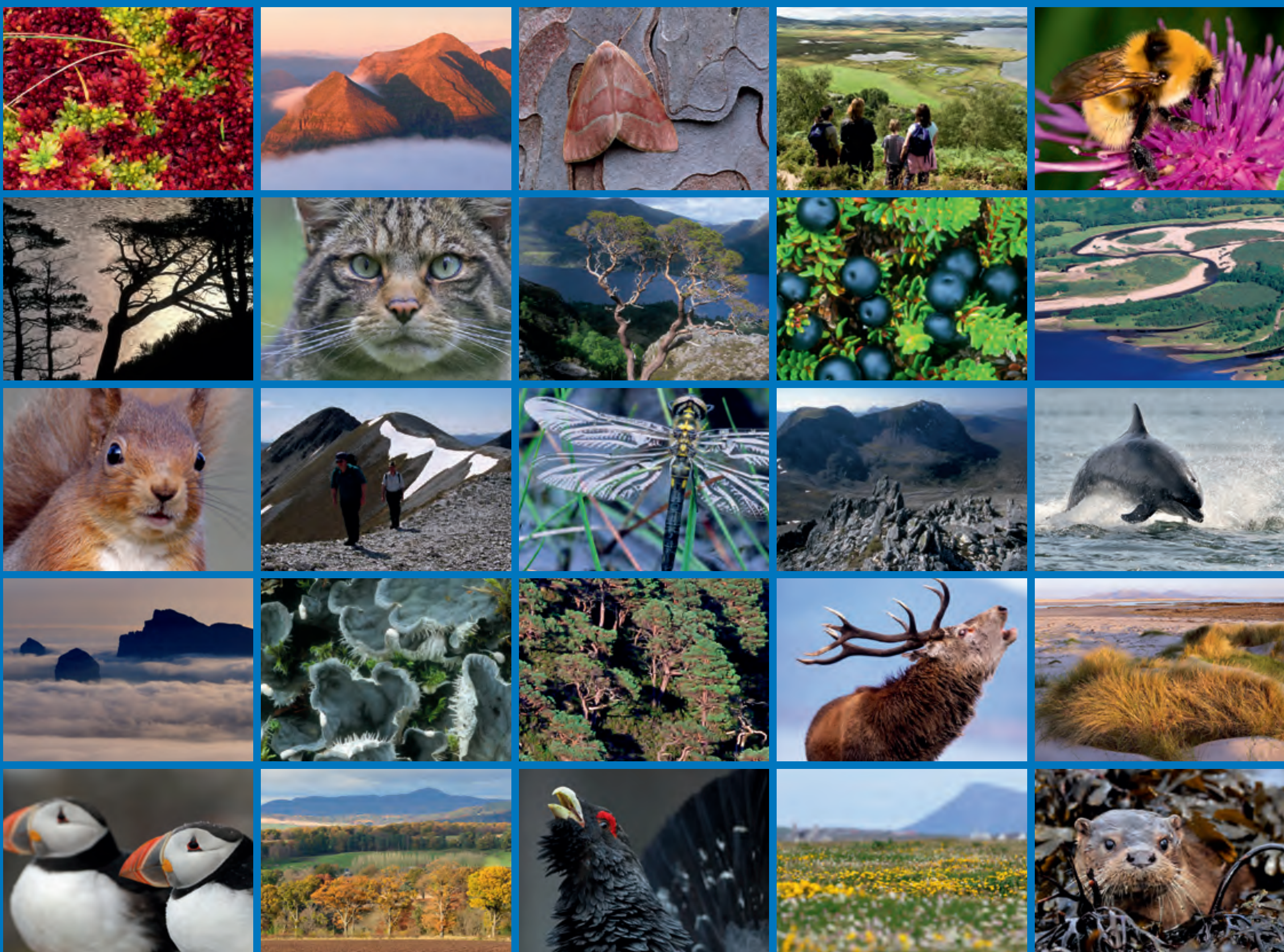
Scottish Natural Heritage
Commissioned Report No. 522

# Analysis and future application of Hebridean Mink Project data



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# COMMISSIONED REPORT

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# Analysis and future application of Hebridean Mink Project data


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COMMISSIONED REPORT

# Summary

## Analysis and future application of Hebridean Mink Project data

**Commissioned Report No. 522**
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### Background

SNH's Hebridean Mink Project (HMP) uses intensive and systematic trapping by professional trappers to achieve eradication of American mink (*Neovison vison*) in the Western Isles. Phase 2 of the project started in 2007 and is scheduled to end in March 2014. It implements a standardised trapping regime over multiple years, so a large data set has been assembled which can be used to inform management decisions in the HMP area as well as in other areas where mink eradication is envisaged. Statistical analyses of these data to date have been limited.

The aim of the present project was to optimise the amount that can be learned from the HMP by providing a scientific analysis of what has happened to the population of mink in the Outer Hebrides during the project. It also aimed to examine how the findings can be applied more widely and in future mink control schemes elsewhere in areas where similar habitats are occupied by mink.

### Main findings

- A hierarchical statistical model based on capture histories of mink caught in four habitat compartments over three seasons fitted to the HMP data yielded credible estimates of the number of individuals that escaped capture and of demographic parameters of the culled mink population.
- In the model, mink that escape capture in the fraction of a given habitat trapped during a given season, as well as those mink in the non-trapped portion of that habitat compartment, contribute to the population in the next season. These mink may survive, reproduce and/or move between compartments.
- The daily probability that a mink in the vicinity of open traps was caught varies between 0.15 and 0.30, increasing over the study years. A probability of capture of 0.3 implies that about 24% of females present in an area escape trapping after 4 days. There was no evidence of evolving trap-shyness under selection imposed by trapping.
- It is estimated that there is a mean of 0.33 independent female offspring per adult female and almost no mortality due to causes other than trapping.
- There are very high movement rates between habitats by individuals or their offspring, especially during the summer to winter transition. A high proportion of these individuals were found to move into the large mountain and moorland compartment which was treated as a single habitat type in this report
- We estimated there were 350 females in SPRING 2008. Our last reliable estimate is that 61 females bred in 2011 across the whole of HMP area. The number of breeding females was estimated to have been reduced by approximately 80% in 4 years. The rate of

decline of the mink population in each habitat was roughly constant from 2009-2010, but slowed down in 2011 relative to previous years.

- The statistical model, which fully accounts for all sources of uncertainty, yields a wide range of predictions on the dynamics of the Lewis and Harris mink population beyond 2011. The possibilities that the population recovered in late 2012 or is nearly extinct are both consistent with the data at hand.
- A model initialised with mink population size from SPRING 2011 and ignoring the uncertainty around demographic rates, was used to simulate the likely outcomes if systematic (as opposed to reactive) trapping had continued beyond 2011. This yields a distribution of likely times to extinction with the earliest extinctions occurring in 2014 and the latest in 2021. The most common outcomes are the Lewis and Harris mink population would have gone extinct in 2015 or 2016. In 80% of simulations mink had gone extinct by 2017. Those dates could be brought forward if the current trapping regime was more effective, but no data were available to explore whether this is the case.
- The key features that affected success are the combination of high mink mobility, the fact that not all mink are caught in a trapping session and, crucially, the fact that only a fraction of a habitat compartment could feasibly be trapped in a season.
- Thus scenarios involving redeployment of trapping effort to maximise the proportion of habitat trapped in two seasons, shorter trapping sessions, no trapping in one season, and reduced trapping in the habitat with highest emigration rate hasten extinction.
- Modelling approaches similar to those used here could be applied to data with a different structure but this would require substantial further model development.

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## 1. INTRODUCTION

Systematic persecution sustained over many years has had an enormous impact on native carnivore species in Europe and beyond. The wolf (*Canis lupus*), lynx (*Lynx lynx)* and bear (*Ursus arctos*) have been driven to extinction in much of Europe, including the whole of Britain (Yalden, 1999). Populations of smaller carnivores, including the wild cat (*Felis silvestris*), the pine marten (*Martes martes*) and polecats (*Mustela putorius*) have also been decimated as a direct result of persecution by game-keepers, although complete extinction across Britain was averted by the inception of World War I (Langley & Yalden, 1977). In Scotland, the polecat disappeared from its last refuges in the north but the pine marten survived persecution in remnant populations in Inverness-shire, Ross and Cromarty and Sutherland, and the wildcat was reduced to these counties and Caithness (Langley & Yalden, 1977). Pine martens are now recovering in Scotland following protection (Balharry *et al.,* 2008). The above demonstrates that, while ruthless persecution of small carnivores may lead to extreme rarity and much reduced range, it does not always lead to extinction. Recent recoveries of previously much depleted carnivore populations demonstrate the potential for substantial bounce-back and spatial spread of such species after cessation of lethal control (Grenier *et al.,* 2007).

Small carnivores, including mustelids, cats and mongooses have been introduced to many locations worldwide where they often severely impact native fauna. Eradication of invasive non-native vertebrates is increasingly achieved on oceanic islands through the use of toxins that can be spread aerially (Cromarty *et al.,* 2002, Parkes *et al.,* 2006). Poison-based eradication programmes of carnivores are deemed not feasible in Europe because of higher human density and perceived acceptability by the public (Genovesi, 2005). Management of vertebrate non-native species in Europe is therefore undertaken using techniques such as live trapping, sometimes assisted with devices that facilitate the detection of individuals at low density (Reynolds *et al.,* 2004, Porteus *et al.,* 2012, Gosling & Baker, 1989). The management objective is eradication on islands without immigration (Macdonald & Harrington, 2003) and, elsewhere, control to levels where native prey are not severely affected.

Variation within mustelid populations in their propensity to explore and enter traps is considered to be a substantial impediment to achieving eradication through live trapping followed by euthanasia (Craik, 2008; Harrington *et al.,* 2008; King *et al.,* 2009). Based on a telemetry study, King *et al.*(2009) argued that inefficiency in the trapping of wide-ranging mustelids such as ferrets (*Mustela furo*), stoats (*Mustela erminea*) and American mink (*Neovison vison*) is probably commonplace. This may arise if traps are too thinly spaced such that not all individuals readily encounter a trap or if some shy individuals actively avoid or refuse to enter traps or to take bait. Furthermore, if avoidance of novel objects and associated trap shyness have a sufficient heritable basis, trapped populations can be expected to be under strong selection favouring ever increasing trap shyness, further precluding eradication. Though plausible and often raised as an obstacle to eradication, we know of no evidence of such evolutionary processes affecting pest animal control efforts.

Because of the increased search time, as well as the need to vary detection techniques and the diminishing return per trapping effort, the per capita cost of removing the last animals toward the end of some eradication campaigns commonly escalates. For example, the majority of the 79,569 goats removed from Pinta island in the Galapagos cost between US$10–100 per goat to remove. In contrast, the cost of removing the final goats was over $10,000 each (Carrion *et al.,* 2011). It is important to keep in mind that the time a declining population takes to reach extinction has a random component to it. This is because many demographic processes (birth, death, sex ratio) have a chance component as has the control process of, for example entering traps. Thus wildlife managers and funders must bear in mind that predictions on potential dates to eradication should encompass a range of possible values rather than a single set date. The contribution of processes operating in very low density populations, such as the failure to find a mate, are poorly understood and make prediction even more difficult. Embarking upon eradication thus requires a sustained commitment to the objectives by stakeholders and funders.

The American mink is a mustelid species that escaped or was released from fur farms in a wide range of locations outside its native range. Numerous studies have revealed their impacts on native wildlife and the species is the target of numerous control programmes with stated goals ranging from containment, to control, to eradication in much of Europe (reviewed in Bonesi & Palazon (2007)). In Scotland, mink invasion has proceeded for more than 50 years with only the northernmost fringes of the mainland as yet unaffected (Fraser *et al.,* 2013). This invasive species is one of four mustelid species established outside its natural range in Scotland. Feral ferrets are widespread and stoats have recently been reported from the Orkney Islands where they are likely to threaten the endemic (but non-native) Orkney voles (*Microtus arvalis orcadensis*) as well as ground nesting birds (Macneil, 2010). Pine martens are known to have bred recently on Mull, an island where there is no historic evidence of their presence (Roy *et al.,* 2013).

SNH's strategic approach to mink management currently focuses on two approaches. These are the Hebridean Mink Project (HMP) which uses intensive and systematic trapping by a team of professional trappers to achieve eradication in the Western Isles (Moore *et al.,* 2003; Roy *et al.,* 2009), and the Scottish Mink Initiative (SMI) using a network of mink rafts, operated largely by volunteers, to effect a landscape-scale population reduction leading to eventual extinction (Bryce *et al.,* 2011). The use of unpaid volunteers to monitor rafts and then set traps only following detection of mink presence has given the SMI the potential to achieve substantial reductions in mink abundance with lower resource inputs than a professional-based system relying on salaried trappers. There is, however, as yet no evidence that it could be sufficiently effective to facilitate eradication in the face of immigration from the periphery of the controlled area. The HMP approach has been developed to deal with initially perceived very high mink densities in island habitats of the Outer Hebrides. It is capital-intensive and resource-intensive, owing to the deployment of large numbers of traps and the employment of salaried trappers. The HMP approach has achieved quality-assured levels of control and follows a specific control design that can be modified by decisions of the Project Manager.

A benefit of the volunteer approach is that information on the residual distribution and abundance of mink, including the extent of re-colonisation of previously cleared areas, is potentially obtained through the repeat checking of rafts for the presence of mink footprints. The challenge is to maintain a comprehensive spatial coverage of rafts in the face of low mink incidence and potential loss of motivation by volunteers. The professional trapper approach does not suffer from this challenge: trapping effort is quantified but capture per unit of effort, especially at low density, only provides limited information on the size and distribution of the remaining mink populations.

Given the scale of the conservation problem caused by American mink, and limited resources, SNH identified a need to develop an appropriate strategy for Scotland which does not rely on resource-demanding systematic, intensive trapping. Because it implements a standardized trapping regime over multiple years, HMP has collated a large trapping dataset which has been used throughout the project to help inform management decisions and to provide an indication of the likely time to extinction under various management scenarios.

Statistical analyses of these data have been limited. They included linear extrapolations of the rate of decline in mink capture, predicting the likely time to extinction in July 2011 (Shirley & Rushton, 2011 unpublished), as well as a more substantial simulation modelling exercise inspired by the data. In order to assess the population of American mink within

Lewis and Harris, Newcastle University produced a model of the population and the impact of the project's trapping effort on this population (Shirley & Rushton, 2011 unpublished). The model was an individual-based simulation with movement, habitat selection, mating and dispersal rules as well as demographic parameter estimates taken from the literature. The model was detail-rich and used to investigate the predicted effect of a spatially and temporally explicit representation of HMP control efforts. The model predicted that more than 500 mink would be present at the end of March 2011, when the project's first tranche of funding was due to come to an end. This was at least a factor or two above what was generally believed by all project staff. A separate paper produced by the HMP management team reported that 'despite considerable efforts during the iterative process of finalising the model, the modellers and the project staff have found it difficult to make use of existing parameter data that provides a population structure that properly mimics the real population without losing objectivity within the **model'**. A key issue was how to treat the 'boggy moorland' habitat compartment that the HMP team considers harbours only transient mink, while the Newcastle team considered that it could not be ignored without strong evidence. This illustrated well the issue that, as is often the case with detail rich models (Ginzburg & Jensen, 2004), predictions were strongly dependent upon assumptions on parameters and initial values of population size that were not estimated from the data but gleaned from peer reviewed published studies.

Two years after this attempt to synthesise the evidence on the effectiveness of HMP in driving mink towards extinction, the present project aimed to optimise the amount that can be learned from the trapping data. It aimed to achieve this by providing a scientific analysis of what has happened to the population of mink in the Outer Hebrides during the project. It also aimed to examine how the findings can be applied more widely and in future mink control schemes elsewhere in areas where similar habitats are occupied by mink.

## 2. OBJECTIVES

The objectives of this project are, through appropriate analyses of HMP trapping data, to:

1) Describe the decline in the Outer Hebrides mink population in a robust statistical manner;

2) Subject to fluxes being estimable from the available data, analyse the contributions of the control features, such as the way traps were operated which contributed most to this decline;

3) Identify components of the control strategy which contributed very little to the decline;

4) Identify the habitats that, owing to different demographic rates, or low or ill-timed trapping effort, have created the greatest challenges for the control programme;

5) Identify any seasonal variation in the above which could guide project resource use;

6) Provide quantitative parameter estimates and an understanding of mink population growth rates in relation to habitat quality, fluxes between habitats and trappability that will be useful for the modelling/design of future control work elsewhere

Further requirements were that the report should:

a) Examine the evidence concerning the progress of the HMP, including the likelihood of achieving its goals when it ends in March 2014. This is vital in order to demonstrate that the decision-making associated with the substantial project expenditure was justified. If the HMP does not meet its target, the model will provide a rigorous analysis of the course of the decline in mink numbers.

b) Specify the data requirements for future projects to enable the modelling tool to be applied as necessary. Examples of the data formats required should also be specified for running analyses.

