Survival on the border: A population model to evaluate management options for Norway's wolves

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Abstract

We present an individual-based model of the Norwegian wolf population, which is used to evaluate the effectiveness of current and potential management policies in fulfilling the Norwegian Government's stated aim of maintaining three breeding packs within a designated wolf zone. The model estimates the 'functional extinction rate' of the population, defined as the proportion of years in which breeding wolf packs are absent. Under current conditions according to estimates from Scandinavia, with observed values of natural survival rates (0.903) and unauthorised mortality (0.203) and allowing for immigration from Sweden, the model predicts that the probability of functional extinction is as low as 0.07. This output variable is highly sensitive to the demographic parameters, and if alternative estimates of natural survival rates (0.73 for cubs, 0.83 for adults) reported for wolves elsewhere and higher rates of unauthorised mortality (0.4) are utilised, the functional extinction rate is 0.67±0.15, and the population is dependent on maintenance by immigration from Sweden. The main determinants of functional extinction rate are the unauthorised mortality rate and the immigration rate from Sweden. The Scandinavian population as a whole shows a rapid non-linear increase in probability of extinction at unauthorised mortality rates above 0.10. Varying levels of the current management interventions (increasing the size of the wolf zone and target number of packs) are ineffective; only when unauthorised mortality rate falls below 0.30 is a self-sustaining population in Norway able to establish. An adaptive harvest policy with culls targeted only at dispersing animals, or taking place only when the population exceeded a threshold level, could be sustainable if the unauthorised mortality rate is reduced. The fact that the Norwegian Government has been explicit about its management strategy and objectives has allowed us to test the ability of this strategy to

meet the objectives, and we have shown that it is dependant upon maintaining the current circumstances alongside a high adult survival rate to be able to do so. Given the potentially critical role of the Swedish population in sustaining Norway's wolves, there is a strong case for joint management of the Scandinavian population. These insights are likely to be relevant for the management of other species living across geopolitical boundaries.

Introduction

Large carnivore management regimes are often controversial. The extremely mobile and wide-ranging nature of these species means that they can rarely be conserved just within protected areas (Linnell et al. 2005a). Successful conservation of large carnivore populations involves management of entire landscapes, often across administrative boundaries. The conservation of trans-boundary populations is particularly challenging, as management regimes may vary hugely as animals move over borders. For example, in Scandinavia, Sweden has a large population of brown bears (*Ursus arctos*), while the Norwegian population is dominated by immigrant young males from Sweden (Swenson et al. 1998). For the wolverine (*Gulo gulo*), the entire northern population in Sweden and Norway is very sensitive to off-take on the Norwegian side of the border (Sæther et al. 2005). Nevertheless, the populations are managed independently.

Throughout much of the northern hemisphere, the most controversial large carnivore species, with a particularly extensive range, is the gray wolf (*Canis lupus*). Wolves have for thousands of years lived in close proximity to mankind, and the relationship has often been volatile (Mech 1970). In recent centuries, the perception of the wolf has been as an agricultural pest, a competitor with hunters, and a direct threat to human safety. Consequently, the wolf has seen a sharp decline globally, and extirpation from much of its former range (Mech & Boitani 2003). However, in common with other large charismatic carnivores, many people now recognise the wolf as a vulnerable component of global biodiversity, a tool for ecological management, and a potent 'flagship' symbol of the wild (Linnell et al, 2000). The wolf thus epitomises many of the issues faced by policy-makers aiming to enable coexistence of people and wildlife (Woodroffe et al. 2005).

Norway's wolves

On the Scandinavian peninsula, having faced deliberate persecution for centuries, wolves were considered functionally extinct by the 1960s (Wabakken et al. 2001b). However, in 1983, a single breeding pack was discovered in South Eastern Norway, close to the Swedish border, which had probably immigrated from Finland or Russia (Wabakken et al. 2001b, Linnell et al. 2005b). Numbers slowly grew, but faltered under the effects of genetic depression and demographic stochasticity (Liberg et al. 2005) until apparently being sustained by the arrival of a third immigrant in 1991 (Vila et al. 2003). Since then, the population has expanded rapidly; by 2005 the total Scandinavian population was generally held to have grown to 119-143, with the Norwegian sub-population numbering ~ 20 wolves (Wabakken et al. 2005).

Since its re-establishment, the Norwegian wolf population has attracted substantial controversy, as well as intensive research and population management (see e.g. Nilsson, 2003, Skogen, 2001, Wabakken et al., 2001a). Politically, the wolf became a focus for the more general conflict between rural and urban communities, the former leaning toward eradication of the wolf as a threat to humans, livestock and big game, and the latter toward its conservation (Skogen, 2001). In the face of strong demands from the anti-carnivore lobby, in 2000 the Norwegian government sanctioned a culling programme. One of the more recent culls, in 2005, killed 5 of the 22-24 individuals in the country, comprising an alpha female and two scent-marking pairs, leaving 16 wolves and only one functional breeding pack. This led to major international concern about the future of Norway's population (information from reports by animal-interest groups such as Proact Mammal Campaigns, 2006, and the WWF and BBC news websites; confirmed through expert consultation).

