

Incorporating evolutionary processes into a spatially-explicit model: exploring the consequences of mink-farm closures in Denmark

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Hammershøj, M., Travis, J. M. J. and Stephenson, C. M. 2006. Incorporating evolutionary processes into a spatially-explicit model: exploring the consequences of mink-farm closures in Denmark. – *Ecography* 29: 465–476.

In this paper, we present an individual-based cellular lattice model, which is based on a real landscape (Denmark). The model predicts the distribution of free-ranging mink from data collated on the geographic locations of fur farms, the number of breeding mink kept per farm, and a range of parameters regarding escape, reproduction, mortality, and dispersal. When evolution was incorporated in the model, the results showed that the degree of adaptation within the free-ranging mink population is likely to vary spatially, with lower adaptation in areas where farm mink density is highest (due to the greater number of escaping mink). We used the model to explore the potential consequences of closing mink farms, or limiting escapes from them, on the evolutionary ecology of the free-ranging population and found that depending upon the parameterisation of the evolutionary processes, several different outcomes are possible. Closing mink farms may result in a crash of the free-ranging population, or alternatively it may result in the establishment of a better-adapted, truly feral population that may ultimately outnumber the population that was present before farm closures. The main purpose of this paper is to raise awareness of the potential importance of evolutionary processes for the naturalisation of mink in Denmark, and to highlight the need for further work. Future field studies should be targeted to reduce the uncertainty in key parameters, allowing the development of an improved version of this model that can be used to generate management recommendations. More generally, we believe that further work linking evolutionary and population biology is required particularly in an applied context. There are likely to be many further scenarios where evolutionary processes may hold the key to understanding both population and community dynamics.

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The American mink *Mustela vison* is not native to Europe, but feral mink populations have become established in many European countries (Stubbe 1993). In Denmark, free-ranging mink populations are also widespread, but it is uncertain whether a truly feral mink population exists. Denmark holds >2000 fur farms, and

a recent study in two areas of Denmark showed that nearly 80% of the free-ranging population consisted of escaped farm mink (Hammershøj et al. 2005).

Artificial selection or adaptation to captive environments typically results in reduced fitness under natural conditions (Tufto 2001, Gilligan and Frankham 2003,

Accepted 12 January 2006

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ISSN 0906-7590

and references therein). In earlier work, we developed a spatial model for sexually reproducing organisms, in which we incorporated a measure of genetic adaptedness to natural conditions (Travis et al. 2005). We demonstrated the use of the model to investigate the evolutionary dynamics of an invasive species, and asked one specific question: how does the number of introductions influence the dynamics of invasion? In the model, an individual's genotype determines the probability that it will successfully establish at a suitable site. If introduced individuals are well-adapted to the wild conditions, the size of the population in the wild always increases with the number of introductions. However, when the introduced individuals are poorly adapted to the natural conditions, as would be expected in the case of farm mink, considerable genetic adaptation is necessary before the population in the wild is able to grow appreciably. Up to a point, increasing the number of introductions increases invasion potential due to simple demographics and because the introduced population contains a greater proportion of the total number of well-adapted alleles. However, as the number of introduced individuals with mainly poorly-adapted genes increases beyond this point it becomes ever more difficult for a population to become well-adapted. Under these conditions, the most rapid invasion occurs for an intermediate number of introductions. Thus, when the number of introductions is high, adaptation to local conditions is dramatically slowed and in some cases a well-adapted population never establishes (Travis et al. 2005). This effect is similar to that described by Kirkpatrick and Barton (1997) in which gene flow from the centre of a species' range can limit adaptation at the periphery and prevent the range from expanding outward.

The high proportion of escaped farm mink in the Danish nature strongly suggests that fur farms have not been adequately secured against escapes of mink. As has been shown in other countries, the impacts of mink on native fauna can be dramatic (e.g. water vole, Woodroffe et al. 1990, Barreto et al. 1998, and waterfowl, Nordström et al. 2003) and in a recent government order (no. 610 of 19 July 2002) restrictions were placed on Danish mink farmers to more effectively prevent mink from escaping. Ensuring that no more farm mink escape from fur farms may result in 1 of 3 outcomes: 1) the free-ranging population will crash and leave only small, isolated populations that may or may not go extinct, i.e. the farms act as sources and nature as a sink, 2) the free-ranging population might crash at first but will then "grow" back to present levels, i.e. the population size is at its carrying capacity, with or without farm mink, or 3) a truly feral population adapted to the Danish environment will become established at a new equilibrium that may be either lower or higher than the current mink density.

In the present study we attempted to determine which outcome is more likely. First, we constructed an individual-based cellular lattice model. The model was based on a real landscape (Denmark), and predicts the distribution of free-ranging mink from geographic locations of fur farms, the number of breeding mink kept per farm, and a range of parameters regarding escape, reproduction, mortality, and dispersal. We then incorporated evolution, i.e. genetic properties, in the model, and looked into the potential effects on the free-ranging mink population in Denmark of stopping/limiting further escapes from farms.

The model

Overview

We have used an individual-based cellular lattice model framework to describe the spatial population dynamics of the Danish mink population. Cellular lattice models have been used quite widely in theoretical ecology in recent years both in deterministic (e.g. Hassell et al. 1994) and individual-based forms (e.g. Travis and Dytham 1998, 1999). Within this framework the landscape is represented by a lattice of cells, each of which represents a patch of habitat. For the model described here a cell represents a 1 km square of Denmark. Input data for the simulation models were generated using ArcView GIS 3.3. A digitised map of Denmark (Top10DK, Copyright, Kort and Matrikelstyrelsen, permit G18/1997) was used to outline the coastline and water bodies thought to be large enough to represent barriers to movement for mink. From this a surface was generated where the value in each grid cell determined whether the 1 × 1 km cell represented land (0) or water (1). The Arcview 3.3 grid function was used to assign a cell as either land or water and this is based on whatever feature constitutes the majority of a cell. Different types of habitat can readily be incorporated into this general framework by allowing cells to have different states (e.g. sea, lake, forest, arable land), and the behaviour of an individual (e.g. reproduction, dispersal) can be made dependent on the habitat type. Here, we differentiated simply between water and land. Good information on the location and size of mink farms in Denmark exists, and we simulated the escape of mink from these farms into the wild. The geographic locations of all Danish fur farms and the number of mink (breeding females) kept in each farm in 1996 were entered into ArcView 3.3 and a density grid of farmed mink was calculated for the whole country (excluding the island of Bornholm) at a resolution of 1 × 1 km (Fig. 1). We used number of farmed mink per km² rather than number of farms. We assumed that the more mink a farm has, the more mink escape, and we thus ignored the possibility that bigger farms are better at keeping mink from escaping relative to smaller farms (or vice versa).