## 3. METHODS

The Hebridean Mink Project started in 2001 with the aim of ‘eradicating mink from North Uist and Benbecula whilst reducing the population in South Harris creating a buffer zone against re-immigration’. The subsequent discovery of mink in South Uist required extension of the spatial extent of the project after funding had been secured. The first phase of the project finished in June 2006 and the Uist mink population at that time was deemed to be ‘effectively eradicated’. There was then a gap in funding during which two staff were employed to maintain a buffer zone in South Harris until the start of Phase II with the aim of eradicating mink from Lewis and Harris. From February 2007 until May 2008, the project twice trapped the mountains and moorland of South Harris, an area that had been nearly completely depleted of mink previously but was being re-colonised from the mink-saturated north of the HMP area. Over that period, HMP gradually increased the buffer zone, trapping from the south of South Harris to the top of North Harris. By 2008, it had put in place a systematic and comprehensive trap structure with 8,741 traps permanently placed at approximately 350 m spacing in areas deemed suitable for mink by HMP staff (Figure 1). Since then, twice-yearly systematic trapping sweeps broadly progressing from south to north continued until the present, except for 2011 when the sequence was reversed, with trapping moving from north to south. Funding was extended in 2011 to March 2014.

Trapping of some areas requires boats and suitable climatic conditions which may result in some areas that had been inaccessible being trapped out of sequence. In winter 2008, systematic trapping targeted the islands of Loch Roag in west Lewis for the first time, an area classified as moorland and perceived by HMP staff as probably the best mink habitat on the island. Similarly, South Eishken to the south east of Lewis, was trapped in summer 2011 after weather-related delays. This contributed to 30 females being caught in moorland in that season.

### 3.1 Structure of the data set

Mink trapping on Lewis and Harris is organised in roughly 100 $km^2$ trap zones, each with a heterogeneous habitat composition. Traps are set in trap lines approximately 350 m apart operated by a single member of staff. These are opened for capture for four days at a time, approximately twice per year.

Rather than analysing trap lines or zones separately, we considered all traps that were found in the same habitat and the capture histories of all mink caught in the same habitat. Given that mink are not released upon capture, capture histories for four day long trapping sessions are simply: 1000, 0100, 0010, or 0001 to represent those mink caught on the first, second, third or fourth day of trapping respectively, and having escaped capture for 0, 1, 2 or 3 days respectively. To ensure a large enough sample size to estimate probability of capture and demographic rates, the analyses required that different trapping rounds/lines be pooled by habitat type and season. All assignment of traps to a habitat category was done at the outset of the project. Two of the six habitat categories used, ‘Cliff’ and ‘Machair’ had already been combined from various sub-habitats. We further simplified this, in consultation with HMP, to four categories (Figure 2), namely CROFTING, boggy moorland (BOG hereafter) and a composite category COASTAL POOR that includes ‘Cliff’ and ‘Machair’, two of the least suitable habitats for mink. A final category MOORLAND includes traps in 'Mountain' and 'Moorland' habitats, as the distinction is fairly subjective and very few traps or captures were at any significant altitude (Iain Macleod, pers. com.).

We assumed that the traps were distributed in all suitable mink habitat and use the classification of each trap provided at the outset. All analyses are thus based on the proportion of each traps in a given habitat that are operated in a given time interval. Thus while the proportion of traps between habitats is 13% CROFTING, 30% BOG, 44% MOORLAND and 13% COASTAL POOR, this does not precisely reflect the relative representations of these habitat types on the islands but rather the representation of habitat deemed worthy of trapping by HMP staff. Deviations are most extreme for the MOORLAND habitat (a combination of moorland and mountain habitats) where trap density is visibly lower than in other habitat compartments (Figure 1).

We focused on the capture histories of all mink caught during one of three seasons we specified based on the key stages in the mink's life history. They are: WINTER (15 September – 15 February), when we assume independent juveniles enter the trappable population and most dispersal between habitat compartments takes place, SPRING (16 February - 7 June) including the period of female territory establishment and the rut, and SUMMER when reproduction takes place and when females remain in their territories with dependent young and some early post weaning dispersal takes place (8 June - 15 September). These seasons were the shortest time intervals over which we could reasonably expect to be able to estimate parameters.

Having pooled all trapping events in a given habitat compartment in a given season, we obtained mink abundance estimates in the fraction of a given habitat compartment trapped in a given session. By extrapolating information from those traps in a habitat compartment operated in a season to all traps in the same habitat compartment, including those not trapped in that season, we then estimated the size of the mink population in that habitat compartment on the whole island. Summing over the four compartments then yielded the mink population size for the whole of Lewis and Harris. These calculations are based on the assumptions of equal mink density within a habitat compartment and random trapping in relation to mink density. We discuss the plausibility of these below.

Data from 2007 are problematic in several respects (below), which may reflect the fact that trapping took place only in the south of the area at this time and that captures must have included a large proportion of dispersing colonists, as the area had been fully cleared of mink previously. We explore below a model that treats data from this year separately in analyses. The HMP team abandoned systematic 'blind' trapping from October - November 2011 and adopted a procedure that involved attempting to detect mink and setting traps reactively in areas with known mink presence. The structure of these data is fundamentally different from the remainder and they are also treated differently in our analyses.

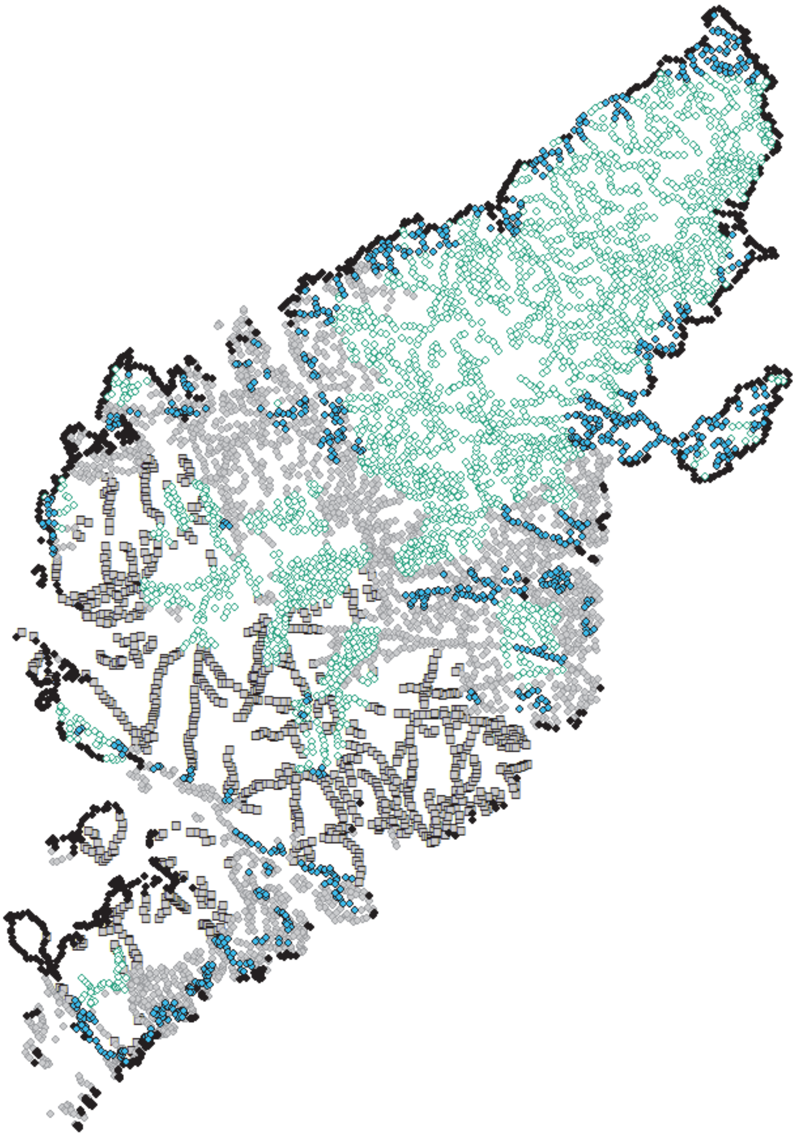

*Figure 1: Map showing the location of all traps operated by HMP with the colour of each circle showing the habitat type assigned to the traps prior to the project start. Key: Boggy moorland (BOG): green dotted; CROFTING: blue; MOORLAND: grey diamonds; MOUNTAINS: grey squares, Cliff and Machair: (COASTAL POOR): black. (© Crown copyright 2013. All rights reserved. Scottish Natural Heritage. 100017908 (2013))*

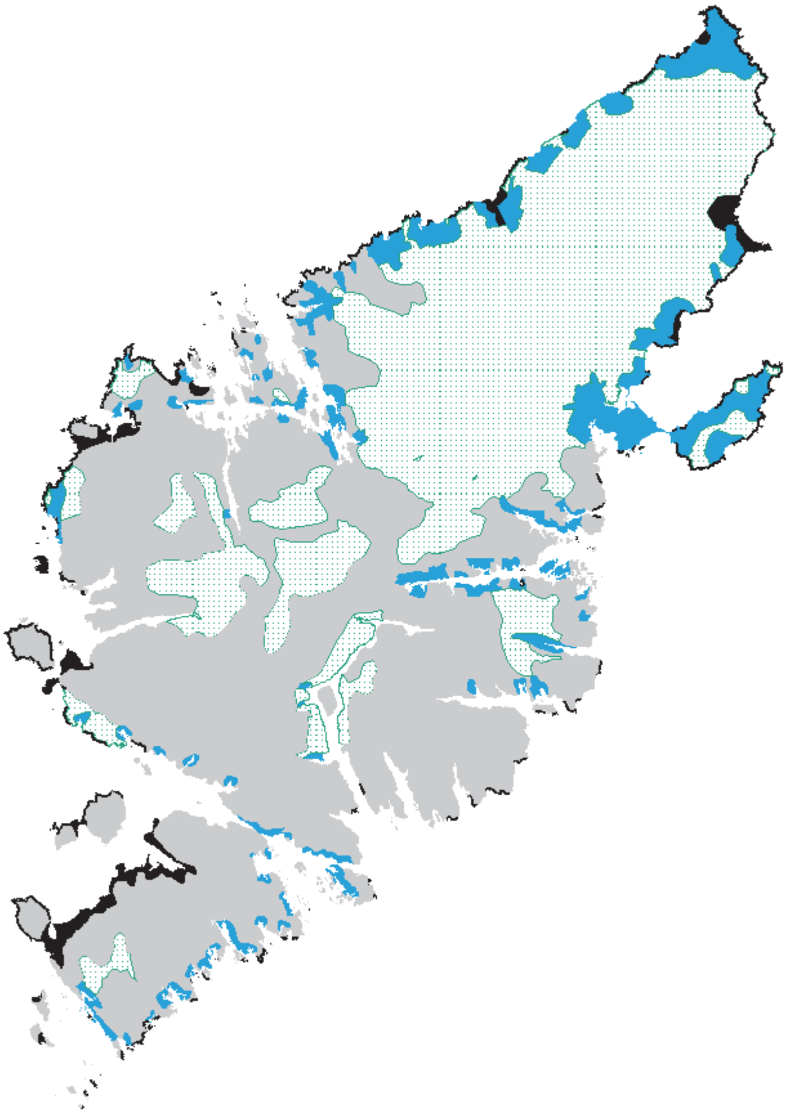

*Figure 2: Map showing the pooled habitat categories. Key: Boggy moorland (BOG): green dotted; CROFTING: blue; MOORLAND: grey; COASTAL POOR: Black(© Crown copyright 2013. All rights reserved. Scottish Natural Heritage. 100017908 (2013))*

## 3.2 Formulating a state-space model fitted to the HMP trapping data

The data were fitted to Bayesian hierarchical models that have both an observation and a population dynamics component. The observation component relates the observations (number of mink caught) to reality (number of mink present) and the population dynamics component links population size in successive time periods by demographic rates (birth, death and movement). In the model, mink that escape capture in the fraction of a given habitat trapped during a given season, as well as those in the non-trapped portion of that habitat compartment, contribute to the population in the next seasons. These mink may survive, reproduce and/or move between compartments.

### *3.2.1 Observation model*

The observation component of the model follows the structure of closed population capture-recapture models using existing trapping data, whereby the sampling process generating observations on the size of the population is explicitly modelled. The description below gives a brief description of our approach which is slightly modified from that given in Forsyth *et al.*, (2003). (The computer code with comments explaining each step of our statistical analyses is available from SNH on request). We extended previous work estimating population size based on constant sampling effort with removal of individuals (Zippin, 1956, 1958). Our model estimated the number of mink in each (sampled portion of) habitat and the probability of an individual mink being captured as a function of the number of mink caught in each consecutive night. The number of mink escaping capture is a multinomial function of capture probability (p) and actual population size over the first four nights. The capture probability per day of trapping can be estimated from the number of mink caught after one, two, three, and four days and from this the number of mink that escaped capture after four days can be estimated.

Our model was a modification of a model by Royle & Dorazio (2006) to allow capture probability to vary with many other covariates as in standard regression modelling. For the effect of habitat, year, season and sex, we considered models in which p varied with year and season (or habitat), but differently for the two sexes. Since the sex-ratio of mink populations – including that of the Outer Hebrides – is roughly balanced, estimates of female population sizes are usually sufficient to model the population dynamics. This is because in species for which males can mate with several females and do not provide paternal care such as mink, females are the limiting sex to population growth, provided all females encounter a mate. However, if males and females have the same trappability, including the male data in the observation model increases the power of the analysis and, ultimately, the precision of the female population size estimates.

The number of trapping days was variable, with 73% four-day sessions, 26% of sessions under four days and 1% over four days (Figure 3). Rather than adding complexity to the model, we made the pragmatic simplifying assumption that all sessions lasted four days, by adding the missing number of days with no captures for the shorter ones and by truncating the longer ones after four days. This is expected to slightly under-estimate the probability of capture per day. Initial attempts to use the data augmentation approach, described in Royle & Dorazio (2008), did not succeed when applied to data where no recaptures occurred over four consecutive days, as is the case in removal trapping.

Capture probability is the probability (i.e. a value between 0 and 1) of an individual mink present being trapped per night. Variation in capture probability may be dependent on a variety of factors, including behavioural aversion to entering traps, hormonal state, home range size, and the positioning of traps in relation to areas of activity. The models assume that there is a finite population around the set of open traps that is experiencing no mortality, recruitment, emigration, or immigration over the four days of trapping. It also assumes that capture probability is equal within the set of traps considered, but can vary between groups of traps. It is the magnitude of this variation that was modelled as a function of season, habitat, sex and year in the analyses below.

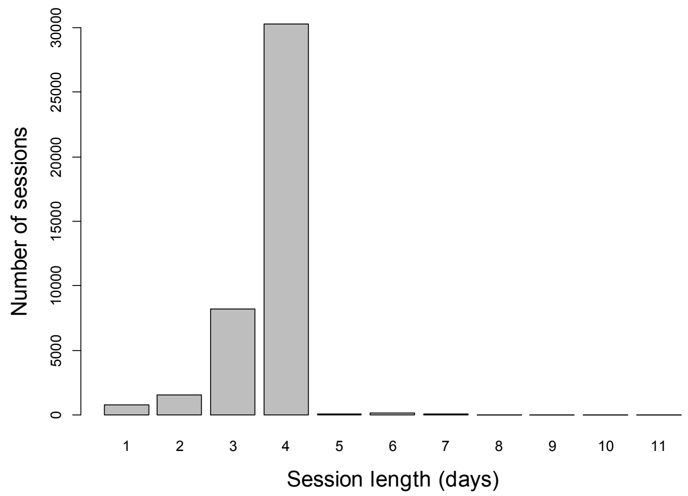


*Figure 3: The distribution of the length of trapping sessions up to 2011.*

All models were fitted in OpenBUGS 3.2.2 (Lunn *et al.,* 2009)[1]. The programme uses an iterative sampling algorithm to identify the most probable distribution of the parameter values (Bayesian posterior distribution) for models that may be too complex to solve using traditional maximum likelihood estimation (MLE).

### *3.2.2 Population dynamics model*

The observation model informs a demographic process model reflecting the dynamics of the culled mink population. This encompasses the contributions of birth, death and movement rates of mink between four different compartments that were defined by habitat. The model used the three seasons defined in Section 3.1.

The population dynamics model is structured by habitat but not by age or life stage (e.g. adults and juveniles) since mink are sexually mature in the year following birth. The model assumed that birth, death and movement rates within and between habitat compartments are density independent. As such it is a simplification of what is likely to occur in the natural environment, but one that should be acceptable where mink populations have been depleted by trapping and live in an unsaturated environment. It also precludes the need to estimate parameters describing the shape of density-dependent functions. Female population size for each habitat is estimated during each season using the trapping data (observation model), and the different estimates are linked to each other by demographic rates described by the population dynamics model. For the latter component, we assumed the following transitions. 1) WINTER to SPRING: dispersal between habitats and survival; 2) SPRING to SUMMER: survival; 3) SUMMER to WINTER: production of independent juvenile females and early post-breeding dispersal between habitats. For transition 3, survival was omitted as it is indistinguishable from reproduction based on the available data (i.e. only the combined product of reproduction, survival and dispersal could be reliably measured). Models assumed that fluxes between habitat compartments are not constrained by distance which we deemed reasonable given the size of the focal area and the long dispersal distance of mink, with individual movements sometimes exceeding 50 km (Gerell, 1971; M. Oliver,

[1] A full introduction to the use of BUGS for modelling population processes can be found in Royle & Dorazio (2008).

unpublished data). HMP staff considered that there are strongly unequal fluxes of individuals between habitat compartments with, for example, boggy moorland sustaining low numbers of resident breeding females. The model, therefore, allowed for this to occur and for a 4x4 matrix describing dispersal to be asymmetric. Initial models that also allowed for different production of independent young in different habitats were unstable and did not yield reliable parameter estimates because *in-situ* recruitment could not be distinguished from dispersal.

