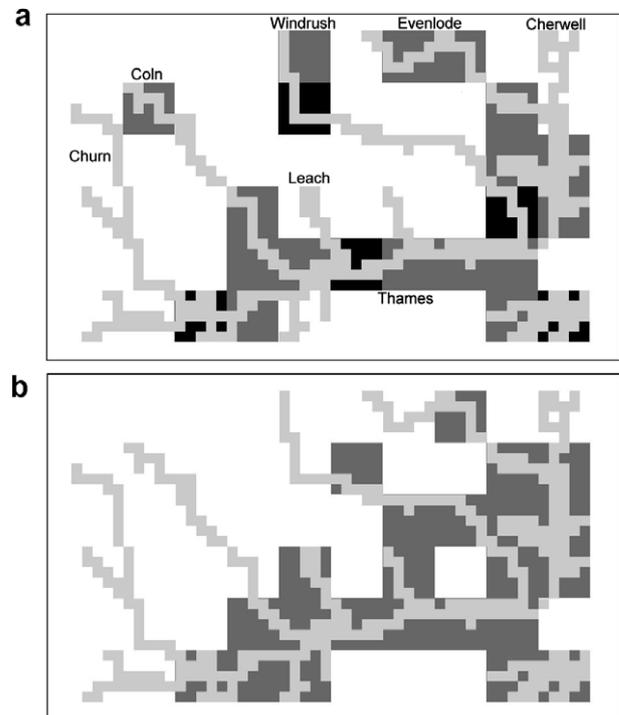


Fig. 8 – Maps of the observed (a) and predicted (b) distribution of mink in the Upper Thames in 1995. The grey squares represent the distribution in 1995; the black squares represent the observed distribution of mink in 1975 (All squares that were occupied in 1975 were still occupied in 1995). The distribution of mink is reported at 5 km resolution while the river sections in lighter grey are reported at 1 km resolution. The names of the main rivers are also reported.

that we considered, but also on other factors, such as habitat, that were not included in the model and therefore must be considered with caution. Indeed, a number of authors have suggested that demographic models may be better employed in the generation of relative rather than absolute predictions (Akçakaya et al., 1995; Beissinger and Westphal, 1998). The model has higher credibility (sensu Rykiel, 1996) when suggesting the best periods in which to trap. The model identified a mixed strategy of trapping during the mating, late dispersal, and winter seasons as the best one to achieve maximum suppression of mink densities, instead trapping during the gestation and weaning season was not profitable. While trapping during the mating season has long been recognised as important for mink control, trapping during the juvenile dispersal season has not always been considered, in the belief that most juveniles would die during dispersal anyway. The failure of early attempts to control coypus was attributed to immigration into cleared areas, which was not given sufficient consideration (Gosling and Baker, 1989). Because of the importance of targeting juveniles, once mink have been reduced to low densities in a core area, it may be necessary to trap in peripheral areas to prevent immigration from nearby non-controlled populations. In this way, one could reduce

the cost of control, if trapping in peripheral areas did not exceed additional costs of trapping in core areas. It is important to remember that the suggested trapping strategy is valid for open populations of mink, where immigration is expected. If the objective is to eradicate a closed population of mink, the best strategy may be different (e.g. Macdonald et al., 2002b).

In the model we considered the parameter called ‘trappability’ which takes into account the likelihood of an individual mink being trapped. This parameter depends both on the actions of the trapper and on the behaviour of the mink. Levels of trappability may vary, for example, with mink density (with mink being easier to trap at higher densities), type of habitat, and the ability of the trapper (Macdonald and Harrington, 2003), and for stoats *Mustela erminea* it has been shown that it can vary also with levels of food supply (King and White, 2004). The model highlighted that the level of trappability may be an important factor to take into account when choosing the trapping periods (Fig. 2). For example, at low levels of trappability, trapping during the mating (January–March) or dispersal season (August–October) seems to give similar results, whereas at high levels of trappability, trapping during the dispersal season becomes decisively more effective. These variations are represented by the variation of the slopes of the function that links trappability to the number of mink in the different periods (Fig. 2). In particular, slopes are less steep in the two periods when males are relatively more trappable than females, i.e. during the ‘mating’ and ‘gestation and weaning’ seasons. Increased success in trapping males might not actually benefit overall population control since individual male mink are promiscuous fertilising many females, and traps holding males reduce the opportunity for catching reproducing females.