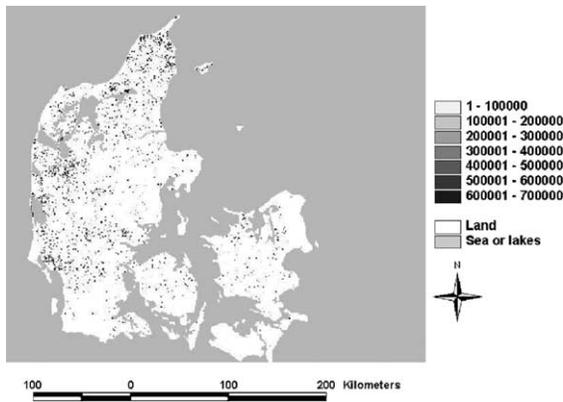


Fig. 1. Map of Denmark showing the number of farmed mink per 1×1 km square.

The model simulated the reproduction, mortality, and dispersal of mink, incorporating (as far as possible) empirically observed differences due to age and sex. Data from a questionnaire of Danish hunters that captured mink in the hunting season 1996/1997 (Hammershøj and Asferg 1999) was used to generate a density grid of killed mink per 10×10 km.

In the evolution model, we allowed for adaptation to occur within the mink population by explicitly modelling the genotypes of every individual. We assumed that adaptation to the wild is an additive trait controlled by 100 independent loci (although we varied the number of loci involved in sensitivity analyses). Sexual reproduction was incorporated in the model. Mortality of individuals born in the wild was determined by their genotype. Below, we describe in more detail how escape, reproduction, mortality and dispersal were modelled.

Escape

For each cell on the lattice we held the total number of mink that are farmed within that 1 km^2 area. We assumed that for every 100 mink in captivity there is a probability, e , that one escapes into the wild. The genotype of an escaping mink was determined by setting each allele equal to 1 (well-adapted) with probability a , and to 0 (poorly adapted) with probability $1 - a$. A recent count of autumn numbers of farmed mink in Denmark resulted in an estimate of 2.5 million breeding females, and ca 12.5 million pups with a sex ratio of ca 50:50 (Hansen pers. comm.). The age distribution of females was ca one third 2 yr olds and two thirds 1 yr olds. Each male was allowed to mate with up to 6 females, and 90% of males used in breeding were 1 yr olds. Rather than trying to incorporate all this detail, and because we had no information on the differential probabilities of escape for mink according to age or sex, we made a few simplifying assumptions in the model. The sex of each escapee mink was assigned at random

according to a 1:1 ratio, and in most runs of the model all escaping mink were assumed to be juvenile, i.e. < 1 yr of age.

Reproduction

Females and males can both breed from the age of 1 yr. For simplicity, we assumed that fecundity is age-independent once maturity is reached, and that on average a reproducing female will have 4 young, based on reported litter sizes from Sweden (Gerell 1971) and Germany (Stubbe 1993). Due to limitations of resources, e.g. space and food, we assumed that an upper limit exists for the number of females that reproduce within a 1×1 km cell. The value of this upper limit was set by a parameter b , and was set at 2 for the majority of simulations. This was no more than a best guess, and represents one of the parameters that we had least information about. We chose this limit following consultation with an expert on American mink ecology in Scotland (Helyar pers. comm.) who indicated that “1 or 2 mink per km^2 sounds reasonable but 4 is probably too high”. Research both from the species’ native range (Allen 1986) and from Sweden (Gerell 1967) also suggest that the home range requirements of female mink are quite substantial and that it would be unlikely to find > 4 breeding in 1 km^2 . Where there were more than b females in a cell, those that reproduce was determined at random. A female’s mate was determined as follows: if there were mature males within the same cell as the female then one would be selected at random to be the mate. Otherwise, if there were mature males in any cells up to 5 km distant, one of those was selected to be the mate. Otherwise the female failed to mate and did not reproduce. A reproducing female gave birth to 4 young, whose genotypes were determined by simulating meiosis. At each locus, mutation from captive-type to wild-type and vice versa occurred with probability m . Each offspring was male or female with equal probability.

Mortality

The probability of mortality depended on age and history of the mink (Hammershøj 2004). For wild mink, this probability was dependent upon how well adapted the mink was. For juvenile wild mink, mortality equalled $0.8 - (A/200) \times A_i$, where A is the number of well-adapted alleles that the mink possesses (a number between 0 and 200) and A_i scales how important being well-adapted is to the probability of mortality. For adult wild mink, mortality equalled $0.7 - (A/200) \times A_i$. For escaped mink, the probability of mortality was not dependent on genetics, but was fixed at 0.8 for juveniles and 0.75 for adults.

Dispersal

As is almost always the case in constructing spatially-explicit models, parameterising dispersal is very challenging: it is usually the ecological process that we have the least information about. In this case we reviewed the available data on mink movement (Birks and Dunstone 1991, Larivière 1999, and references therein), and constructed a dispersal function that generated movement behaviour that was (subjectively) consistent with these data. It is a crude approach, but without further data it is difficult to do more.

Dispersal of mink was simulated by employing a correlated random walk that was constrained by the presence of large water bodies (e.g. sea and lakes) (Kareiva and Shigesada 1983). First a number of “steps” made during the dispersal phase was assigned to each individual. This number was drawn at random from the discrete uniform distribution between 0 and s , where s depended upon the sex, age, and history of the mink (Table 1). A “step” refers to the movement of a mink from one cell on the lattice to one of the 8 adjacent cells.