The model aimed to capture the essential feature of the HMP that not all trap lines were trapped in all seasons. This meant that less than the whole of each habitat compartment was trapped. This was achieved by specifying varying proportions of each habitat suffering trapping mortality at different time steps to reflect HMP practice and explore different control strategies subsequently. We assumed that population size per unit trap (a proxy for density) was equivalent in the trapped and un-trapped portions of the habitat before trapping, (removed and escaped mink). Following this assumption, the total population in a given habitat is obtained by dividing the estimated population in the trapped portion of the habitat by the proportion of the habitat that was trapped.

Such models can then be iterated across a number of years, with consecutive estimates of population size constraining values that could be taken by the demographic rates (e.g. survival, and number of independent young produced by non-trapped individuals, as well as their movement rates). At the same time, the estimated population sizes are also constrained by the estimated demographic rates, as the model fitting procedure tries to find the most probable parameter values given the observed data and the set of modelling assumptions. Indeed the mink population in a habitat compartment of the island at a given time step must reflect the number of surviving mink at the previous step discounted by survival, the productivity of those mink (if the time interval allows reproduction) and immigration by surviving or newly born in other habitat compartments.

At the outset of the project, it was not known how informative the data would be, but we ensured biological realism with respect to the estimated rates by using informative Bayesian priors on production of independent young, survival and dispersal rates, reflecting knowledge of the biology of the species from the literature. We used so-called vague priors that set upper and lower bounds to parameters such as survival and the number of offspring produced but gave similar weighing to all values within the specified range. Essentially, when the data are information-rich, the values of the estimated Bayesian posteriors should be strongly influenced by the data from the Outer Hebrides.

The model, including both observation and demographic components, is referred to below as the ‘combined model’. For simplicity, we first ran the observation model alone in order to obtain capture probability per day and population size estimates informed solely by the capture data (step 1). We then ran the combined model to estimate population sizes and demographic rates using both the capture data and the hypothesized demographic processes (step 2). In the latter step, capture probabilities were fixed at their values estimated in step 1, in order to accelerate computations. The computer code with comments explaining our demographic statistical analyses is available from SNH on request.

### 3.3 Simulations of parameterised models to explore hypothetical scenarios

The model, parameterised to represent the Outer Hebrides mink population can be used to explore, through simulations, different control scenarios and to explore retrospectively the control features which contributed most to the steep decline in estimated mink abundance. Thus we sought to identify whether trapping effort in some habitats contributed little to the decline, identify the habitats that have contributed most to the population's resistance to control, as well as identify any seasonal variation in the above which could guide resource use.

### 3.3.1 *Starting conditions*

For each simulated scenario, the starting population conditions mirrored those for SPRING 2008. Thus, the population was allocated as 90, 100, 40, and 119 female mink into BOG, COASTAL POOR, CROFTING and MOORLAND habitats respectively.

### 3.3.2 *Dispersal*

Model simulation used estimates of dispersal rates in two seasons derived from the model. These were taken as fixed and we did not explore the sensitivity of the model simulation to variation in those estimates

### 3.3.3 *Starting Reallocation of effort*

To assess the relative importance of each habitat, season and the duration of trapping toward reducing mink population size, each of these factors were varied whilst keeping the overall effort constant. In total 8,741 traps were set across the island. Following our correspondence with HMP, and inference from the trapping data, we considered each trap to be open for four days and that 43% of each habitat was covered per trapping session, per season (equivalent to each trap being set once per year). This defined the 'Standard' scenario for the project and meant that 3,759 (0.43 x 8,741) traps were set per average trapping season. The Standard scenario was used as a baseline to investigate the effects of varying effort by season, habitat and trapping duration. In the first instance, however, the mean 'Observed' by-season, by-habitat efforts across the years 2008 – 2011 were used in comparison to the Standard scenario, to make inferences about how the project may have been more or less successful than if trapping had been equally deployed across all habitats and seasons. These observed efforts are shown in Table 3. When simulating alternative scenarios (i.e. varying the proportion of habitat, number of seasons, or duration of trapping sessions), the Standard effort was redeployed accordingly, to reflect the fixed manpower available. For example, if the number of trapping nights was reduced from four to three, the proportion of habitat trapped (equivalent to traps used) was increased by the same relative magnitude, thus keeping the effort, in terms of trap days, constant.

### 3.3.4 *Running the simulations*

The demographic components of the model (e.g. productivity and survival) were stochastic. As such, the same population starting conditions and trapping strategies could result in different outcomes. Therefore, each scenario was simulated across a number of repeats to achieve a robust 'average' outcome. We first established the appropriate number of repeats by looking at when the average outcome stabilised (i.e. varied very little as additional runs were added). The measure of interest was the time to population extinction, and after experimenting with a number of scenarios, we found this varied little after 50 repeat runs. Subsequently all scenarios were simulated 100 times.

We emphasise that such simulations are based on empirical estimates of the probability of mink capture derived from the data of HMP in 2010. As such they do not reflect any changes in trapping strategy such as to move from blind to 'reactive trapping' implemented from November - December 2011, or trapping sweeps targeted at areas where mink were detected that may result in departures from 2010 trappability estimates.

## 3.4 Prospective analysis of the contribution of trapping regimes to future eradication efforts

In order to apply the lessons learned from the HMP, and to estimate effort and the likely outcomes in other potential target areas, we simulated trapping in two other relevant habitat scenarios based on GIS data of the focal areas and extrapolation from the HMP data.

Simulations assumed land masses with different representations of the four habitats considered on Lewis and Harris. By necessity, we used strictly the same classification and demographic rate as estimated from the HMP so as to have simulations driven by data. Woodlands are not represented in the HMP project area, thus we lack any information on their value to mink. Here they were pooled with bogs under the strong assumption they also are marginal mink habitats. Simulations were started with the same initial conditions (349 females) as in Lewis and Harris but we distributed these according to the habitat prevalence. The two scenarios considered were loosely inspired by land use in a 'Skye/Mull' scenario, where the habitat consisted of 14% BOG (and woods), 7% COASTAL POOR, 7% CROFTING and 71% MOORLAND; and a scenario loosely inspired by 'Sutherland/Wester Ross', where the habitat consisted of 5% Bog, 2% COASTAL POOR, 2% CROFTING and 90% MOORLAND. Given the model is not spatially explicit, the spatial arrangement of the habitat components was not taken into account.

## 4. RESULTS

Overall, within Phase II of the HMP, 1,514 mink were caught of which 784 were females. The number of mink caught increased from 277 in 2007 to 524 in 2008 and then declined by roughly 60% annually to 367 (2009), 208 (2010), 135 (2011) and 78 in 2012. Across all years, 48.5% of mink were caught in MOORLAND which accounts for 44% of traps, 21% in BOG which accounts for 30% of traps, 16% in CROFTING, slightly in excess of the 13% of traps in this habitat, and 14% in COASTAL POOR habitat, roughly in line with the 13% of traps being placed in this habitat. The sex ratio was slightly more male-biased in BOG habitat (48% females) than in other habitats (53% females), a possible indication of the habitat being used more intensely by transient individuals.

### 4.1 The trappability of mink caught as part of HMP

There was substantial variation in trapping effort over time and between habitats with an overall increase to an average of 43% of traps in a given habitat being opened in a given season (Table 1, Figure 4). Overall, a lower proportion of traps in BOG habitat were operated and a very low fraction of traps in MOORLAND was operated in WINTER 2011 as the HMP team shifted from a strategy based on regular trapping rounds to a system based upon detection followed by targeted trapping (Figure 4). There was a steady decline, down to values approaching zero in the mink capture per unit of effort (Figure 4) but it is noteworthy that a spike in trapping success in MOORLAND habitat in summer 2011 was followed by no trapping effort in this habitat.

Analyses are based on the history of captures and the distribution of mink caught on the successive days of capture. Overall, 39% of mink were caught on the first day of trapping, 29% on the second day, 20% on the third day and 13% on the fourth and final day before traps were closed (Figure 5). There was, however, some between year variation in this pattern, including less of a decline over time in 2012 (dotted line), though sample size is low.

Estimated probabilities of capture per night range from 0.16 [95% credible interval: 0.06 - 0.25] in SPRING 2007 to 0.34 [0.23 - 0.46] in summer 2010. Estimates varied with time, increasing over the first four years of the project, and with season, and there was an interaction between sex and season with males more trappable than females in WINTER (Figure 6). Our models indicated that there was no evidence of a difference in the trappability of males and females in SPRING and SUMMER. They also indicated that the difference in trappability between habitats was negligible. We therefore assumed in the final observation model that the trappability of males and females was equal in SPRING and WINTER and across habitats, in order to increase the precision of trappability and population size estimates.

The capture probability ($p$) = 0.34, for the summer trappability in recent years, implies that about 28% of females present in an area escaped trapping after three days $(1-p)^3$, and 19% of individuals are predicted to have escaped trapping after four days $(1-p)^4$. This value rises to 36% in WINTER 2010. Similarly, our estimate of p=0.15 in WINTER 2007 implies that as many as 52% of resident females escaped capture after four days of trapping at the start of Phase II of HMP (Figure 7).

*Table 1 - Proportion of traps deployed in a given habitat that were activated in each season and years used for our analyses and model.*

| | BOG | COASTAL POOR | CROFTING | MOORLAND |
|---|---|---|---|---|
| 2007 | | | | |
| SPRING | 0.02 | 0.38 | 0.27 | 0.08 |
| SUMMER | 0.04 | 0.19 | 0.24 | 0.16 |
| WINTER | 0.15 | 0.09 | 0.22 | 0.24 |
| 2008 | | | | |
| SPRING | 0.14 | 0.15 | 0.22 | 0.27 |
| SUMMER | 0.23 | 0.11 | 0.19 | 0.23 |
| WINTER | 0.41 | 0.63 | 0.50 | 0.20 |
| 2009 | | | | |
| SPRING | 0.32 | 0.25 | 0.26 | 0.38 |
| SUMMER | 0.13 | 0.56 | 0.44 | 0.45 |
| WINTER | 0.33 | 0.46 | 0.72 | 0.65 |
| 2010 | | | | |
| SPRING | 0.31 | 0.39 | 0.40 | 0.42 |
| SUMMER | 0.29 | 0.33 | 0.25 | 0.37 |
| WINTER | 0.37 | 0.85 | 0.93 | 0.47 |
| 2011 | | | | |
| SPRING | 0.36 | 0.27 | 0.46 | 0.45 |
| SUMMER | 0.18 | 0.24 | 0.17 | 0.34 |
| WINTER | 0.79 | 0.40 | 0.39 | 0.01 |
| 2012 | | | | |
| SPRING | 0.20 | 0.05 | 0.10 | 0.03 |
| SUMMER | 0.00 | 0.00 | 0.00 | 0.00 |
| WINTER | 0.08 | 0.04 | 0.12 | 0.11 |

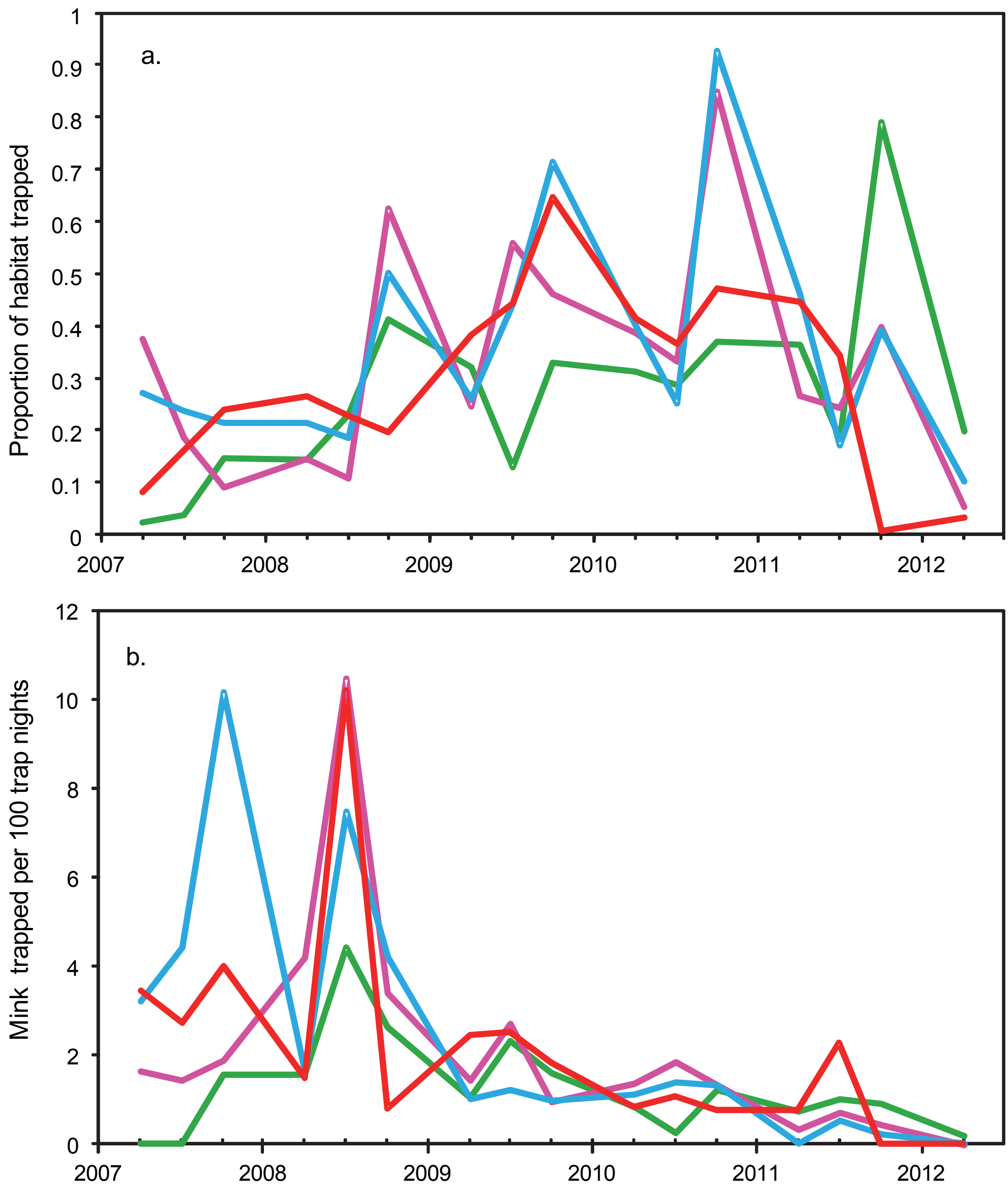


*Figure 4: (a) the proportion of each habitat type trapped per season, 2007 – 2012; (b) The capture rate per unit of effort (/100 trap nights) of female mink per habitat type. Key: Red = MOORLAND; Blue = CROFTING; Pink = COASTAL POOR; Green = BOG.*

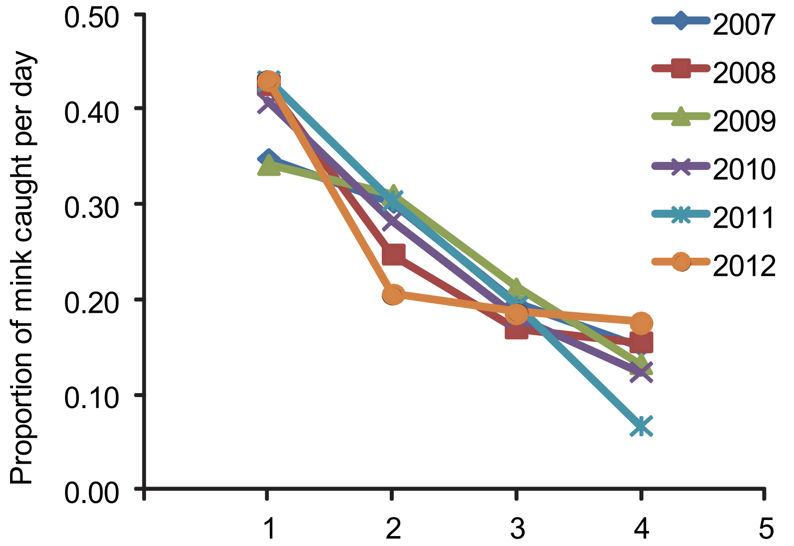


*Figure 5: The proportion of mink caught on first to fourth day of trapping session in each year.*

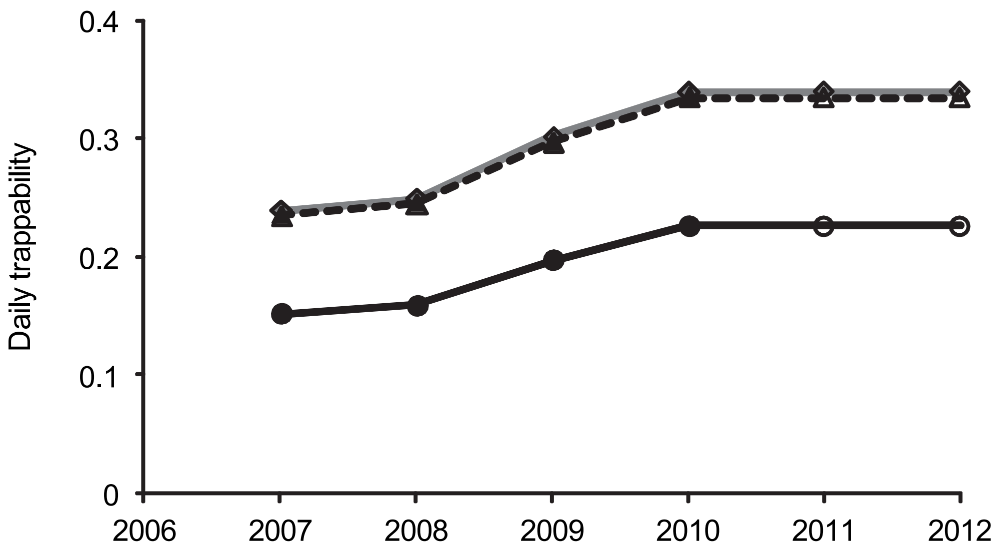


*Figure 6: Estimated female trappability per day showing the increase in probability of capture over time and the difference between seasons (solid line and circles: SPRING, grey and diamonds: SUMMER; dashed line and triangles: WINTER). Values for 2011 and 2012 (symbols not filled) could not be estimated and were set to the 2010 value in population models.*

### 4.2 Estimated demographic parameters of mink in HMP area

There is currently no standard tool for comparing the goodness of fit of state-space models, meaning that the choice of modelling assumptions must be guided mostly by ecological expertise. A model simultaneously assuming that the number of juveniles produced varied between habitats, and that individuals moved between habitats during the SUMMER to WINTER transition, yielded estimates of between 0.05 and 0.15 female offspring produced per adult female in BOG, MOORLAND and COASTAL POOR habitats and around 18 in CROFTING areas. These unrealistic estimates (respectively too low and too high) reflected the challenge in separating the contributions made by reproduction and mink movement between habitats to changes in abundance.