The level of immigration from nearby non-controlled areas is another factor that the model suggested needs to be taken into account when choosing the control period. While the level of immigration does not seem to affect trapping success when trapping is done in periods that comprise the dispersal season, if trapping is done outside the dispersal season then it is important to take into account the likelihood of mink immigrating from nearby areas. When immigration is expected to be low it may be possible to consider trapping only during the mating or winter season, otherwise trapping should always include the dispersal season.

Although maximum suppression of mink densities (low mink strategy) was obtained by trapping during the mating, late dispersal and winter seasons, to preserve water voles in the long-term (water vole protection strategy), it was more important to concentrate trapping during the mink juvenile dispersal and winter seasons (Fig. 4). This difference is likely to be due to two reasons. First, trapping in the mating season becomes less important to preserve water voles because primarily adult male mink are targeted during this season. In order to maintain maximum water vole densities, however, it is important to target adult female mink because they most heavily predate on water voles due their small size and ability to enter water vole burrows. (Strachan and Jefferies, 1996). Second, by trapping during the mink dispersal season (August–October), mink numbers are lowered at a time when water voles are reproducing and dispersing, themselves. Protection during the reproductive period may be particularly

important in species like water voles, whose individuals are short-lived and thus likely to reproduce during only one reproductive season.

The number of water voles after 20 years responded to a well-defined threshold in the number of female mink, whereas water voles tolerated greater variability in the number of male mink (Fig. 5). The different reactions of water voles to male and female mink densities were probably due to the greater vulnerability of water voles to predation by female mink.

4.2. Model limitations

One of the limitations of the model is that habitat was not modelled explicitly as we assumed all river corridors to be suitable for both mink and water voles. In reality, this is unlikely to be the case. In Britain, the water vole shows a spatial distribution that goes from fragmented. (Aars et al., 2001), through clumped (Telfer et al., 2001), to semi-continuous (Stoddart, 1970; Bonesi et al., 2002). Within this context, our model is more likely to be representative of populations of water voles living on the main channels of lowland rivers in the central and southern parts of England rather than populations living either in upland rivers, such as those in Scotland, or in the upper tributaries, where their distribution is naturally more fragmented. A greater degree of fragmentation due to the underlying habitat structure is likely to increase the probability of water vole extinction when water voles are subjected to mink predation (Rushton et al., 2000a). All other conditions being equal, we would expect that if the model was to be applied to areas where water voles are already naturally fragmented, mink control should need to be even more intense to allow water voles to persist in the long term. Two studies conducted in areas where water voles are naturally fragmented showed that mink tended not to establish resident populations, due possibly to a lack of alternative prey (Aars et al., 2001; Telfer et al., 2001). In such cases, to ensure the long-term survival of the water vole populations ad hoc mink removals upon their sporadic colonisations may be the best option.

Dispersal is one of the behavioural factors that is likely to have the most impact on the output of individual-based models (Rushton et al., 2000a), but it is also one of the most difficult factors to model because of the difficulty of gathering data. Not much is known about dispersal in water voles and mink and therefore it is difficult to assess whether we realistically modelled the dispersal process. In effect we had to assume a plausible behaviour that might not have actually occurred in the field. We assigned dispersing juveniles, both in mink and water voles, to areas along the river characterised by being below carrying capacity. We did not take into account that there could be obstacles along the route to reach such areas; consequently our model might have underestimated mortality during dispersal. In mink, we attempted to overcome this problem by considering juvenile mortality in the pre-dispersal phase, when mink undertake exploratory excursions from the mother’s home range before dispersing.