First, we will describe the correlated random walk that we implemented as it would occur if there were no constraints due to landscape characteristics. There are 8 possible directions that a mink might take in each step (relating to the position of the adjacent cells); these can be thought of as NW, N, NE, E, SE, S, SW, and W. The initial direction that a mink took as it moved from its start location was determined by drawing a direction at random from the 8 possibilities. The mink then “stepped” to the cell located in that direction. With a probability, k , the direction of movement remained the same for the next step: with a probability $1 - k$, the mink changed direction for the next step. We set $k = 0.50$, and changing directions was primarily allowed in the same general direction. Thus, an individual that started by stepping S would have a 50% probability of continuing S for the next step, but a 20% probability of moving SW, and 20% probability of moving SE. Animals were given a 10% probability of moving in a randomly determined direction. These probabilities were fixed in all simulations. An individual continued moving until it had made the number of steps that it was assigned.

Table 1. Maximum number of steps assigned to each mink depending on age, sex and whether it is escaped or wild. These values are somewhat arbitrary but have been selected such that they result in ranges of dispersal distances consistent with those reported for mink of different ages and sexes (see Birks and Dunstone 1991, Larivière 1999, and references therein).

| | Escaped mink | | Wild mink | |
|---------|--------------|----|-----------|----|
| | Juv | Ad | Juv | Ad |
| Males | 40 | 20 | 60 | 30 |
| Females | 40 | 5 | 60 | 10 |

The constraints imposed on movement were due to the likely difference of movement across large areas of water. For example, if a step would have resulted in a mink moving from land into an area of water then it was allowed to occur only 5% of the time; the other 95% of the time, the mink was reassigned a random direction. We also incorporated an increased risk of mortality due to being away from land: any step that resulted in the mink being >1 cell away from land had associated with it a 0.02 probability of death. Finally, a mink was not allowed to conclude its movement while in a watery cell. If an individual used up all its steps and was away from land, it was assigned more steps and kept moving until either it suffered mortality or arrived on land.

Ordering of events

We ran the model using an annual time-step. Each year we simulated the various processes outlined above in the following order: Escape, Mortality, Reproduction, Dispersal. Following dispersal all the individuals' ages were incremented. The parameters that were varied between runs of the model are listed in Table 2.

Sensitivity analysis

We attempted to parameterise the model using all the available data, and where that was lacking, we canvassed the opinion of experts. For example, we were unable to find any information on how many loci are involved in determining a mink's degree of adaptation to wild conditions. However, consulting mammal geneticists resulted in a “best guess” of 100 loci. This was considerably more than we were anticipating and was not ideal for model purposes as it considerably slowed computation. We believe that our model parameterisation captured the empirical data available and otherwise incorporated expert opinion. However, inevitably there was still considerable uncertainty regarding the parameterisation of several processes within this model. To establish how robust the results were to changes in the parameter values we varied several of the parameters in a large number of simulations. Specifically, we varied 1) the number of loci that act to control the degree of adaptation to wild conditions, 2) the proportion of mink escaping from the farms, 3) the maximum number of female mink that can breed within a grid cell, 4) the dispersal behaviour and 5) the probability of a mutation.

Results

Before describing the main results, we first highlight the type of dispersal behaviour that the correlated random walk produces (see Fig. 2). Some mink settled within a few km of the farm from which they escaped while others settled >20 km away.

Table 2. List of parameters varied in the model, their default values, and the ranges tested.

| Parameter | Description | Range | Default |
|-----------|--|-------------|---------|
| e | Initial rate of mink escape. | 0.01–0.04 | 0.02 |
| e2 | Altered rate of mink escape. Only used when a change in regime is simulated. | 0–0.04 | 0 |
| Myear | Total number of years that the model is run for. | 100–200 | 100 |
| Cyear | Year that change in e occurs. | 0–50 | 25 |
| b | Density dependent parameter: max. no. of females breeding in each cell. | 1–4 | 2 |
| m | Prob. of mutation at each locus. Implemented during reproduction. | 0.0005–0.01 | 0.001 |
| a | Prob. that each allele is well-adapted in escaping mink. | 0.01–0.1 | 0.03 |
| A_i | Determines the importance of being well-adapted. The greater A_i , the larger the fitness costs of being poorly adapted. | 0.1–0.6 | 0.5 |

When the model with no evolution was run for 50 yr mink density varied considerably across Denmark with the greatest concentrations being found in the regions with large numbers of farmed mink (Fig. 3). These numbers were converted into proportions and summed in 10×10 km squares in Fig. 4A. The proportion of total mink bagged by hunters per 10 km^2 is shown in Fig. 4B. A visual comparison between these 2 figures reveals reasonable correspondence between those regions of Denmark where many mink are bagged by hunters and those regions that the model suggests should be populated by many mink. This correspondence gives us some confidence that the model is producing sensible output, but certainly does not represent a validation of the model (see Discussion).

When the model with evolution was run we obtained a wide variety of different results both for number of mink in the wild and the mean degree of adaptation (Fig. 5). For our default set of parameter values, the mean degree of adaptation slowly grows from ca 3 to 8, and the number of mink from an initial 4000 to 260 000 (Fig. 5A). We do not wish to put too much significance on the absolute numbers of mink, but will use them to compare different runs of the model, i.e. we compare relative densities. With increased mutation rate adaptation occurred far more rapidly, and this resulted in a much steeper increase in the abundance of mink in the wild (compare Fig. 5J with 5A). A similar pattern of increased adaptation and population abundance resulted from increasing 1) the number of females breeding in each

cell, b, 2) the probability that an allele is well-adapted in an escaping mink, a, and 3) the relative influence on fitness of beneficial alleles, A_i . Only when A_i was reduced from 0.5 to 0.1, did the population go extinct.

We ran a set of simulations to illustrate the potential outcomes of mink farm closures (Fig. 6). In these simulations the model was run as before for 25 yr, and then the farms were shut down, i.e. no more mink escaped. The response of the mink population to farm closure was sensitive to the parameterisation of the model. In a first example closing farms resulted in a steady increase in the population's mean degree of adaptation (Fig. 6B). Initially in this case, there was a decrease in population abundance, but once adaptation progressed sufficiently, the trend was reversed and the population expanded so that ultimately it exceeded the original abundance. In a second example (Fig. 6D) closing farms resulted in a rapid decline in mink abundance despite a transient increase in the degree to which the population was adapted to the wild conditions.