Alternative options were then explored, which assumed that productivity varies according to habitat and there was no early post-breeding dispersal, or that allowed for early post-breeding dispersal between habitats where there was no difference in productivity. The first option produced estimates of productivity varying widely between habitats (i.e. between 0.25 and 0.8 independent female offspring per adult female produced in BOG, MOORLAND and COASTAL POOR habitats and around 10 in CROFTING areas). The latter estimate is biologically unrealistic given that productivity in the model does not relate to litter size at birth but to a combination of the number of young that weaned and survived the post-independence period and are trapped between September and February. It thus includes the period when most juvenile mortality takes place. Variation between habitats was not implausible though, as it may reflect the combined impact of reproduction and movement into this habitat, consistent with the suggestion that some females give birth in the inland portion of their territories and move back to the coast with their young (Iain Macleod, pers. com).

A model assuming early post-breeding dispersal between habitats and uniform productivity in all habitats yielded a productivity estimate of 1.49 female offspring surviving to capture between September and February, per adult female [95% credible interval: 1.21-1.80]. This value is still much too high given that, when combined with our adult survival estimates, it equates to a population multiplication rate of about 2.5 from one year to the next. While no formal estimates have been published for American mink, this value is well in excess of estimates of the maximum feasible multiplication rate of related American martens (*Martes americana*), feral domestic ferret and black footed ferret (*Mustela nigripes*) which range between 1.3-1.35 (Grenier *et al.,* 2007, Fryxell *et al.,* 1999, Barlow & Norbury, 2001).

After carrying out further analyses in order to estimate year-to-year variations in population productivity, we discovered that the high average productivity in the previous model was inflated by an improbably high productivity estimate for the year 2007. Given that data from 2007 originate entirely from South Harris that had been virtually emptied of mink in Phase I and was subjected to intense re-colonisation, we interpreted this value as an artefact of the trapping design. As a consequence we specified our final model with two estimates of productivity; one specific to 2007, and one common to all other years (interpreted as an estimate of the real productivity). From this model, we obtained productivity estimates of 11.65 [8.09 - 14.65] for 2007 and 0.34 [0.06 - 1.08] otherwise. The latter estimate corresponds to a maximum population multiplication rate around 1.3, which is within the range of expected values.

Dispersal rates estimated under the same model were also broadly consistent (i.e. correlated) with those estimated independently for the WINTER to SPRING transitions, providing further support for the ecological realism of this model. While further refinements could be made, this was used as the reference model for the reported parameter estimates and the simulation exercise.

The model yielded estimates of probability of mortality through causes other than trapping, in SPRING and WINTER. These were exceedingly small at 0.008 [0.001 - 0.030] over the four months of the period defined as SPRING and 0.018 [0.001 - 0.062] over the five months of the WINTER period.

*Table 2 - Estimated per capita movement rates [95 % credible intervals] of mink between habitat compartments in HMP area during the SUMMER to WINTER transition (top) and WINTER to SPRING transition (bottom). Values in bold on the diagonal are estimates of philopatry.*

| | | TO | | | |
|---|---|---|---|---|---|
| | | BOG | COASTAL POOR | CROFTING | MOORLAND |
| FROM | BOG | ***0.76 [0.28-0.99]*** | 0.12 [0.00-0.37] | 0.04 [0.00-0.18] | 0.08 [0.00-0.45] |
| | COASTAL POOR | 0.27[0.01-0.78] | ***0.02 [0.01-0.60]*** | 0.3 [0.01-0.71] | 0.22 [0.01-0.66] |
| | CROFTING | 0.15 [0.00-0.54] | 0.13 [0.00-0.40] | ***0.44 [0.04-0.80]*** | 0.27 [0.01-0.68] |
| | MOORLAND | 0.16 [0.01-0.43] | 0.12 [0.01-0.26] | 0.09 [0.00-0.24] | ***0.62 [0.36-0.82]*** |
| | | TO | | | |
| | | BOG | COASTAL POOR | CROFTING | MOORLAND |
| FROM | BOG | ***0.30 [0.03 - 0.58]*** | 0.15 [0.01-0.35] | 0.08 [0.00-0.23] | 0.47 [0.12 - 0.80] |
| | COASTAL POOR | 0.28 [0.01-0.79] | ***0.31 [0.01 - 0.75]*** | 0.22 [0.00-0.60] | 0.19 [0.00 - 0.63] |
| | CROFTING | 0.22 [0.01-0.60] | 0.24 [0.01-0.61] | ***0.19 [0.01 - 0.47]*** | 0.35 [0.02 - 0.75] |
| | MOORLAND | 0.15 [0.01-0.39] | 0.08 [0.00-0.24] | 0.055 [0.00-0.17] | ***0.71 [0.42 - 0.92]*** |

Estimates of dispersal rate depict a situation with very high movement rates between habitats by individuals or their offspring, especially during the WINTER to SPRING transition (Table 2). Credible intervals are wide for all rates but many deviate from the priors of 0.25 indicating that the data contain information on movement, though they do not allow estimation of movement rates from the COASTAL POOR habitat in SUMMER with any useful level of precision. Overall early philopatry is high with the notable exception of rates from CROFTING to MOORLAND. Combined emigration rate estimates for SUMMER to WINTER are 24% from BOG, 52% from COASTAL POOR, 55% from CROFTING and 37% from MOORLAND habitat. SUMMER to WINTER movement rates between habitat compartments are unequal with the highest estimated migration rate from CROFTING to MOORLAND (Table 2).

Estimated movement rates during the WINTER to SPRING transition were higher overall, with 70%, 69%, 81% and 28% per capita emigration rates from BOG, COASTAL POOR, CROFTING and MOORLAND habitats respectively. They also show unequal movement rates between pairs of habitats. High WINTER movements are directed towards the MOORLAND compartment as well as much higher per capita probabilities of moving from CROFTING to BOG than the converse, and from CROFTING to MOORLAND than from MOORLAND to CROFTING.

It is important to note that the movement rates shown here are on a per individual basis and that there are large differences in the sizes of habitats and hence the number of mink potentially moving. Thus the estimates shown should neither be taken as estimates of the total number of individuals moving or net fluxes, nor as proxies for dispersal distance as, for example, much shorter movements are required for a mink leaving CROFTING habitat than MOORLAND habitat. Estimates of fluxes, i.e. the number of individuals transferring from one habitat to another, are derived by the combined model when estimating population size.

### 4.3 Observed and modelled dynamics of mink in HMP area

The total estimated population size at the start of the project in SPRING 2007 was 1,334 mink (Figure 9). This initial value, however, is very uncertain given it is based on extrapolation from trapping in Harris only and in the only season when the sex ratio of captured mink was strongly male biased: 37% females in SPRING 2007, 55% in 2008, 56% in 2009, 58% in 2010, 57% in 2011, 50% in 2011%. Given that estimates are based on the trappability from both sexes combined, and the sex ratio does not deviate from 0.5 later on, either females were less trappable than males on that occasion, or the area had been disproportionately re-colonised by males relative to females. These potentially anomalous estimates are somewhat corrected by the demographic model (below). Thus one way to arrive at a plausible initial population size is to double the SPRING 2007 male population size estimate, yielding an initial population size of the order of 1,700 mink. Alternatively, using SPRING 2008 as the starting point would suggest an initial population of 600 to 700 adults. We use SPRING 2008 as the initial population size below.

The estimated population size declined steadily throughout the project with an island-wide estimate of the breeding population, including males and females, of 640 mink before the spring trapping cull. In SPRING 2008, we estimated there were 350 females of which 28 were removed in that season. This equates to up to 322 litters produced. In SPRING 2009, we estimated 266 females were present. As 32 females were removed in SPRING, up to 234 litters were produced in that year. In 2010, we estimated the number of females had declined to 133 females in SPRING, of which 31 were removed, leaving 102 litters. Our last reliable estimate is that out of 155 mink estimated to be present in SPRING 2011, 88 were females, of which 21 were removed before the production of young. We thus estimate that 67 females bred in 2011 across the whole of the HMP area (Figures 8 & 9). Thus according to our estimates, the number of breeding females was reduced by approximately 80% in 4 years.

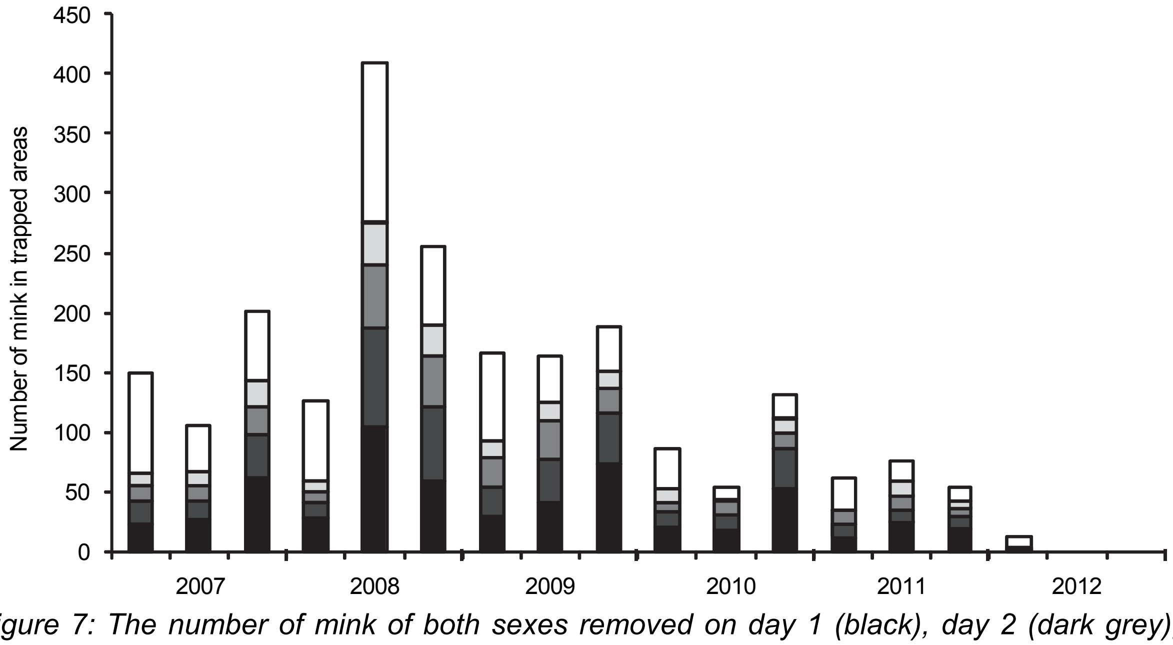


*Figure 7: The number of mink of both sexes removed on day 1 (black), day 2 (dark grey), day 3 (light grey), day 4 (lightest grey) of trapping session, and estimated number of mink that escaped capture (white) despite residing in proximity of traps and hence contributed to*

*the population in the next season, together with mink residing in non-trapped areas. For a given year, the three columns correspond to SPRING, SUMMER and WINTER.*

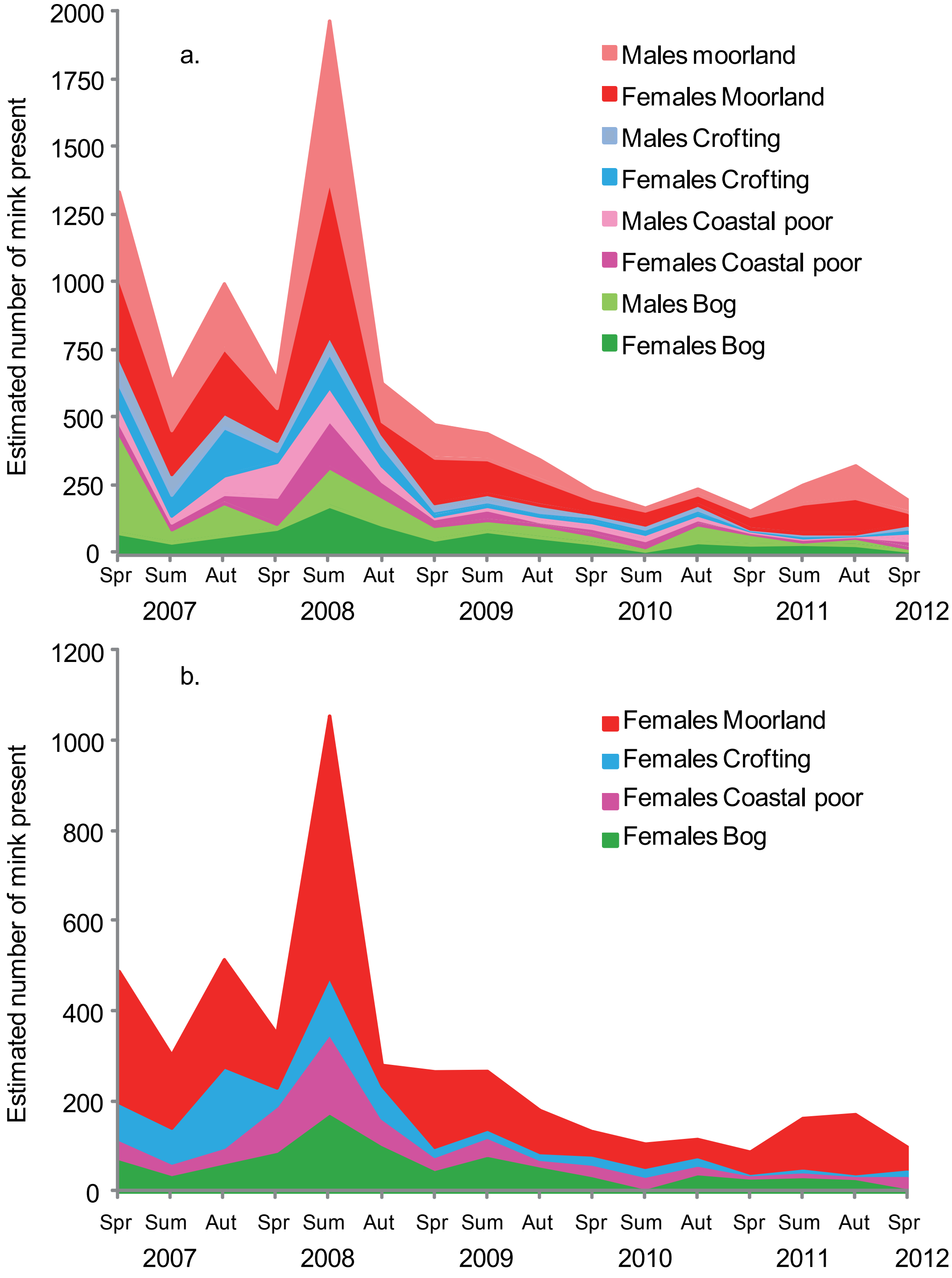


*Figure 8: The estimated number of mink calculated to be present in four habitat compartments of Lewis and Harris before trapping. Estimates are from the capture model (observation component) only and extrapolated values from the portion trapped to the whole island. The areas for each habitat are stacked such that area of plot shows the cumulative number of mink. (a) both sexes, Males in lighter colour; (b) females only. Key: Red = MOORLAND; Blue = CROFTING; Pink = COASTAL POOR; Green = BOG.*

Observation model estimates indicate that in SPRING 2011, 88 female mink were distributed unevenly between habitats, with 35% in BOG habitat, 8% in COASTAL POOR habitat, 3% in CROFTING habitat, and 53% in MOORLAND habitat. Estimates beyond SUMMER 2011 are unreliable, especially for MOORLAND, because a tiny fraction (0.9%) was trapped in that season and the trapping regime changed. Note however that the rise in the MOORLAND population size from SUMMER to WINTER 2011 (2011.05 - 2011.75) is well supported by both the modelling of captures (observation model) and cruder trapping efficiency (catch per unit of effort, Figure 4). No increase coinciding with reproduction is evident in other habitat compartments.