A further limitation of the model is that it did not take into account changes in life-history traits following changes in densities, because it did not consider reproductive output to vary according to density. In reality, control measures can

result in the realisation of a larger reproductive output compared to that at carrying capacity. This has been observed in coypu and muskrat *Ondatra zibethicus*, where the low densities obtained during control operations are believed to release the populations from density dependence, thereby increasing reproductive output (Gosling et al., 1981; Verkaik, 1989; cited in Usher, 1989). A larger reproductive output following control is likely to occur in mink as well, as suggested by Gerell (cited by Usher, 1989). The effect of a higher reproductive output on the model would probably result in the even greater need to trap juveniles during the dispersal season.

The conceptual validity of the model inevitably rests on its assumptions – if they are valid and if the model is internally consistent then we can cautiously use the model as a decision-making tool, and resources should be spent on monitoring and re-evaluating how the model is used (Starfield, 1997). The main assumptions in our model concerned the likelihood of mink entering traps as a function of the sex and age of mink and the time of year, and were justified based on physiological and behavioural observations. The model assumed that greater numbers of adult males could be trapped during the mating season, that more juveniles could be trapped during the dispersal season, and that fewest adult females could be trapped during the lactation and weaning season. These observations are supported by many authors that carried out mink trapping for their studies (Gerell, 1971; Chanin, 1976; Birks, 1981; Ireland, 1990; Smal, 1991; Yamaguchi, 2000). However, the model did not take into account the likelihood that mink trappability can vary with other factors such as population density, or with external factors such as resource abundance or the presence of competitors. However, it is will not be possible to quantify the relationship between these variables until further data become available.

4.3. Application of the model

The mink model predicted relatively well the spatial distribution of mink in 1995 on the Upper Thames, locating mink mostly in the eastern areas and along the river Thames as observed (Barreto, 1998; Barreto et al., 1998; Strachan et al., 1998). This result may be a consequence of the particular distribution of mink in 1975, whereby they were found predominantly in the east and along the river Thames from where they spread to other areas. It is also possible that one of the reasons why the model concentrated mink in these areas was because they hosted a greater density of river cells (density of 1×1 km river cells per each 5×5 km square in the area where mink present = 11 ± 3 ; in areas where mink absent = 7 ± 3) thereby making the establishment of a population more secure. Despite the good agreement between our predictions and the observed data, additional factors not considered in the model, such as for example den availability (Halliwell and Macdonald, 1996), may also influence the distribution of mink populations in the Upper Thames. Indeed, a relatively good match between the predicted and observed distributions of water voles, was obtained by adopting values for the mortality parameters in the upper range of the reported values (Table 2). This result may be rationalised, at least in part, by considering the fact that, in reality, the presence of mink may have secondary negative effects for the

voles which were not considered in the model, such as reduced foraging periods, that may further increase mortality (e.g. Gosler et al., 1995). Predicted distributions of water voles coincided with the observed ones in the upper reaches of the rivers Churn and Coln, although, interestingly, the model also located voles on the Cherwell and on the Evenlode in an area that was also occupied by mink. This area was characterised by a relatively high density of river cells per each 5×5 km square (density of 1×1 km river cells per each 5×5 km square on Cherwell and lower Evenlode = 12 ± 2) and it is possible that this larger availability of habitat has ensured a longer survival of the water voles in the model. Indeed, it has been shown that a high connectivity of suitable habitat increases the probability of water voles being present (Bonesi et al., 2002) and that large water vole populations tend to be more persistent (Telfer et al., 2001). Therefore one of the reasons why the model predicted only in part the distribution of water voles in 1995 may be that in the model habitat was considered to be homogeneous while in reality habitat is variable and it is known that habitat characteristics may influence the likelihood of coexistence of water voles with mink (Macdonald et al., 2002a; Carter and Bright, 2003).

5. Conclusions

The results of the model suggest the following considerations regarding mink trapping. First, a combined strategy of trapping during different phases of the mink annual cycle is preferable to trapping only in the mating season. Second, targeting immigrating juveniles as well as reproductive adult mink is important for a successful control strategy. Finally, it is possible to achieve successful mink control providing the strategy adopted is systematic and not occasional, as has often been the case in the past (this is probably one of the reasons why the MAFF campaign in the 1960s was not effective). A complete eradication of mink from the UK is highly unlikely, but the model suggests local reductions that allow water voles to survive in the long term is possible, provided that there is unwavering commitment to long-term control.

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