The stated aim of the Norwegian government is to maintain 3 breeding pairs within a designated wolf zone, as a compromise between wolf conservation and livestock rearing in the region (Miljøverndepartementet, 2004). This three pack limit does not include packs that straddle the border. From a biological point of view, Norway's wolves form one contiguous population with Sweden's animals. In Sweden, Government policy at the time of writing is to have 20 breeding packs within the country, but the whole wolf population is likely to be affected by the Norwegian culling given that the current population is still only around 140 animals. This has led to correspondence between Sweden and Norway, regarding their joint responsibility for wolf conservation under the Convention on Biological Diversity and the 'Bern' Convention; however, the Minister of the Environment of Norway recently stated that there will be no joint management of large carnivores with Sweden (Erik Solheim, official statement on 25th October 2007).

Modelling wolf behaviour

There have been several Individual Based Models (IBMs) developed for wolves (e.g. Vucetich et al. 1997, Haight et al. 1998, Chapron et al. 2003, Nilsen et al. 2007), while Nilsson (2003) used a structured matrix approach to investigate the effects of catastrophes, hunting and inbreeding on the Scandinavian wolf population. Population modelling is a useful tool to guide the management of endangered species, allowing the exploration of the impact of different management strategies on population viability for a given set of limiting factors (Coulson et al. 2001). Socio-political considerations determine the acceptability of particular strategies, but modelling can evaluate the likely impact of different strategies on the viability of Norway's wolves, and hence on the Government's ability to fulfil its stated management objectives. We can also use models to explore the biological consequences of the objectives themselves. In this paper we develop a stochastic individual-based model for wolf population dynamics, and use it to explore the effects of key demographic parameters on the viability of the Norwegian wolf population. These include variation in mortality, dispersal, pack number and pack establishment rates linked to different management strategies, as well as the extent of unauthorised killing. We then ask what effect the target of three breeding packs and the current size of the wolf zone have on the viability of both the Norwegian and the wider Scandinavian population, and hence whether Norway's management aim is compatible with Sweden's. This modelling framework is applicable to wolf population dynamics more broadly, while the exploration of management options is both an interesting case study of the interactions between social and biological factors in carnivore management, and of the quantitative evaluation of the implications of a government's stated conservation objective.

Methods

Due to the importance of the wolf's social structure for its population dynamics and the small size of the Scandinavian population, we used an individual-based model (IBM). We modified the model developed by Nilsen et al. (2007) to reflect the biology of the Scandinavian population. Other than Nilsson (2003), which is not an IBM, previous models of wolf population dynamics have mainly focussed on the interaction between wolves and their prey. In this study we change the focus towards assessing options for wolf population management. Given this focus, and the fact that the Scandinavian population is not likely to be prey-limited due to its small size and the abundance of suitable prey in the area (Nilsen et al. 2005), we treat wolf-prey interactions in a simplistic manner and focus on the dynamics of the wolf population itself. Also we consider only the demography of the population, and do not include management for genetic variation; Nilsson (2003) warns that inbreeding is a potentially serious threat to the long-term viability of the Scandinavian population, but our focus is on short-term management for population viability and hence genetic considerations are outside our remit. Nevertheless, it is clear that genetics have an important role to play in such a small and isolated population of mammals, and hence the results of this study should be considered in this light (see also Liberg et al., 2005).

The Norwegian subpopulation was treated as an isolated population with a trickle of immigrant wolves from an unstructured outside source (Sweden); there was no spatial demographic sub-structuring of the population as a whole. Each individual within the IBM is uniquely identified and has an age, sex, stage and pack membership associated with it. Transitions between stages are related to age and social status, and all transitions take place probabilistically for each individual in random order. Each pack consists of a dominant pair and their offspring; only the dominant pair can reproduce. The initial population was assumed to be 21 wolves, comprising 3 packs of 6 individuals with 3 dispersers, to simulate the current Norwegian population: each pack contained a 4 year old alpha pair with four descendants (2 male, 2 female) of ages 1-3, and the dispersers (2 male, 1 female) were aged between 2 and 3 years.

The model has four compartments, reflecting different wolf life-stages (Fig 1a), and 6 demographic processes are modelled, in the following order; survival, dispersal, establishment of a territory, anthropogenic mortality, reproduction and immigration from Sweden (Fig. 1b, Table 1). Each year, the previous year's cubs can either disperse, remain in the natal pack as a sub-adult, or die. The existing sub-adults can disperse, die or remain in the pack as sub-dominant adults. Sub-dominant adults each year have a probability of dispersal and mortality and otherwise they remain in their natal pack. Dominant animals have a probability of survival and a reproductive rate. If a dominant animal dies, it is replaced by the oldest sub-dominant animal of the right sex in the pack. If there is no suitable animal available within the pack, the position remains vacant until it is filled by a dispersing animal or until a young individual moves up into the sub-dominant adult stage. The pack cannot reproduce until a new dominant pair is established. If both dominant animals die, the rest of the pack disperses. This assumption was made primarily to simplify the model, but is considered reasonable with regards to the literature: Fuller et al (2003) support the assumption, and in Brainerd et al (2008), the loss of both breeders was noted to cause pack dissolution in 85% of cases, and in only 9% of cases did a pack reproduce the following season under such circumstances.