The estimate of 196 mink (including 98 females) in SPRING 2012, although included here for completeness, must be treated with great caution as the trapping regime employed by the HMP had changed from systematic sweeps to targeted trapping from October/November 2011. Note that 34% of traps placed in MOORLAND were activated in SUMMER 2011 but only 0.1% in WINTER 2011 and 3% in SPRING 2012. These were only in areas targeted based on prior knowledge of mink presence. The island-wide estimations wrongly assume similar mink densities in all portions of a habitat, which is clearly incorrect.

Our best, putatively reliable, most conservative description of the dynamics of culled mink in Lewis and Harris is provided by the combined model (Figure 9). The upper panel of Figure 9 allows a comparison of population size estimates from the capture model only (triangles) and estimates constrained by the demographic model (circles linked by lines). It is apparent from examining this upper panel that the fit between both estimates is rather good except for values from MOORLAND in 2007, WINTER 2008 and SUMMER and WINTER 2011 when capture estimates (red triangles) exceed those compatible with the demographic parameters (red circles and lines). According to HMP staff (Iain Macleod pers. com.), each of those instances corresponds to unusual trapping circumstances (discussed above). At other times, observation and combined model estimates agree closely.

The combined model estimates are those most compatible with both capture-derived abundance estimates and the demographic rates estimates. Note that, with the exception of 2007, demographic rates are here assumed to be constant from 2009-2012. Thus the very high abundance of females in MOORLAND in WINTER 2008, for instance, is incompatible with previous population size and demographic rate estimates. Given that abundance is estimated based on a low fraction of MOORLAND being trapped and hence has a high uncertainty attached to it, it is 'easier' for the model algorithm to infer that the true population size in this habitat compartment is lower than suggested by the trapping data alone than to adjust all demographic rates upward. Thus the MOORLAND abundance estimate from the joint observation/abundance model for WINTER 2008 is brought in line with the longer term trend, a desirable property of our model.

Notwithstanding the discrepancies visible in 2007 that reflect the manner the HMP expanded the buffer zone between the islands of North Uist and Harris, the combined model estimates demonstrate very clearly a steady reduction of the mink population from 2008 to 2011 in all habitats when approximately 88 female mink were estimated to remain. The largest estimated populations were in the two large habitat compartments deemed least suitable by the HMP, namely BOG and MOORLAND. The model suggests that mink abundance has been reduced to a very low density in CROFTING and COASTAL POOR habitats. However, examination of the lower panel of Figure 9 where mink abundance is plotted on a logarithmic scale shows that, while the rate of decline of the mink population in each habitat was roughly constant from 2009-2010, it had slowed down in 2011 relative to previous years.

A hierarchical model can predict likely values for the total mink population size based on demographic rates and population size at the previous time step. This is possible using either only observed values of the number of mink caught per habitat without data on the proportion of each habitat trapped (as in 2012), or without any data at all (as in 2013). The model projects what could happen in the future if rates remained as they were previously. We produced such estimates from WINTER 2011 onwards (shown with black crosses on the right hand side of each panel of Figure 9) using only the number of mink caught in 2012. The abundance estimates from the MOORLAND habitat in SUMMER 2011, while consistent with 30 females having being caught, is probably unreliable as an island wide estimate (Iain Macleod pers. com.), and accordingly we left out the value from this habitat only from model predictions for 2011. As shown in the top panel of Figure 9, credible intervals become very large in the absence of real data to anchor estimates. This is because of the uncertainty surrounding the different components of the estimates. Credible intervals are only shown on the upper panel of Figure 9 to avoid cluttering. These model predictions emphasise that little is known about the likely population size under model assumptions because there are no data on trapping effort after SUMMER 2011 that meet the assumption of 'blind trapping'. For instance, it is not implausible that the population recovered in late 2012 through the production of juveniles. The possibility that the population is nearly extinguished is also consistent with the data at hand.

An alternative approach to exploring the likely outcome of the HMP is to use model estimates of demographic rates (survival, productivity, SUMMER to WINTER and WINTER to SPRING movement rates) taken as known, together with the last reliable estimates of mink population size from SPRING 2011, to simulate the likely outcomes of given trapping scenarios. Here we used the proportion of the four habitats trapped in each season that was achieved in 2009 and 2010 which averages 43 % (Table 3). Such simulations can be seen as showing 'what could have happened had the systematic trapping sweeps continued'. Although they do not reflect the subsequent adoption of 'reactive trapping' and do not fully reflect the uncertainty around estimates of population sizes and demographic rates, such simulations are easier to interpret. Using 100 replicate populations and subjecting these to the chance events of survival, reproduction, dispersal and probability of capture yields a distribution of extinction times, with 11 years between the first and last simulated extinctions, with the earliest extinctions occurring in 2014 and the last in 2021 (Figure 10). Approximately 40 % of simulated populations go extinct in 2015 and in 2016. Eighty per cent of simulations are predicted to have gone extinct by 2017 (Figure 10).

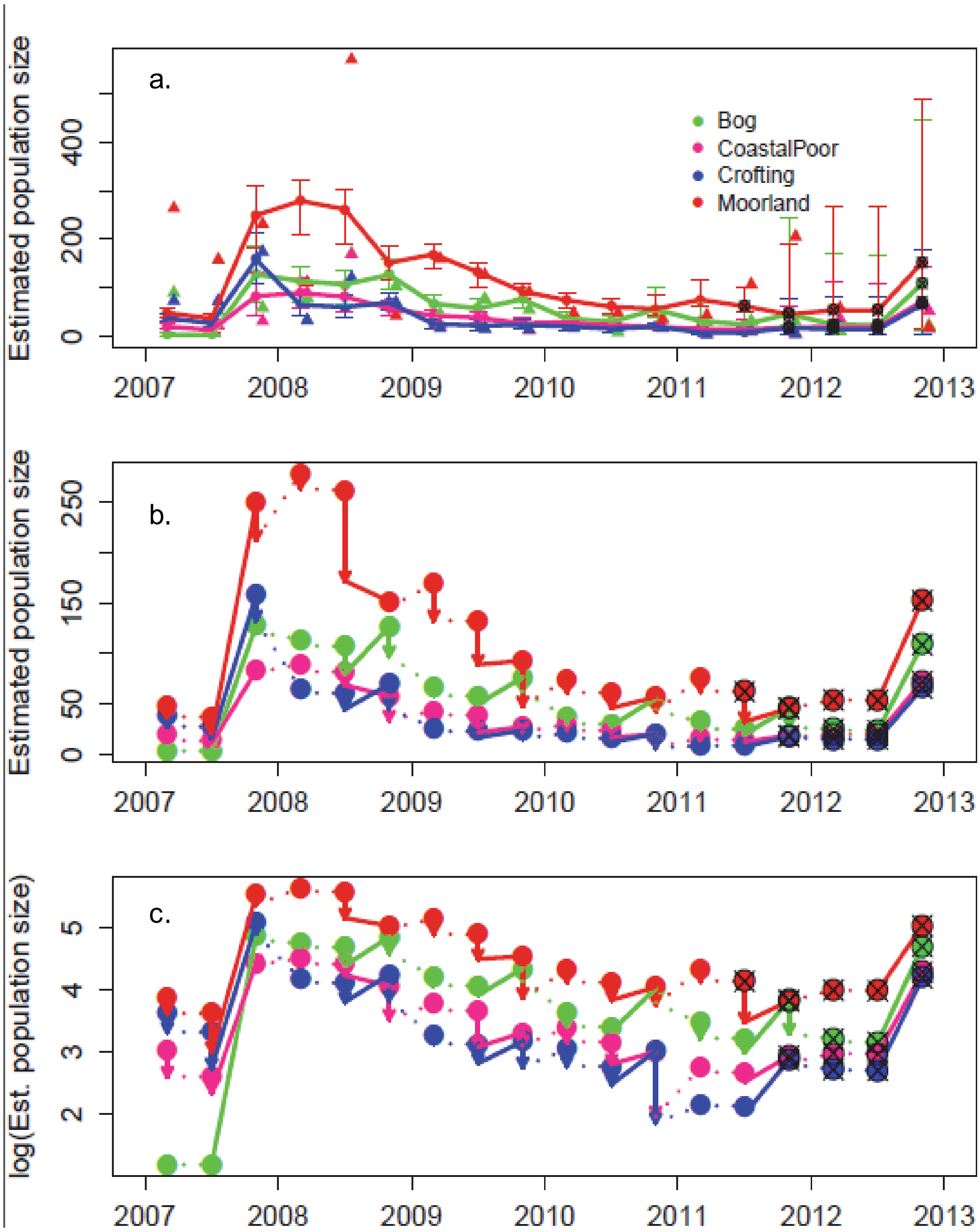


*Figure 9: (a) Comparison between (non-stacked) estimated female population size using the capture model only (triangles) and estimates constrained by including the population dynamics model. Error bars show 95% credible intervals. (b) Modelled mink dynamics showing estimated female numbers. Vertical arrows reflect the depletion of mink by trapping. Solid lines show increase through reproduction and movements, dotted lines show changes through movement only. Estimates with black crosses are 'reverse estimations' from the model based on the number of female mink caught in 2012, but without any reliance on values of the proportion of each habitat trapped (see text). (c) As for (b) but on a logarithmic scale to emphasize rates of change. Key: Red = MOORLAND; Blue = CROFTING; Pink = COASTAL POOR; Green = BOG.*

*Table 3 – Average proportions of habitat trapped in 2009 and 2010 used in simulations of likely extinction scenarios of mink populations in the HMP area using SPRING 2011 estimates as initial values and demographic parameters estimates from the combined model from 2008-2011.*

| | BOG | COASTAL POOR | CROFTING | MOORLAND |
|---|---|---|---|---|
| SPRING | 0.32 | 0.32 | 0.33 | 0.40 |
| SUMMER | 0.21 | 0.45 | 0.35 | 0.41 |
| WINTER | 0.35 | 0.66 | 0.82 | 0.56 |

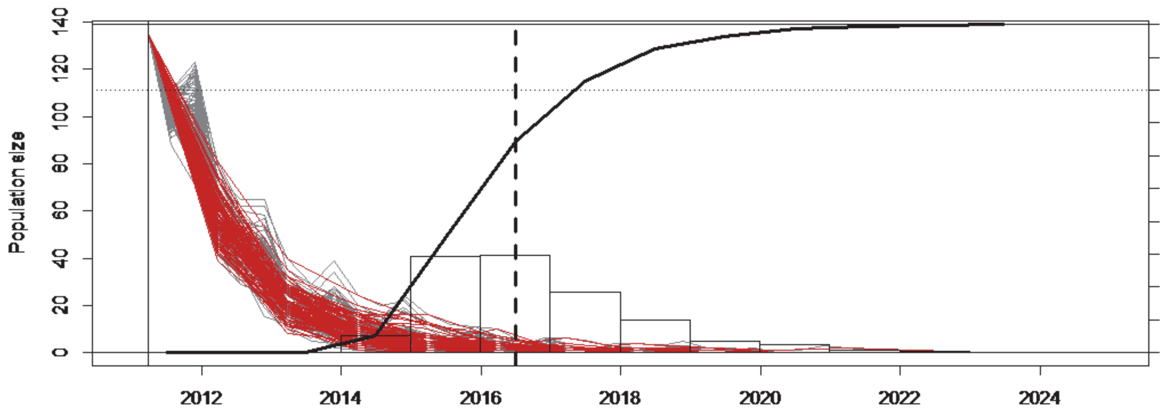


*Figure 10: Simulated annual (red lines) and seasonal (grey lines) dynamics of mink populations subjected to the trapping regime imposed by the HMP in 2009 and 2010 and starting at the abundance estimated to have occurred in SPRING 2011. The histogram shows the distribution of extinction years. The vertical dotted line shows the median scenario of extinction occurring in 2016. The curved solid black line shows the cumulative probability of extinction (right axis). The horizontal dotted line shows that the mink population has gone extinct by 2017 in 80% of the simulations.*

## 4.4 Retrospective analysis of the contribution of trapping effort to changes in mink dynamics

A range of simulations were performed with a parameterised demographic model with the same structure as the model fitted to the data. This was done in order to analyse the control features of the HMP which contributed most to the observed decline in mink numbers and to identify components of the control strategy that contributed very little to the decline. The analyses also incorporated the habitats that, owing to different demographic rates, or low or ill-timed trapping effort, have created the greatest challenges for the control programme. Throughout we attempted to restrict ourselves to plausible scenarios, whereby the modelled distribution of trapping effort was not completely impracticable given the number of staff employed by the HMP.

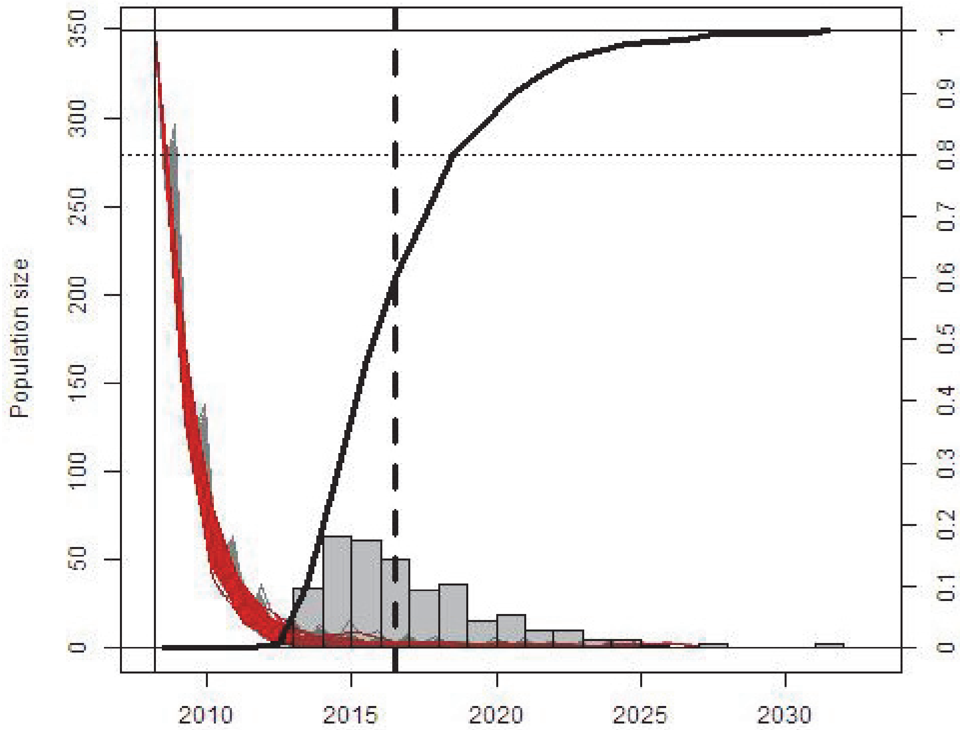


*Figure 11: Simulated annual (red lines) and seasonal (grey lines) dynamics of mink populations subjected to the trapping regime imposed by the HMP in 2008 - 2011 and starting at the abundance estimated to have occurred in SPRING 2008, earlier than on Figure 10 and illustrating the reduction of uncertainty on likely time to extinction.. The histogram shows the distribution of extinction years. The vertical dotted line shows the median scenario of extinction occurring in 2016. The curved solid black line shows the cumulative probability of extinction (right axis). The horizontal dotted line shows that 80% of simulated mink populations have gone extinct by 2017.*

Model simulations starting with population size estimates and the observed scenario in terms of trapping effort, but not using any empirical data other than demographic rates, yield outcomes very similar to those starting in 2011. The median time to extinction from 2008 is 9 years, but with a wider range of plausible years to extinction, (compare Figures 10 and 11).

### *4.4.1 Varying the length of trapping sessions*

In order to determine the impact of varying the number of days of trapping, we simulated the dynamics of mink under three, four or five day trapping sessions. Without a redeployment of effort, three days represents a 25% reduction in effort and five days a 25% increase. The mean time to extinction increased from 9.1 years [95% Confidence Interval 6 - 15.5] to 12.8 years [95% CI 7.3 – 26], a 35% increase when using a three day trapping schedule. Time to extinction decreased by 10% to 8.9 years [95% CI 5 - 17.5 when using a five day trapping schedule (Figure 12). Therefore, with the observed allocation of effort across habitats, and without redeployment of effort, neither a three day nor five day trapping schedule provides a more efficient approach.