The same pattern resulted from running the model with twice as many and half as many escapees per farm (not shown), although the mink in nature became well-adapted and numerous more rapidly when escapes were fewer but continuous throughout the 100 yr. The drop in mink numbers immediately following the closing down

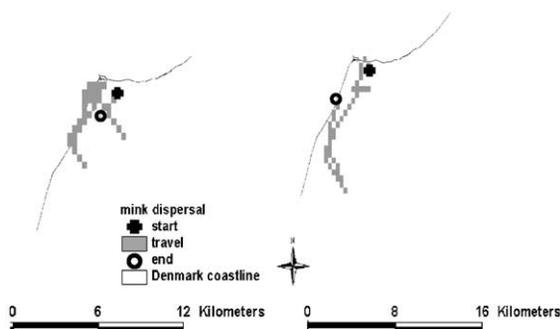


Fig. 2. Dispersal of mink from fur farms in northern Jutland, Denmark. Each figure represents the movements of one individual. Notice the different scales.

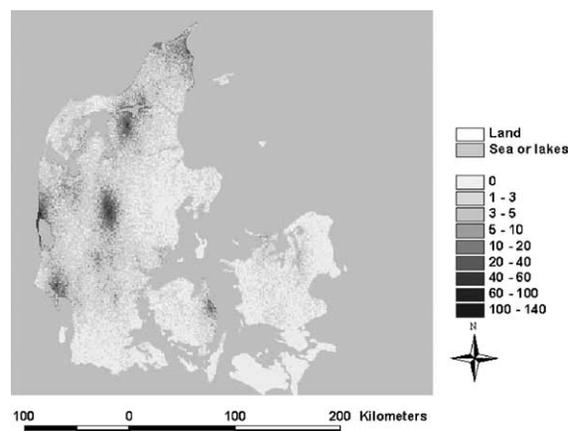


Fig. 3. Map of Denmark showing the number of dispersed mink per 1×1 km square resulting from running the model with no evolution for 50 yr. $N = 666\,000$.

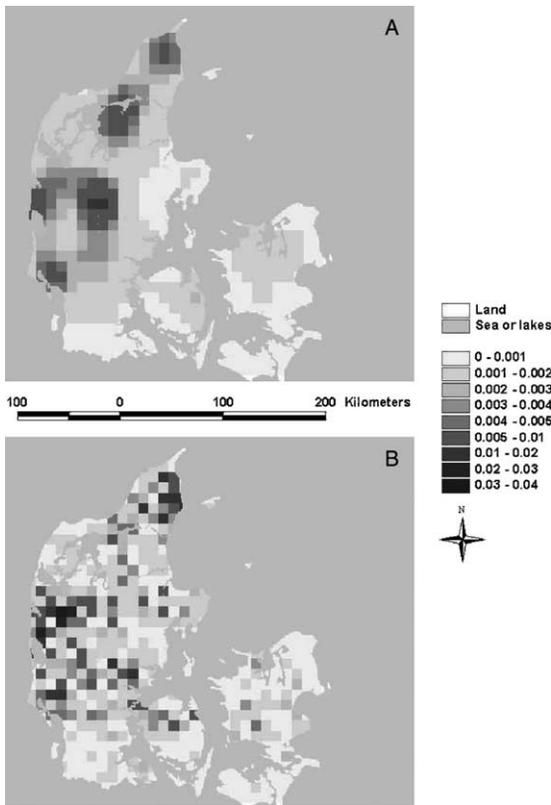


Fig. 4. Maps of Denmark showing A) the proportion of total dispersed mink, $N=666\,600$, and B) the proportion of total mink bagged by hunters, $N=31\,79$, in 10×10 km squares.

of farms was more pronounced with a higher escape rate, but the mean degree of adaptation remained the same in the 3 scenarios, and after ca 20 yr the curves showing numbers of mink were practically identical (not shown).

Complete closure of the farms resulted in mink numbers and mean degree of adaptation rising more quickly than when the escape rate was reduced in year 25 from 0.02 to 0.005 and 0.01, but each scenario resulted in quicker adaptation and population increase than without closing down farms (not shown). Increasing the escape rate in year 25 from 0.02 to 0.04 resulted in slower adaptation and population increase (not shown).

With continuing escapes, the degree of adaptation and the number of mink in nature increased as distance to areas with high concentrations of mink farms increased, a pattern that was especially obvious in year 90 (Fig. 7A). When we simulated farm closures, mink gradually became better adapted and population size increased through time, and by year 90 there were well-adapted mink all over the country (Fig. 7B).

In a similar run of the model with A_i set at 0.01, without closing farms, the pattern remained the same throughout the 100 yr (not shown), and the maps were nearly identical to the year 20 maps shown in Fig. 7. However, as time progressed beyond year 25 (when all the

farms are closed), numbers of mink in the wild declined, and by year 50 there were only small, scattered groups of mink remaining. By year 130, there were no mink left. The mink did become somewhat better adapted after farms were closed down, but the degree of adaptation remained relatively low and was unable to rise high enough for a feral population to move from being a sink (with negative growth rate) to a source (with positive growth rate).