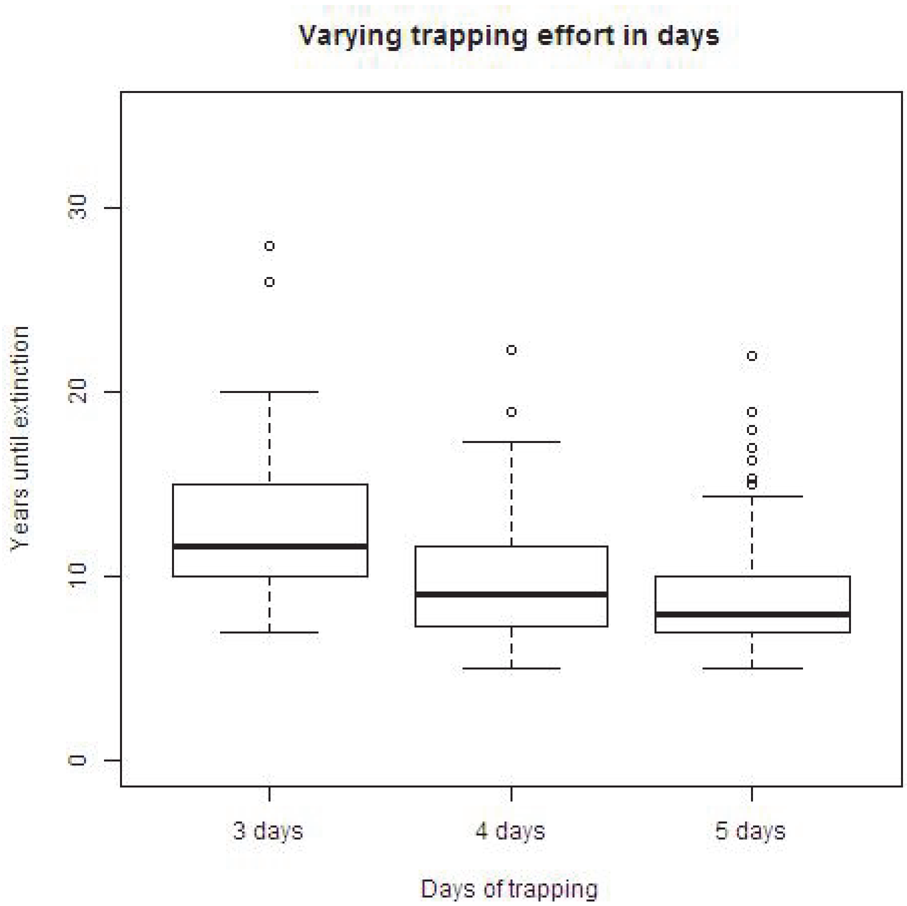


*Figure 12: The effect of varying the duration of trapping sessions on mean expected time to extinction for 100 simulations. Boxplot shows the lower whisker, the lower hinge (first quartile), the median, the upper hinge (third quartile) and the extreme of the upper whisker for one group. Whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box.*

The HMP did not deploy an equal amount of effort across all habitats and seasons, but rather increased effort in some seasons and habitats in favour of effort in others (Table 3). Was this approach more efficient than simply deploying an equal amount of effort (43% coverage) across all habitats and seasons? By comparing the outcomes of simulating these two scenarios, it appears that the observed strategy was more efficient than using equal effort across all seasons and habitats, with a decrease in the mean expected time to extinction from 11.3 years [95% CI 6.3 - 19.5] to 9.1 years [95% CI 6 – 16] (Figure 13). So what factors may have contributed to this difference?

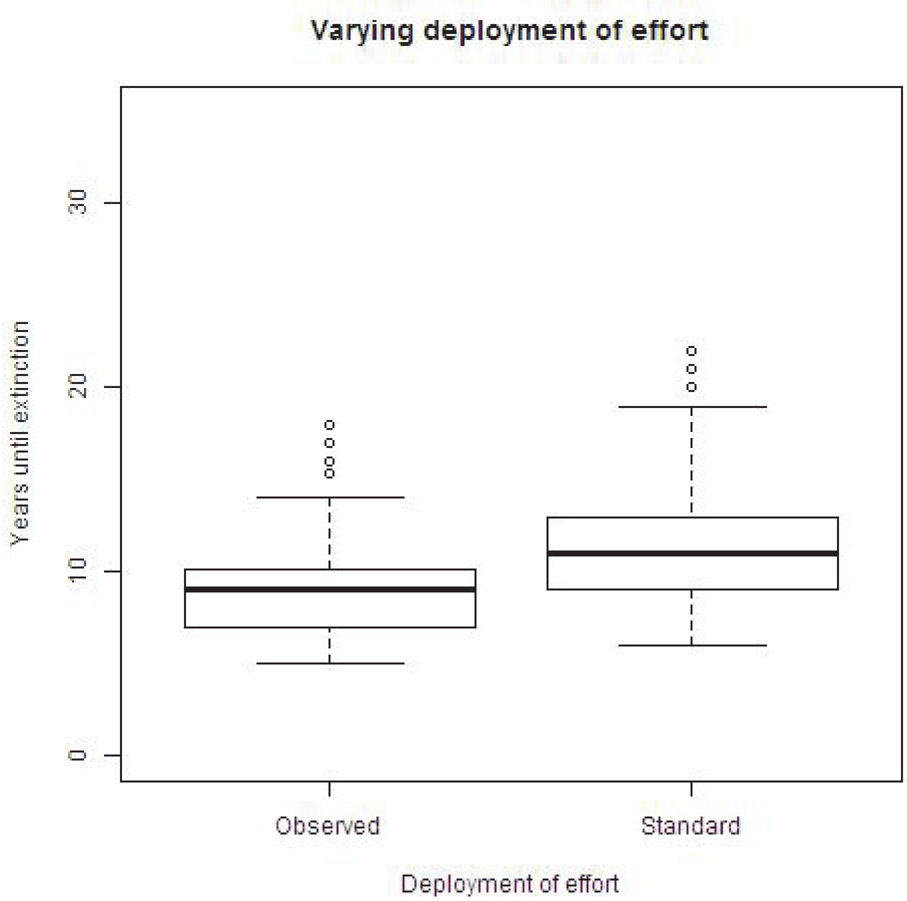


*Figure 13: The effect of varying the deployment of effort on mean expected time to extinction, from 43% in all seasons and habitats, the standard scenario, to those efforts described in Table 3, the observed scenario, for 100 simulations.*

#### *4.4.2 Varying seasonal effort*

One possibility is that increasing efforts in a particular season, and thus removing a larger proportion of the standing population, could reduce population size more effectively, depending on the ability of the population to compensate demographically in those seasons not trapped. In fact, not trapping in any season with a subsequent effort, from 43% coverage per habitat to 64.5% coverage per habitat in the seasons trapped, greatly increased the efficiency of control. It appeared that not trapping in SPRING would most effectively reduce the mean expected time to extinction to 4.9 years [95% CI 4.2 – 6], though this was only marginally more effective than dropping WINTER [5.5 years; 95% CI 4 -7], or SUMMER [6.6 years; 95% CI 5.2 – 9] (Figure 14). All of these compare favourably to a mean expected time to extinction of 12 years [95% CI 6.5 - 25.5] for an equal coverage of 43% of traps in each habitat and season.

#### *4.4.3 Varying effort by habitat*

Another possibility is that varying the trapping effort in different habitats could affect the time taken to reduce the Hebridean mink population size to extinction. The standard scenario was only improved upon by not trapping BOG and redeploying the effort to the other habitats, which reduced the mean expected time to extinction to 8 years [95% CI 4.2 – 6]. Not trapping any of the other habitats resulted in an increase in expected time to extinction, with the worst case scenario being not to trap MOORLAND, where the mean expected time to extinction became 13.5 years [95% CI 6.5 - 25.5] (Figure 15).

### *4.4.4 Varying effort by duration of trapping sessions*

Another alternative is to vary the trapping strategy by reducing the number of trap nights per session, but redeploying the effort (i.e. keeping the number of trap days constant) *pro rata*, to include a greater proportion of the habitat (a larger number of traps) per session. As shown in Figure 16, the simulations indicate that when trapping in all seasons and habitats, it would be more efficient to reduce the number of days that a trap is set per session, if the effort was used to open more traps in a habitat. Ultimately reducing the session length from four to three trap days with an increase from 43% to 57% coverage reduces the mean expected time to extinction from 12.3 [95% CI 7 - 24.6] to 10.2 years [95% CI 5 - 21.6]. However, an increase in trapping duration to five days, with a reduction in effort to 34% coverage, would increase the expected mean time to extinction to 13.4 years [95% CI 7 – 27].

If we consider an 'optimal' strategy that encompasses the most effective pattern of redeployment from varying trapping duration, season and habitat, from the above we could infer trapping for three days, with reduced effort in BOG habitat, and no trapping in SPRING would be optimal. To keep the effort consistent on a pro rata basis, the reduced effort from trapping for three rather than four days, and no trapping in SPRING, means that all MOORLAND, COASTAL and CROFTING habitats can be trapped with 100% coverage in SUMMER and WINTER. However, there is also a sufficient surplus of effort (total trap days) to also trap BOG with 54% coverage in these two seasons. This strategy substantially reduces the expected time to extinction to 4.6 years, with a greatly reduced level of uncertainty in the outcome [95% CI 4 – 6] (Figure 17).

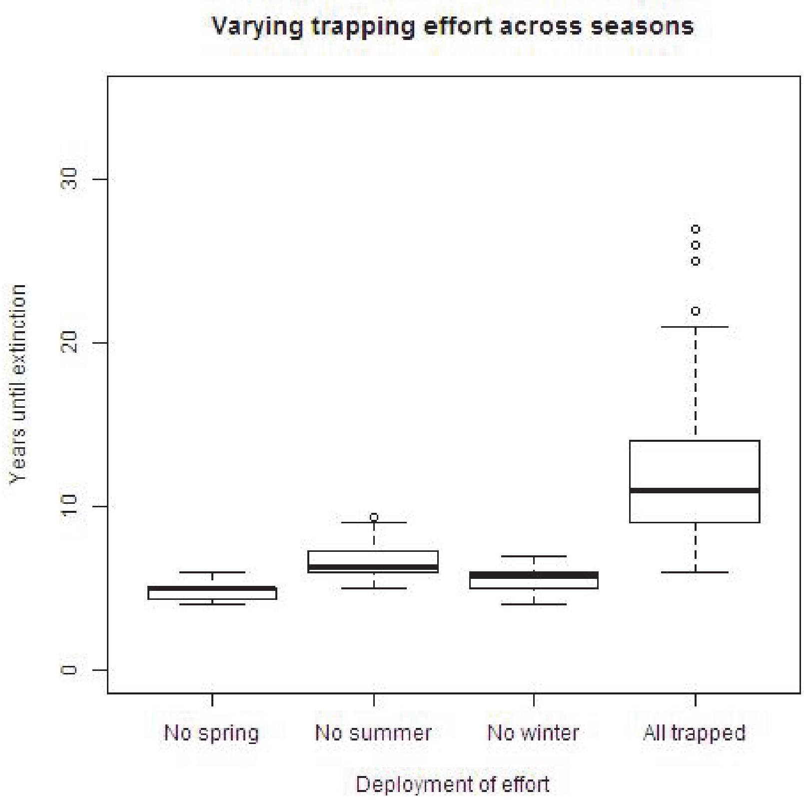


*Figure 14: The estimated time to population extinction when varying seasonal trapping effort with redeployment of trapping.*

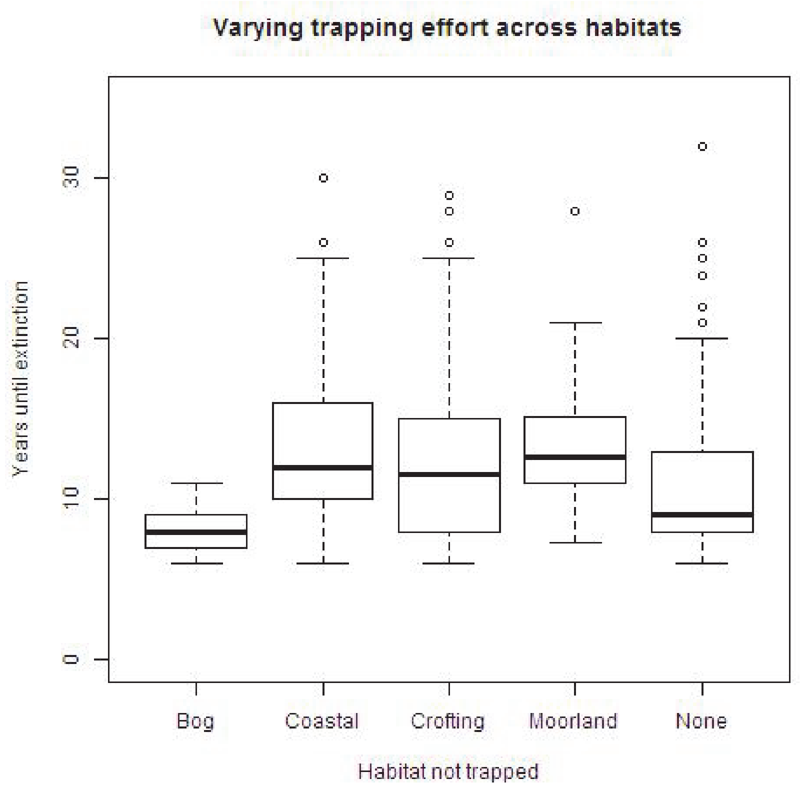


*Figure 15: The estimated time to population extinction when varying trapping effort across habitats with redeployment of trapping.*

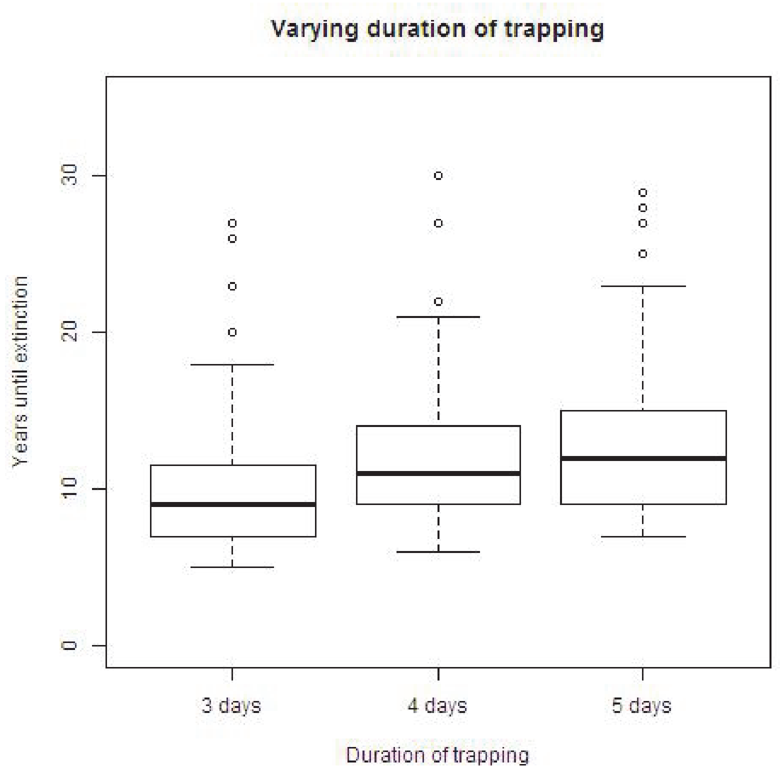


*Figure 16: Contrasting the estimated time to population extinction for varying durations of trapping sessions with pro rata redeployment of effort.*

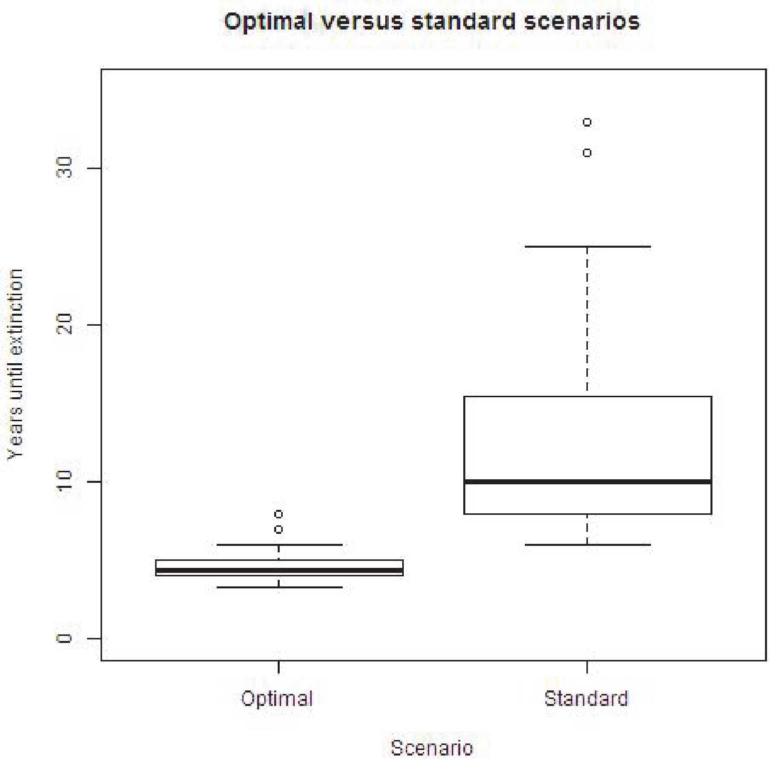


*Figure 17: Contrasting estimated time to extinction for optimal (i.e. three day trapping sessions; not trapping in SPRING; 54% coverage of BOG and 100% coverage of other habitats) and standard (i.e. four day trapping sessions with 43% coverage of all habitats in all seasons) scenarios.*

### 4.5 Prospective analysis of the contribution of trapping regimes to future eradication efforts

In order to apply the lessons learned from the HMP, and to estimate effort and outcomes in other potential target areas, we simulated trapping in two other relevant habitat scenarios based on GIS data of the focal areas and extrapolation from the HMP data. These were a 'Skye/Mull scenario', where the habitat composition consisted of 14% BOG, 7% COASTAL POOR, 7% CROFTING and 71% MOORLAND; and a 'Sutherland/Wester Ross scenario', where habitat consisted of 5% Bog, 2% COASTAL POOR, 2% CROFTING and 90% MOORLAND. Based upon inferences from the HMP in SPRING 2008, the relative densities of female mink (calculated as estimated female mink per trap) were 0.034, 0.089, 0.035 and 0.031 for BOG, COASTAL POOR, CROFTING and MOORLAND, respectively. These values were used to define starting conditions and the allocation of 350 female mink (equivalent to the starting population size for the HMP SPRING 2008) across habitats. This gave starting populations of 46, 65, 26, 214, and 18, 24, 9, 299 female mink in BOG, COASTAL POOR, CROFTING and MOORLAND for Skye/Mull and Sutherland/Wester Ross, respectively. With the area specific habitat proportions, redeployment of effort over three day trapping schedules, favouring SUMMER and WINTER over SPRING, and avoiding BOG, meant that 100% and 91% of all other habitats were trapped in SUMMER and WINTER in the Skye/Mull and Sutherland/Wester Ross scenarios, respectively.