Sensitivity to parameterisation

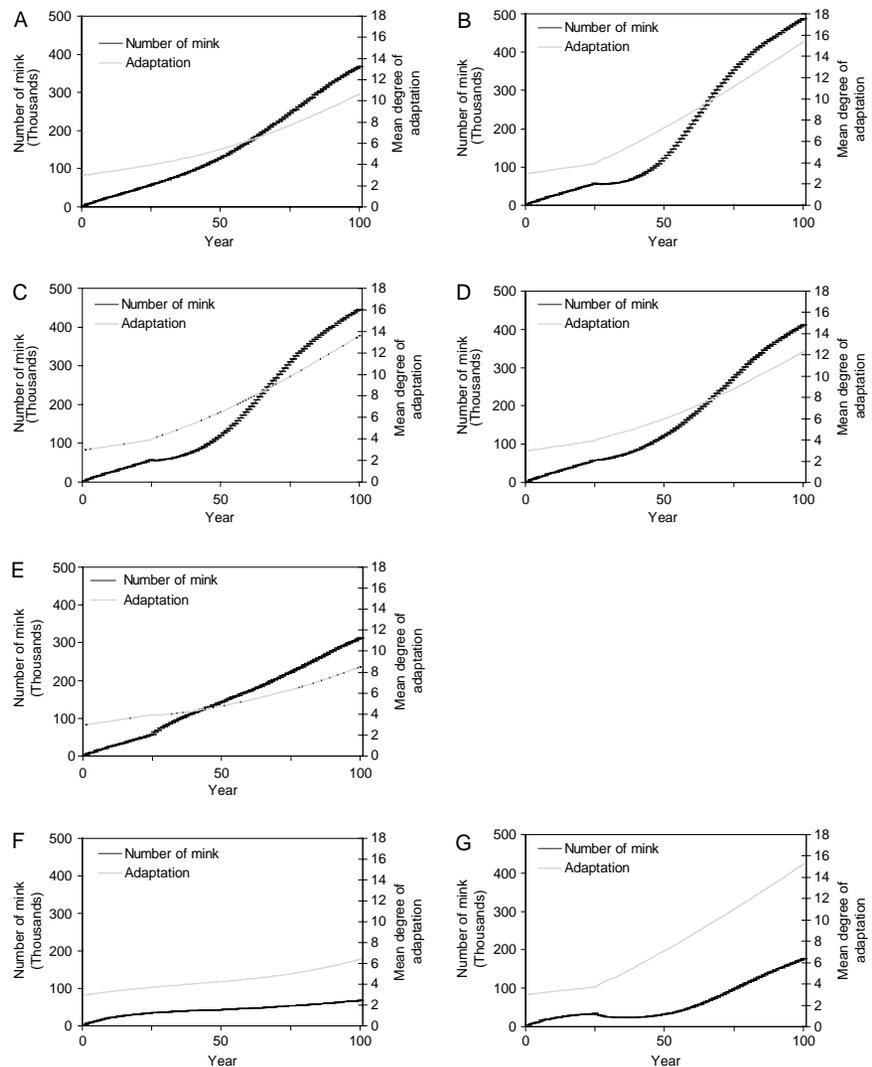
As we emphasised previously in the methods section, there was considerable uncertainty surrounding the parameterisation of several processes within the model, and it was important to establish how sensitive the results are to changing the values of these parameters. We varied 1) the number of loci that act to control the degree of adaptation to the wild conditions, 2) the proportion of mink escaping from the farms, 3) the maximum number of female mink that can breed within a grid cell, 4) the dispersal behaviour and 5) the mutation rate (results described above). Changing most of these altered the qualitative dynamics very little. However, the assumption regarding the number of loci involved in controlling fitness was key to the dynamics.

We looked at a range of loci between 5 and 200 (the default was set at 100 based on the opinions of two mammal geneticists). This parameter proved extremely important in determining both the population and the evolutionary dynamics. When far fewer loci were involved, adaptation was more rapid and population growth was accelerated. This result makes intuitive sense: fewer mutations and recombination events are required before substantially fitter individuals are present in the population.

We varied the maximum number of females that could breed in a grid cell between 1 and 4. Information from elsewhere (Gerell 1967, Helyar pers. comm.) suggests that it is highly unlikely that mink will breed at a higher density than 4 females per km^2 . The results were not unexpected: population abundance increased more rapidly when K was higher, and reached a higher final density. Also, adaptation to the wild conditions was enhanced somewhat by higher K , and this was because the strength of gene swamping from escapees was dampened by the higher abundance of mink in the wild.

We varied both the number of moves made by a mink during dispersal, and the spatial correlation among the moves. Unless the dispersal behaviour was altered substantially from the default values, the results changed very little. Only when dispersal distance was decreased substantially (either by reducing the number of steps, or making the step direction less spatially correlated) did we see a major difference. Then, we found that there was

Fig. 5. Number of mink in nature and mean degree of adaptation resulting from running the evolution model with different parameter values. All figures show means \pm SE from six runs with default values (cf. Table 2), unless otherwise stated. A) Without farm closures (NC), B) with farm closures, C) Escape2 = 0.005, D) Escape2 = 0.01, E) Escape2 = 0.04, F) $d = 1$ NC, G) $d = 1$, H) mutation = 0.0005 NC, I) mutation = 0.0005, J) mutation = 0.01 NC, K) mutation = 0.01, L) $A_i = 0.3$ NC, M) $A_i = 0.3$, N) $A_i = 0.1$ NC, and O) $A_i = 0.1$.

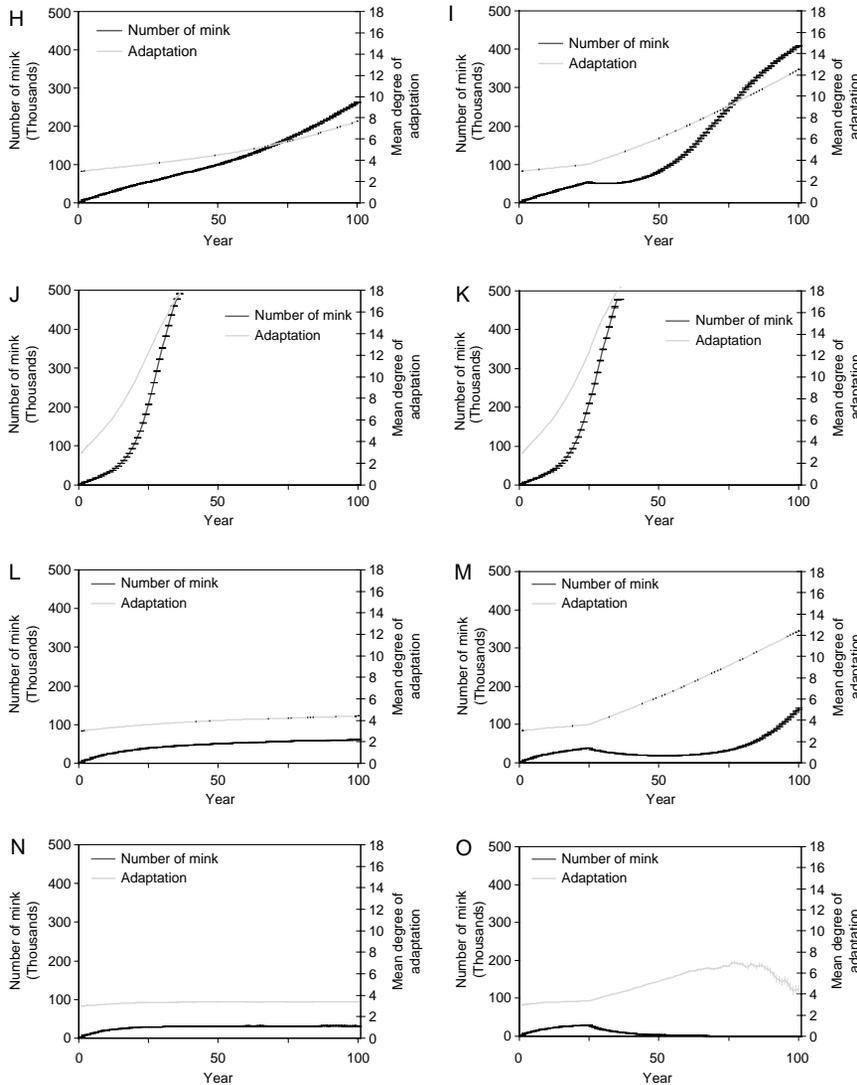


more opportunity for locally well-adapted wild mink populations to establish, as the effects of gene swamping from recent escapes was more limited in spatial scope. If dispersal distance was increased substantially (and well beyond what we believe to be realistic) then the effect was to spatially homogenise the population and local effects were nullified.

As we mentioned briefly above, we varied the rate of mink escape, and also considered the possibility that escaping mink are not exclusively juveniles. Changing the rate of escape is important as it determines the strength of gene swamping. The fewer the escapees the lower the strength of gene swamping and the more likely a well-adapted population is to establish. Interestingly, our sensitivity analyses indicated that this parameter acts in combination with the number of loci parameter in determining the rate of adaptation to wild conditions (and therefore determining the population abundance of mink in the wild).

Discussion

We developed a spatially explicit, individual-based model that simulated the population and evolutionary dynamics of mink in Denmark. To the best of our knowledge, this is one of the first times that a model incorporating evolutionary ecology has been developed for a real species in a real landscape (but see Heino and Hanski 2001). We first used the model to predict the current distribution of mink in Denmark, assuming no evolution, and parameterised the model with data collected in 2 regions of Denmark (Thy and Bornholm). We obtained reasonable correspondence between the model results and hunting data. When evolution was incorporated, the results of the model highlighted that the degree of adaptation within the free-ranging mink population is likely to vary spatially, with lower adaptation in areas where farm mink density was highest (due to the greater number of escaping mink). We have used



the model to explore the potential consequences of closing mink farms on the evolutionary ecology of the free-ranging population. We have found that depending upon the parameterisation of the evolutionary processes, anything is possible! Closing mink farms may result in a crash of the free-ranging population, or alternatively it may result in the establishment of a better-adapted wild population that may ultimately outnumber the population that was present before farm closures.

The no-evolution model

The model output on mink distribution was similar to the distribution of mink bagged by hunters. This gives us some confidence that the model is producing sensible results. Existing data do not allow a full model validation: similarities between the model output and the

hunting data would probably occur for any population incorporating local dispersal, and the hunting data are not of sufficient quality for us to determine whether our model performs better than other possible models. Discrepancies between the model results and the hunting data are not necessarily only a result of the model being wrong; the hunting data will give a biased picture of mink distribution, e.g. some areas could have especially eager hunters, hunters who found a “good spot”, or perhaps no hunters at all, and the data are not corrected for hunting effort. In addition, misreporting of catches on the map in Fig. 4B indicates that mink were caught in that grid square; the absence of a shaded square does not necessarily indicate the opposite, only that bags were not recorded. Future work, that attempted to correct these hunting data for effort would be valuable for providing data that might be used for model validation purposes.