Based on extrapolation from the HMP data, it is clear that the optimal strategy whereby effort is deployed towards trapping MOORLAND, CROFTING and COASTAL habitats, in WINTER and SUMMER, for three days trapping session duration, is more efficient than four days trapping with equal relative effort across all habitats and seasons (Figure 18). Otherwise, the expected times to extinction for both Optimal and Standard strategies are comparable between the two prospective areas and the HMP.

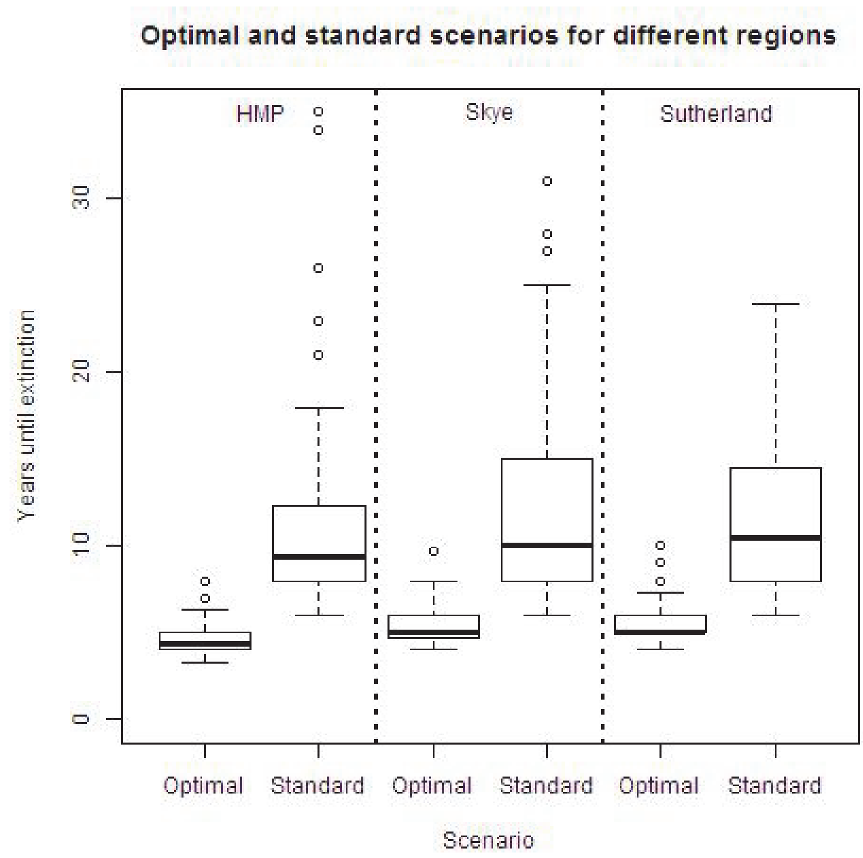


*Figure 18: Mean expected time to extinction for scenarios based on the relative habitat composition of HMP, Skye and Mull. The standard scenario = four day trapping sessions, 43% coverage of all habitats with trapping in each season; the optimal scenario = three day trapping sessions, no trapping in BOG habitat or in SPRING, with pro rata deployment of coverage for other habitats in WINTER and SPRING.*

## 5. DISCUSSION

There were three broad reasons for analysing the data from the Hebridean Mink Project.

1. Forensic: if the project were to rapidly eliminate the last mink, the analysis would provide a retrospective means of rigorously describing the time course of decline in mink numbers and an understanding of the relative contributions made by the various components of the control programme in securing eradication.
2. Strategic: American mink, in common with other introduced mustelids, impact protected species and designated sites across a wide range of areas including some where expenditure to contain their numbers is on-going. Should there be further attempts to eradicate mink elsewhere the analysis could help to optimise these efforts.
3. Greater understanding of the system under management: given that current funding of the HMP runs to 2014, the model provides a prediction on the range of likely extinction times under specific management practices.

## 5.1 Modelling methodology

Describing the decline in the Outer Hebrides mink population in a robust statistical manner and examining the likelihood of achieving its goals of eradication by March 2014 required formulating models and estimating parameters from data on the number of mink captured.

As with any modelling exercise driven by data availability, adjustments and simplifications to a complex ecological reality had to be made to represent population dynamic processes. We briefly discuss the key elements.

Our observation model, which depends on the pattern of decline in the number of individuals in successive trap checks, assumed no (non-trap) mortality, recruitment, emigration, or immigration over the period of trapping (i.e. demographic closure). While most individual trapping rounds included four trap nights, we pooled all trapping rounds in a given habitat over a four month season. Thus, while the assumption of demographic closure was met for the constituent rounds that form our sessions, it is likely that some mink that escaped capture in one trap line may have been caught during the same season in another line. This would result in overestimating the number of mink that escaped capture. Conversely, mink moving away from the trapping zone into a previously trapped zone would lead to underestimation. Both are plausible.

In order to model demographic processes, we divided the continuous process of demography and year-round trapping into three discrete seasons. The seasons we chose relate to key stages in mink life history as well as on a pragmatic decision to avoid inflating the number of parameters to estimate. Considering within season variation in parameters was structurally impossible with the model structure chosen and considering the impact of other cut-off dates was beyond the scope of this project. We also had to assume that mink populations in portions of habitats not trapped in a time interval had the same density as those in sections that were trapped in a season. This was possible because our analyses of trapping data yielded both estimates of the number of mink that escaped trapping and the total number of mink present before trapping commenced (number removed plus the number that escaped). We extrapolated this value to all portions of the same habitat that had not been trapped in that season, using the number of traps in that habitat to estimate the proportions trapped and not trapped. The underlying assumptions that all habitats are suitably covered by traps and random trapping in relation to mink density are plausible given the systematic a-priori selection of trapping sites and scheduling of trapping rounds by the HMP manager. The assumption of equal mink density within a habitat compartment is certainly only a pragmatic starting point dictated by constraints on the number of parameters that can be estimated from the data, but one based on expertise on the ground and knowledge of the ecology of the species elsewhere in its range.

We modelled the female component of the population only, assuming no mating limitation, but used capture data from both sexes to estimate better the probability of capture. Excluding males also leaves out transient males that might be visiting marginal habitat such as boggy moorland. It is exceedingly unlikely that mating limitations occurred in the early stages of the project, but it may possibly have occurred in more recent years when mink numbers were severely depleted, despite the fact that male mink can be highly mobile during the rut (Gerell, 1970). In the absence of empirical evidence on the occurrence of mating limitation, we deemed it wise not to make assumptions that might lead to overly optimistic estimation of how soon the mink population can be eradicated. Similarly, our estimates of likely extinction time were based on the (modelled) death of the last female mink, rather than assuming that a very small population would no longer be viable (the concept of quasi extinction). Again, in the absence of any real data on when a small mink population is no longer viable, it would be unwise to use guesses, especially when all other model parameters are estimated from data.

The demographic model specified was structured by habitat but not age or reproductive stage. Distinguishing between captures of juveniles and potentially reproductive adults might help separate the contribution of movement and reproduction to population growth. We did not access age data in this contract but this could be explored in future work. For instance, we are aware that some female kits were caught at the maternal den in summer. In the absence of data on their numbers and identity, these were treated as if they were adult females, which was an obvious simplification.

The model further assumed constant demographic parameters, implying there was no density dependence despite culling starting when the population was at its putative carrying-capacity in 2007 and becoming reduced to 20% of its initial size by SPRING 2011. These simplifications were motivated by the concern that complex models with many parameters capturing many of the real complexities of ecology, may suffer from 'parameter non-identifiability'. Parameter non-identifiability arises when the data available do not permit the estimation of some parameters. There is an inherent lack of information that keeps some parameters from being estimated due to over-fitting. There is thus a need to find a judicious compromise between how faithful to reality a model structure is and whether it is possible to estimate the model parameters needed to describe this complexity.

We experienced problems with parameter non-identifiability when we attempted, and failed to estimate habitat-specific reproduction. Insufficient data were available to allow for this degree of realism. The absence of information to estimate separately post breeding movements and habitat specific production of independent young, forced us to constrain fecundity parameters to a constant value for all habitats, so as to estimate the production of independent young. This restricts the scope for identifying the habitats that, owing to different demographic rates, or low or ill-timed trapping effort, have created the greatest challenges for the control programme. Indeed, in our model the only habitat specific rates are emigration rates.

### 5.2 Demographic parameters of the Outer Hebrides mink population

The observation component of the model yielded, for the first time, estimates of the probability of capture of American mink from which we could calculate the probability of mink escaping capture in a trapping round. The probability of capture per night ('trappability') started at 0.15 in SPRING 2007, rising gradually to 0.34 in SUMMER 2010. The values of trappability compare very favourably with estimates of daily probability of first capture of 0.14 for stoats in New Zealand (King *et al.,* 2003) and the probability of ferrets escaping capture over six nights of 52%(Morley, 2002). A probability of capture value of p=0.34 translates into 28% of females escaping capture after four days, the duration of 73% of trapping rounds (Figure 3). These values emphasise the probabilistic nature of eradication, a key issue we return to below.

The rise in daily trappability between 2007 and 2010 must reflect improvements in practice on the ground over time, such as trap placement, care in setting traps, use of lures, etc. The pattern runs contrary to what would be expected if trap-shyness was evolving under strong selective pressure imposed by trapping. However, these estimates are averages and do not preclude the existence of a portion of mustelid populations that avoids traps and may not trigger them. For instance, Zuberogoitia *et al.* (2006) detected tracks in the sand of 17 mink that actively avoided traps and urged projects seeking to eradicate American mink to consider those individuals that never trigger traps, such as females living in very small streams and the non-territorial population living in other habitats. King *et al*. (2009) reported similar observations with ferrets and stoats in New Zealand. Furthermore, there was a relative excess of mink caught on the fourth day of trapping, despite assuming all trapping sessions lasted four days, while only 73% did. These may be symptomatic of within group (e.g. females in SPRING) variation in the response of individuals to traps that should be explored further. This may delay eradication beyond what models overlooking such variation predict.

The combined observation/demographic model yielded a range of plausible demographic estimates, demonstrating that the data are informative and giving confidence in model performance. The estimate of productivity (young females per adult female) was 0.34 (with 95% credible intervals spanning 0.06 - 1.08). While this value is substantially smaller than estimates of the number of weaned young from the literature (Gerell, 1971), it is important to keep in mind that owing to the structure of our model, the estimate combines the production and the mortality of kits from birth to time of census, which are indistinguishable using the data. Newly produced young are trapped between September and February such that productivity in the model relates not to litter size at birth, nor at weaning, but to the number of young weaned that survived the post-independence period, including early winter when most juvenile mortality takes place. The estimate of productivity from the HMP is also commensurate with estimates from Aberdeenshire derived from genotyping culled mink and reconstructing parentage (M. Oliver, unpublished data). Adult survival estimates suggest little or no mortality attributed to causes other than trapping in WINTER and SPRING. While natural mortality was trivially small, at 1% per five month period, the estimates exclude newly independent juveniles expected to suffer most mortality. Other studies of mustelids, including island-dwelling feral ferrets also report low mortality in winter (Bodey *et al.,* 2011).

Estimates of dispersal rates depict a situation with very high movement rates between habitats by individuals or their offspring, especially during the WINTER to SPRING transition as well as strong post-breeding movement towards the MOORLAND compartment. The literature lacks quantitative estimates of per capita dispersal rates of mink and the values produced were seemingly high, but certainly not implausible. They partly reflect the inherent habitat patchiness of Lewis and Harris such that relatively short movements amounted to between habitat movements. Overall, the notion that mink redistribute themselves between habitats in late summer and autumn is consistent with population genetics analyses from NE Scotland (M. Oliver, unpublished data) and the HMP staff perception that some coastal females have their kits in inland moorland areas (Iain Macleod pers. com.). The high movement estimates have had large implications for the ability to control the mink population in the Outer Hebrides given only a fraction of each habitat was trapped in each season (below).

As with other demographic rates, the movement estimates in this model were assumed to remain unchanged from year to year. Yet, there are good ecological reasons to expect that patterns of redistribution between habitats changed when the island population changed from saturation to heavy depletion and vacant territories arise in prime habitats. For instance, Bodey *et al.* (2009) suggested that on the Uists, female American mink increasingly made use of coastal resources as control proceeded. While it is technically possible to allow dispersal rates to vary over time, further work is needed to establish whether the data are sufficiently rich to estimate parameters.

### 5.3 The observed decline in the American mink population of Lewis and Harris

When deciding whether to take notice of its diagnostics and predictions, it is useful to ask whether the population abundance estimates from the combined observation/demographic model are credible. We believe they are.

The upper panel of Figure 10 allows a comparison of capture estimates and estimates constrained by the demographic model. There is a good fit between both estimates, except in 2007 and for WINTER 2008 and SUMMER 2011, when capture estimates in MOORLAND alone wildly exceed those compatible with the demographic parameters. Following discussion with Iain Macleod, it transpires that these discrepancies correspond to times when there have been departures from model assumptions in the trapping protocol, with trapping taking place in areas deemed not representative of the habitat compartment in the island. If it is really the case that such anomalous situations only occurred on those occasions, this would increase rather than decrease the confidence in the model's ability to describe the dynamics of the culled mink population despite its many simplifying assumptions.

Some abundance estimates from the capture only model (observation component) appeared anomalous but the way they are arrived at is logical. Estimates reflect the two sources of extrapolation in the data: the estimated number of mink escaping capture in areas trapped in a given season, and the estimated number of mink living in areas not trapped in that season. The latter is extrapolated from the total number of mink (caught or not) in trapped areas and extrapolated pro-rata from the proportion of a given habitat compartment trapped. Thus, if the portion of a habitat trapped is not representative of the whole, a biased estimate will unavoidably be produced by the observation component of the model. This appears to have occurred in three instances mentioned above.

Fortunately, the way a state-space model operates somewhat corrects for such bias. The combined model estimates are those values most compatible with both capture-derived abundance estimates and the demographic rates estimates. All population size estimates are based on a sample of a habitat trapped and thus come with their own uncertainty. Where values are incompatible with population size estimates at the previous time step and demographic parameters are assumed to be constant, it is 'easier' for the model algorithm to give low weight to the anomalous abundance estimate rather than changing demographic parameters across all years and habitats. When anomalous values such as those from 2007 are too influential, we were able to treat them separately. Thus, while the model is imperfect, indeed, it is a caricature of reality; we consider it has sufficient satisfactory features to be used to inform management decisions.

Given the issues with the data from 2007, we have two candidate initial population sizes. Assuming there were as many males as females in 2007, one yields 1,700 mink. This is strikingly similar to the estimate of a carrying capacity of 1,605 (range: 1461-1787) arrived at based on considerations of mink home range size and behaviour by Shirley & Rushton (2011 unpublished). We are, however, much more confident in our estimate of 350 females in SPRING 2008 and used these in the simulations. Both estimates are substantially lower than the estimate of 7,500 – 9,000 females by Hudson & Cox (1989) based on *ad hoc* considerations. We also have a high level of confidence in our estimate of the residual population size in SPRING 2011 as being 155 mink, including 88 females and 67 males. This is a third of the median value of approximately 464 estimated by Shirley & Rushton (2011 unpublished), highlighting the large discrepancies between our data-based approach and the simulation approach used by Shirley & Rushton (2011 unpublished).

## 5.4 Predicting the likely course of the decline in mink numbers on Lewis and Harris

Our combined observation and demographic model suggests that the mink population had declined to 20% of its initial reliable estimate size in SPRING 2008 by SPRING 2011. However, when using the number of mink caught in 2012, but with no estimate of (blind) trapping effort to inform its predictions, the same model predicts that the MOORLAND population may have recovered in 2012. While the model has a good fit to the data (when available), the model predictions have very large uncertainty attached to them when attempting to predict the future, or in the absence of data on trapping effort. As such, the utility of this version of the model that fully propagates all sources of uncertainty in predictions is very limited.