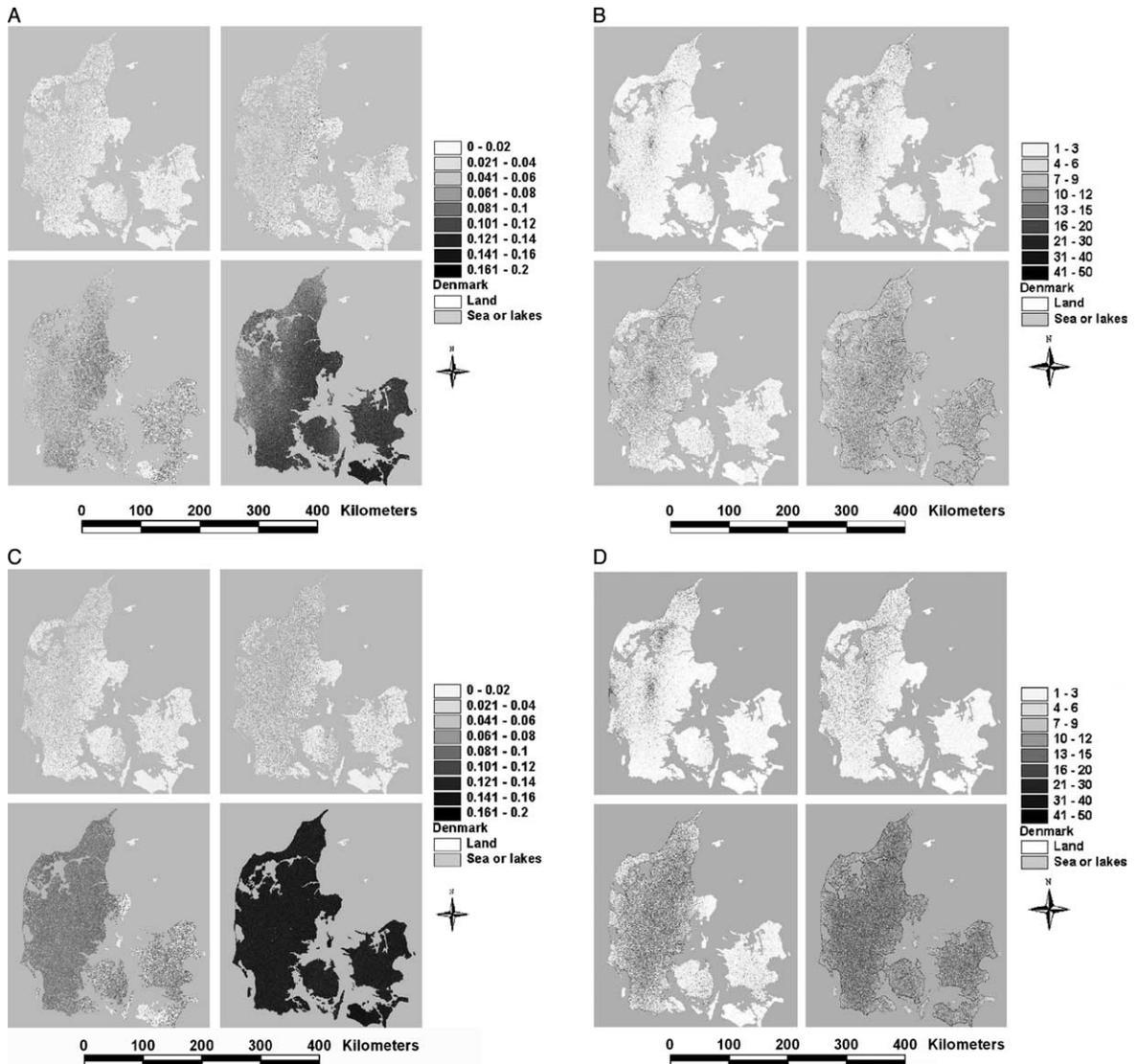


Fig. 6. Spatial distribution of mean degree of adaptation (A and C) and number of dispersed mink (B and D) in 1×1 km squares. One run for 100 yr of the model with continuous escapes from farms (A and B), and one run where farms are closed down in year 25 (C and D). Each four-map block represents "snap shots" from year 20 (top left), 30 (top right), 50 (lower left), and 90 (lower right). $a = 0.03$, $A_i = 0.5$, Mutation = 0.001, and $d = 2$.

Having suggested why the hunting data may not provide a particularly accurate picture of relative mink densities across Denmark, it is only fair that we should point out why the model may also fail to provide an accurate prediction. Predictions of models are only as good as the estimated parameter values (Myers et al. 2000), and some of our parameters (particularly dispersal, the genetic system and density dependence) were based on best guesses. We have compared the predictions made by the model parameterised by data collected from a relatively small region of Denmark. It is quite plausible that survivorship could be quite different in other regions. Furthermore, we have simplified the biology:

we have not incorporated interactions with potential competitors and have simplified the landscape.

Macdonald and Rushton (2003) modelled space use and dispersal of 4 mammal species, including mink, in real landscapes in Britain. In their model, adult mortality of mink and their home-range size were the only significant partial correlates of the total population size in the landscape. Dispersal distance was not a significant factor in determining persistence in the landscape (Macdonald and Rushton 2003). In our study, we used data on mortality from Danish free-ranging mink (Hammershøj 2004), and did not vary the mortality rates between runs. We included an indirect

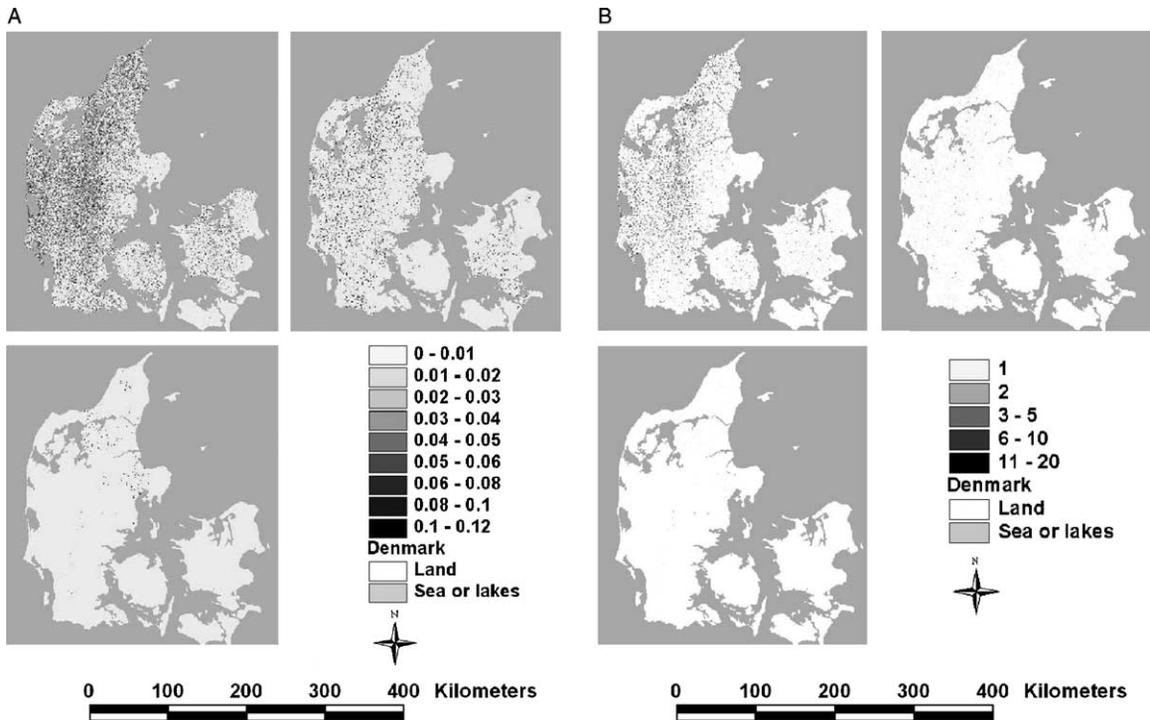


Fig. 7. As Fig. 6, but with $A_i = 0.1$. Only maps from running the model with farms closing are shown, year 30 (top left), year 50 (top right), and year 90 (lower left). A) Mean degree of adaptation, and B) number of dispersed mink.

measure of home-range size in our model, i.e. the number of females breeding in each grid cell, b . The effect of varying b was substantial, and obtaining more accurate knowledge on mink home-range sizes in Denmark would be of great use in improving the model. Future model development could also incorporate spatial variability in habitat quality, which might lead to both a reduction in b and potentially to a reduction in the mean litter size. Unfortunately, we do not currently have the data that would allow us to vary habitat suitability according to habitat type, and we certainly do not know how the different population parameters (e.g. reproduction, dispersal, mortality) vary across different habitat types.

Dispersal of mink in the model was limited by water bodies, which were believed to act as barriers to mink movements. Elsewhere dispersal was assumed to be equally possible. We believe that this is a fair simplification of the landscape, since most 1 km^2 grid cells in Denmark include suitable habitat for mink. Other model studies have assumed that mink disperse through all habitats (Macdonald and Rushton 2003). If and when more data becomes available on the behaviour of mink in different habitat types, this detail could readily be incorporated into the general model framework developed, and potential consequences of habitat specific dispersal behaviour could be established.

The model including evolution

The predictions of this model were similar to those from our theoretical model (Travis et al. 2005). Within most tested parameter ranges, limiting or completely stopping escapes from farms resulted in mink in the wild becoming better adapted to natural conditions and thus, reach higher population sizes, quicker than if escapes were to occur at the same rate. However, when the relative influence on survival of beneficial alleles, A_i , was set at 0.1, this was not the case. With this parameter value, adaptation never reached high enough values for the wild population to persist, and the population went extinct before year 130. This highlights the importance of establishing what the fitness benefits are to mink of acquiring a single beneficial allele. At present, no studies have been made on fitness estimates in the wild and it may take a few years before techniques are adequately advanced to study this complex field. The model results suggest that if the fitness benefit is relatively low, reducing escapes from farms is likely to reduce the population in the wild, while if the benefit is relatively large, closing farms may not have the desired effect.

For mammals in general, mutation rates are in the range of 10^{-4} – 10^{-3} for neutral alleles and of 10^{-2} for non-neutral alleles (Pertoldi pers. comm.). These ranges resulted in very different outcomes in our model. With a mutation rate of 10^{-2} , the mean degree of adaptation and the number of mink in nature increased very rapidly

within the first 25–30 yr, and closing down farms only added slightly to the rate. The default values of A_i and a were “educated guesses”, and since the model showed very different outcomes when varying these parameters, obtaining more exact knowledge about these parameters would allow us to more accurately predict the effect of closing down farms. Nevertheless, for all ranges of mutation rates used in the model, closing down farms always resulted in quicker adaptation and higher population sizes relative to allowing escapes to continue. The same holds true for all tested ranges of probabilities that an allele is well-adapted in escaping mink, a , and most tested ranges of the relative influence on fitness of beneficial alleles, A_i , except in one case as discussed above.

Thus, the results from our model do not really support the hypothesis that fur farms today act as sources and areas away from farms as sinks (cf. Wiens 1990). Quite the opposite can be the case, in that continuous escapes from fur farms may actually keep mink in nature at a genetically less well-adapted stage and thus, at lower population sizes, than would be the case if there were no further escapes from fur farms.

Interestingly, flooding populations with maladaptive genes has been suggested as a control strategy that could be employed to alter population genetic structure and reduce adaptive variation (Sakai et al. 2001). The results obtained from our model suggest that this may in fact, unknowingly, have been practised in Denmark since the mink first arrived there in the early 1930s. The current and historic density of mink farms in Denmark is higher than found elsewhere. Whereas in, e.g. Norway, Sweden, and Finland, mink have become naturalised, evidence suggests they have not done so in Denmark (Stubbe 1993, Hammershøj et al. 2005). While this may be a result of differences in the environmental conditions, especially landscape structure, between Denmark and the other countries, it may also be a result of the higher density at which mink are farmed, and the greater number of escapes that result.

Ideally, at this point, we would have liked to consider what the implications of the results are for management of mink in Denmark. However, given that the model predictions differ so much depending upon the parameterisation, we feel that to do so would be premature. We hope that this model will serve to highlight the additional complexity that evolutionary processes can add to the biology of an introduced species, and that the results will motivate future field-based studies that will seek to reduce the uncertainty associated with those parameters about which we have the least information.

Here, we have developed a sophisticated model to explore the evolutionary ecology of introduced mink in Denmark. The same model framework could be used to make predictions for many other introduced and invasive species, both animal and plant. The results

that we have obtained in this model for mink conform to those in a more theoretical study (Travis et al. 2005) in suggesting that understanding the genetics of the species, the degree to which the introduced population is maladapted to wild conditions, and in particular knowing how much fitness benefit is gained by possessing well-adapted alleles, is critical if accurate predictions are to be made regarding the population dynamics of a species when the rate of introductions is altered.

There is a growing recognition that evolution can occur on a time-scale that is important for ecological processes (Stockwell et al. 2003, Phillips and Shine 2004, Maron et al. 2004). Here we have attempted to construct a model to assess the potential importance of evolutionary ecology in determining the invasion dynamics of the American mink in Denmark. We are able to conclude that contemporary evolution may be extremely important in determining the outcome. However, the outcome of the evolutionary population dynamics is heavily dependent upon the values of several key parameters about which we have the least empirical information. This is indicative of the problem likely to be faced as we attempt to apply evolutionary theory to conservation biology; as the complexity of the models increases they become ever more data hungry. The greatest challenge in applying evolutionary theory to the management of populations will lie in obtaining data of sufficient quality that we can be confident in model predictions.

Acknowledgements – We would like to thank Sander Jacobsen, Jørgen Østergaard and Anne Bertelsen from the Danish Fur Breeders Association, Copenhagen Fur Center for providing data on fur farms in Denmark, and Poul Nygaard Andersen at the National Environmental Research Inst. for helping prepare the GIS data. We are also very grateful to Peter Heinrich for his assistance in running the model scenarios, and to Liselotte W. Andersen and Cino Pertoldi for some valuable comments on genetics.

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Subject Editor: Douglas Kelt.