We used an alternative approach to overcome problems with not having data on trapping effort after SUMMER 2011, and only having the number of mink caught following responsive trapping that cannot be extrapolated to the whole island in 2012. As such, we took model-derived demographic parameters as given, used the last reliable estimate of population size in each habitat in SPRING 2011 as the starting value and explored through stochastic simulations, the range of times to extinction under the *hypothetical* scenario that the method of trapping had continued unchanged. These simulations indicate that the mink population is equally likely to go extinct in 2015 or 2016. The earliest simulated extinctions took place in 2014. Eighty per cent of simulations predicted extinction by 2017.

The outcome is relevant **if** reactive trapping is at least as effective as systematic ('blind') trapping at low density, which is highly plausible and is certainly the belief of the HMP staff and ecologists studying American mink. If reactive trapping is more effective than 'blind' trapping then the predictions may be quantitatively overly pessimistic. Qualitatively, they convey the very important message that predictions of the time to extinction take the form of a distribution of more or less likely dates and not a single date. The distribution of extinction times spanned 11 years when based on a 2011 starting point and 27 years when simulations were initialised using data from 2008. Thus uncertainty is reduced but the modal time is unchanged.

Extinction time takes the form of a distribution because in the model, as in the real world, many of the demographic processes have a random element to them. Individuals have a probability to survive, die, enter a trap and produce a number of young, but when this applies to a small residual number of individuals, a wide range of outcomes are feasible for the same set of parameters. Note that throughout, by using well known statistical distributions such as the Binomial or Poisson laws, we assumed that individuals are homogeneous; they are subjected to the same probability. If some individuals do not follow those rules, e.g. if they are inherently shy and reluctant to enter traps, extinction may be delayed relative to predictions. The converse is true if the probability of reproducing decreases with density.

### 5.5 The contributions of aspects of the trapping protocol to observed dynamics

Our retrospective, model-based exploration of the features of the trapping protocol highlights factors that influence time to extinction. We explored the benefits of varying the length of trapping session, the proportion of each habitat trapped and the season of trapping, singly and in combination. According to our model estimates, habitats only differ in emigration rates, not productivity or survival. The key features that affected success are the combination of high mink mobility, the fact that not all mink are caught in a trapping session and, crucially, the fact that only a fraction of a habitat compartment could feasibly be trapped in a season. Together, these components led to a situation akin to a 'game of hide and seek' that delays extinction relative to what would have happened if the whole island was dealt with simultaneously. The outcome was similar to scenarios much studied by population ecologists, whereby the coexistence of a predator (in this case, the trappers) and prey (the mink) is impossible in a homogeneous environment, but coexisting populations can be stabilised by constant re-colonisation through prey dispersal of areas depleted to extinction by a predator that tracks its prey in time and space (e.g. Holyoak & Lawler, 1996). In that context the rate of dispersal of the prey and of the predators (akin here to the number of trapping zones operated in a season), determine the degree to which spatial heterogeneity and the existence of refuges from trapping facilitate predator and prey coexistence. Thus, scenarios involving the redeployment of trapping effort that maximises the proportion of habitat trapped in two seasons, involves shorter trapping sessions, ceases trapping in one season, and reduces trapping in the habitat with highest emigration rate, will hasten extinction very substantially compared to a baseline scenario.

As mink trappability is relatively high, most mink were removed in four days of trapping. Thus the careful manner in which traps were operated contributed much to the decline. Given this, the benefit of extending trapping sessions to five days was limited and less than what would have been achieved if trapper effort had been deployed so as to operate a greater proportion of traps in a season, even if it was at the expense of a few more mink escaping capture in the trapped areas. While the population was declining to extinction, re-colonisation of all areas from temporarily uncontrolled areas delayed eventual extinction. Thus, adoption of even two day sessions, which might have allowed the same staffing complement to trap twice as many traps, is beneficial.

Manipulating the way in which modelled trapping effort was distributed with respect to the duration of trapping sessions and proportional coverage between habitats and across seasons, greatly influenced the expected time to extinction when simulating projected population declines. To recap briefly, the most effective strategies are those that maximise spatial coverage of the project area even if at the expense of the proportion of mink caught in each trapping zone area. Of the modelled redistribution of trapping effort, those involving not trapping in SPRING, not trapping BOG and trapping for three rather than four days, all decreased the expected time to extinction for the HMP area. Moreover, applying these strategies in combination substantially decreased the expected time to extinction from nine to –4-6 years. This could be considered an 'optimal approach' even though there are no doubt logistic constraints that would make its implementation difficult. These are best considered by field staff with an intimate knowledge of the area, the distance that can be covered by field staff and the many constraints of field work. The simulations also indicated that the approach used by the HMP over the period SPRING 2008 – WINTER 2011, was more effective than simply having distributed effort evenly across all habitats and seasons. The mean standardised trapping effort, by habitat, during this period was 0.22, 0.26, 0.28 and 0.24, for BOG, COASTAL POOR, CROFTING and MOORLAND respectively. This has improved efficiency compared with an even distribution of effort, as BOG had the lowest effort deployed. The mean standardised trapping effort by season over the same period was 0.29, 0.24 and 0.47 for SPRING, SUMMER and WINTER respectively. Again this would be expected to have a beneficial effect, as a relative increase in trapping effort in any season, with a pro rata redeployment of effort, improved efficiency in terms of reduced time to extinction. Notwithstanding, the expected time to extinction under the deployment of effort in the HMP over the period 2008 – 2011 was around 9 years (i.e. extinction in 2017). Altering this approach towards the 'optimal strategy', as described, was predicted to reduce this to 4-5 years (i.e. extinction in 2012 – 2013).

Why did these alterations in trapping strategy lead to varying outcomes? Modelling estimated high trappability rates (0.15 – 0.34), which intuitively suggest that decreasing the duration of trapping sessions in favour of increasing the proportional coverage of habitats should result in an increase in the proportion of the standing population removed. Indeed this was the case, a decrease from four to three days resulted in a pro rata change in coverage from 43% to 57%, and the nature of the proportional change in removal, resulting from this trade off, is clearly illustrated in Figure 12.

Not trapping in BOG habitat, with redeployment to other areas, also reduced the expected time to extinction, although not trapping in any other habitat did not improve projected outcomes. It may be generally expected that not trapping in a particular habitat creates 'refuges' from trapping, which could hinder eradication efforts. However, the observed outcomes may be explained, in part, by the high estimated flow of individuals from BOG to MOORLAND (47%) during over-winter dispersal. This very high rate means that as long as MOORLAND is being trapped, a very large proportion of those individuals born in BOG should be exposed to trapping. Firmer conclusions on the relative contributions of different habitats would require estimates of habitat-specific rates of production of independent young. While we attempted to obtain such estimates, this proved impossible with the data available.

Ceasing trapping in any season, with a pro rata increase in effort in the other seasons, was also predicted to have a substantial beneficial effect for eradication outcomes. Again this is likely to be attributable to the high trappability of mink. Ceasing trapping in any season with pro rata redeployment of modelled trapping effort meant increases in coverage from 43% to 64% and, as illustrated in Figure 12, this should lead to a large proportion of the population (ca. 40%, with four day trapping schedules) being removed during every trapping session. With three trapping sessions per habitat per year, such removal rates will cause rapid population decline, even when intrinsic demographic rates are high. An odd observation, contradicting accepted wisdom, was that not trapping in SPRING was slightly more effective than not trapping in the other seasons. This may reflect the fact that SPRING is the only season without dispersal in the model and dispersal seems to play a key role in the resilience of the mink population to control. Furthermore, given that young mink enter the modelled population during the transition from SUMMER to WINTER and not SPRING to SUMMER, this is not as counter-intuitive as it seems. Demographic considerations dictate that reducing the pre-breeding population in the last transition before reproduction and after natural mortality has taken place should be more effective than doing it before mortality affects potential breeders. In practice, however, demographic considerations must be balanced against seasonal variation in mink behaviour that are believed to lead to relatively higher trappability of females before than after they have kits such that it is difficult to trap females until their kits leave the den. The main lesson is that minimising the availability of spatial refuges is key. Given a fixed number of person hours that can be deployed to achieve high spatial coverage in one time interval, the difference in the different scenarios to make this possible are relatively minor. Clearly practical considerations such as the length of daylight, must play a large role in any implementation of the general advice. Refining the division of the year into shorter time intervals might provide further insights into the contribution of each season if it revealed finer scale variation in the demographic or trappability parameters. This was beyond the scope of this project and probably of the data.

Overall, our simulations indicate that, owing to high mink mobility, scenarios that maximise the proportion of a habitat trapped will hasten extinction. This conclusion is wholly in line with accepted best practice in island eradication procedures being implemented with increasing success around the world.

While it is paramount to minimise the scope for re-colonisation through synchronised trapping of as large a portion of the islands as feasible, reaching a suitable scale is very challenging when dealing with a species as mobile as mink. Mink not only disperse at high rates but dispersal distances are such that individuals can potentially cross the whole island in a few days (Gerell, 1971; M. Oliver, unpublished data). In this respect, a key feature of the HMP which is the systematic, sequential trapping of zones, has contributed to the challenge of rapidly achieving eradication. Note that each HMP trapping zone approximates to 100 km$^2$ of often very challenging terrain and there are limits to what a trapper can achieve in a day without the aid of technology. While there certainly are logistical challenges to implementing our ‘optimal scenario’, including re-deploying existing staff time to trap over two seasons only, performing shorter three day long trapping sessions over 100% of three out of four habitats amounting to 70% of the island, and trapping only 54% of BOG, the financial and biodiversity benefits of hastening extinction can be substantially improved. If mink can be eradicated in 4-5 years, there is much greater scope to undo the damage they cause to Scotland’s biodiversity, despite resource limitations. Given the minimal differences between seasons and habitats in our model, it is likely that there is scope to substitute one for the other, so long as high proportional coverage is achieved and the scenario of ‘Hide and Seek’ with repeated re-colonisation is avoided. Thus, mustering a sufficiently large professional work force able to cover as high a proportion of the area as practically feasible simultaneously, may deliver more rapid benefits to conservation, though the careful systematic deployment of traps at regular intervals that took place in Lewis and Harris would be a prerequisite to large scale trapping.

### 5.6 Applicability of the model to other sites and data types

The small influence of habitat composition on the time to extinction was illustrated by applying HMP-derived mink parameters and an initial female population size per unit of habitat to hypothetical scenarios based on Skye and Mull, and Sutherland and Wester Ross. Despite sizeable differences in habitat composition, the presence of less BOG and much more MOORLAND, resulted in predicted extinction times that were similar to those predicted under both the optimal and observed scenarios in the HMP area (Figure 18). Any inference should be limited to the lack of relative differences between hypothetical sites and trapping scenarios, as no information on initial mink density at either site was included in simulations and both areas have been only recently and partly colonised by mink (Fraser 2013). While using HMP-derived demographic parameters should be a sensible first approximation for mink elsewhere, strong assumptions had to be made on how to treat habitat types not present in Lewis and Harris. The message here is that challenges in controlling mink will be similar in those areas, and that similar benefit to achieving synchronised large scale trapping are also likely to be accrued, but with the added challenge of on-going immigration from uncontrolled peripheral areas.

When considering whether our modelling approach can be applied to projects that use other protocols, it is important to remember that fundamentally, the approach developed here depends upon the assumption that estimates of mink population size in trapped areas can be extrapolated to areas that are not trapped. This assumption was met for most of the duration of the HMP, when the whole mink habitat was saturated with traps and these were operated in systematic sweeps, yielding a good depiction of patterns of change in mink abundance. This assumption breaks down when trapping becomes directed. This was well illustrated when we first attempted to use trapping data from 2012, not knowing that trapping was no longer random in relation to mink distribution, but targeted at those areas where HMP staff knew mink survived. Model predictions were of a rapidly growing mink population from 2011 to 2012, spreading from moorland to other habitats. Should information from a few areas with remnant mink be extrapolated to the island as a whole, it is not surprising that large population estimates ensue. Thus, while it seems highly sensible to target trap, a consequence is that the present model loses its utility in interpreting the data that arise from this.

The behaviour of the model from late 2011 illustrates that it cannot estimate rates based on data of a mixed nature, such as a combination of systematic ('blind') trapping and trapping in response to the detection of signs on rafts and land-based tracking tunnels. Thus there is a degree of tension between the need to deviate from a rigid systematic trapping protocol in the face of low catch per unit of effort and the desire to estimate rates and assess the progress of the project towards ultimate eradication.

Based on the experience gained here, there is no doubt that in its present state, the model is not applicable to mink control projects using raft-based detection to guide trapping (Reynolds *et al.,* 2004). This is not for conceptual, but rather practical reasons. Indeed, mink trappability subsequent to detection and attempted trapping on a raft can readily be quantified. What is required is, additionally, an estimate of the probability of detection of a mink on a raft or other detection device (given that a mink is known to be present). Reynolds *et al.* (2010) estimated that the detectability of an individual mink, per monitoring raft, over a two-week check period, varied between 0.4 in late summer and 0.6 in late autumn. By inference, it is possible to estimate the risk of failing to detect a mink, according to the number of independent opportunities to detect it. This would depend on the number of rafts being checked during an interval. Thus, theoretically, provided data are available on the distribution, frequency and outcome of checks for footprints, it should be possible to specify a model that combines probabilities of detection and capture probability, given detection, in an observation model, and then link these through a demographic model. This, however, would require substantial model development and precise data on effort. A severe constraint on doing this, in practice, is the difficulty to convince volunteers to keep detailed records. Indeed, it is worth noting that the volunteer-based mink control project, the Scottish Mink Initiative (SMI), decided not to collect data on the length of time a trap has been set on a raft until a mink is caught, or on the number and length of trapping attempts that do not lead to a capture[2]. It is only recently that progress has been made in obtaining records of raft checking from a subset of volunteers. Similarly, it remains difficult to convince some volunteers and wildlife professionals to avoid using speculative 'blind' trapping, or to leave their traps permanently opened. This variation in the approach to mink trapping would make it impossible to apply the approach designed here to data from the SMI. This is because the observation model used here is not applicable.

### 5.7 Data requirements for future use of the modelling tool and its variants

If future projects were to apply the modelling tool developed here, or one of its variants, they should collect, and organise in databases similar to that used by the HMP, the following information as a minimum requirement:

1) Data on sampling effort including, specifically:
    - The number of traps activated;
    - The habitat in which all traps are placed;
    - The dates when these are activated. Ideally the length of trapping sessions should be standardised and certainly not exceed a length of time over which it is reasonable to assume that the population is demographically closed (e.g. a few days).

    Additionally, if procedures are not as standardized as they were in the HMP,
    - Any variation in the use of bait, lures or trap placement that might result in variation in trappability, such as trapping only in response to the detection of mink footprints on a raft, including setting traps not only on a focal raft but also its neighbours.

2) Data on trapping success, specifically
    - The number of mink caught on each day of trapping
    - The number of trapping attempts that result in no capture

3) Data characterising mink caught
    - The sex of mink
    - The age of mink. This can be as simple as juvenile or '11 month or older'. Hence potentially reproductive specimens can cheaply be determined by taking X-rays of the canines and would allow the fitting of the model structure by stage, (not attempted here). Where resources allow, full age estimation by *cementum* analysis would give scope to fit fully age-specified models. In both instances, however, it is unclear how uncertainty in ageing would affect the results and hence the use of informal, *ad hoc* methods for ageing mink may actually degrade the quality of this information.

[2] Note that recording information on trapping effort and success, not only captures was achieved, albeit with a degree of difficulty and many gaps, by the predecessor of SMI, the Cairngorms Water Vole Conservation Project Bryce *et al*. (2011).

## 6. CONCLUSIONS

We used modern methods to estimate the size of the mink population on Lewis and Harris, including the fraction that escape capture after bi-annual trapping sweeps of the island. We found that approximately 24% of females escape trapping after four days, but importantly, that mink are highly mobile with substantial transfers of individuals between habitats. We were able to document that the population had declined by 80% between 2008 and 2011but were unable to estimate reliably the magnitude of any subsequent change in abundance. This was because the reactive trapping approach adopted by the HMP when confronted with very low capture per unit of effort does not contain as much information on population size at the scale of the islands. Our predictions, based on the statistical estimates of demographic parameters, do unambiguously predict that the Outer Hebrides mink population should become extinct in the near future, with the modal year of the scenario being 2017 under the systematic trapping regime. Under this scenario, extinction could be as early as 2014 and 80% of our simulated population had gone extinct by 2017. Given the high likelihood that the current procedure, focused on detecting and removing the few remnant mink, is almost certainly more effective, it is likely that the population will shortly be eradicated, but funders should be prepared for the possibility that the final stages of eradication may be protracted due to chance factors. Our analysis of the factors that contributed to the outcome, highlighted the important role of dispersal by mink, combined with the fact that only subsets of the islands could be trapped at the same time. This is to avoid the constant re-colonisation of areas cleared of mink by highly dispersive mink. Given the relatively high effectiveness of trapping, the trapping of a large proportion of the island simultaneously with shorter sessions, is substantially more effective than the approach used. There are, however, obvious practical obstacles to implementing the modelled optimal trapping regime.

The innovative manner in which we analysed data from a culling programme to inform its course is novel, and has the potential to be applied more widely to provide a sound evidence basis to the assessment and optimisation of invasive species control programmes in Scotland and elsewhere.

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