The first step in the annual cycle is that each individual other than the dominant pair has a probability of joining the pool of dispersing animals. Each disperser over two years old then has a probability of establishing a territory. If an animal is establishing a territory, it first looks for an existing pack with a missing animal of the correct sex, and next establishes a new territory in which to wait for a pair. If neither is available, it remains in the disperser pool. It is assumed that the probability of any disperser being successful in establishing a new territory (and hence the total number of territories available) is linearly related to the size of the designated wolf zone.

Once the territory establishment process is complete, dominant pairs reproduce, producing a large or small litter with a given probability, the size of the litter being defined from the literature. For instance, the number of pups in a small litter was taken from Mech, 1970; and relates to data from a study of thinly distributed wolves in Alaska. Next, immigration from Sweden occurs, with the immigrants joining the disperser pool. These immigrants are assumed to be sub-adults and are assigned a sex with a probability based on empirical observation (Mech, 1970); note that these observations relate to studies of a small population in Finland, which was repopulating at the time and hence far from carrying capacity, so was appropriate for this model.

Next, survival of each individual is modelled, as a function of overall wolf population density and prey availability. As prey are not considered limiting, but to fluctuate from year to year due to climatic conditions, the prey availability was modelled by adding an error term to each survival rate, drawn from a uniform distribution with a mean of 1.0 and a standard deviation of ±10% and varying on an annual basis. In the absence of explicit feedback between the wolf and prey populations, density dependence was modelled in a ratio-dependent manner; that is, beyond the threshold population size at which density dependence begins to act, all survival rates were multiplied by the ratio of the threshold population size and the current total wolf population (Eberhardt et al. 2003). This threshold was set at 100 wolves based on expert consultation; this is the number estimated to fit comfortably within the current wolf zone (Pedersen *et al*, 2005). Basic survival rates were age-dependent, and not related to other factors such as the life stage of the wolf (e.g. survival rates were not modified based on whether the wolf was sub-dominant, dominant or dispersing). This is ecologically unrealistic; dispersing wolves in particular are likely to be at greater risk of mortality than wolves resident in a territory (Pletscher et al, 1997). However, in this model dispersing wolves do not materially affect the functional extinction rate until they find a territory, and therefore disperser mortality is subsumed into the other parameters.

Finally, anthropogenic mortality of two kinds was applied; legal culls and unauthorised mortality. The latter includes both deliberate and accidental killing, such as road deaths, shooting or poisoning. We assume that unauthorised mortality targets individuals from all stage-classes with equal probability, while legal culls could potentially target individuals from particular stage-classes. The parameters in Table 1 were the result of a full literature review and are referred to as the 'baseline' parameters throughout. Liberg et al.'s (2008) estimates of survival rates (including unauthorised mortality) for wolves in Sweden are substantially different to the values obtained from the literature. We explicitly considered the effect of using these values instead of the baseline values, due to the sensitivity of the model to these two parameters.

The model was coded in R (R Core Development Team 2007), and each simulation was run 50 times over 100 years in order to generate the main results; 50 was the minimum number of repetitions considered necessary statistically to keep the confidence intervals (CIs) acceptably narrow, and this minimum was used due to the time taken to run the model. The output parameter of interest is the number of years in the 100 year simulation in which there are no functional breeding packs. This may occur when the total population size is above zero, and does not represent population extinction partly because of internal recruitment of animals to breeding from the sub-dominant stages and partly because of immigration from the contiguous Swedish component of the population. A true probability of extinction is not possible to calculate for a population receiving continuous immigration, but because the Government of Norway’s stated aim is to maintain a breeding population of wolves, this metric is a policy-relevant measure of management failure. We shall call this metric the “functional extinction rate”; hence, the functional extinction rate is equivalent to the proportion of the 100 year time span of the model in which no alpha pairs were left in the population.

Sensitivity analyses were run by varying all parameters simultaneously both over a feasible range, given in Table 1, and by picking values from a distribution with a standard deviation of 10%, according to the method of McCarthy et al. (1995). The model was run for 500 random parameter combinations, each repeated 50 times. The wolf population’s functional extinction rate was used as the dependent variable in a general linear model (GLM) with a binomial link, including all parameters and their interactions. The linearity of the relationship between the parameters and the functional extinction rate was examined by plotting the parameter values against the logit of the extinction risk (McCarthy et al. 1995), and the significance of each parameter as a determinant of extinction risk was inferred from the coefficients of the GLM.

Sensitivity analyses revealed that the parameters to which the model was most sensitive were the immigration rate from Sweden and the unauthorised mortality rate. These are the two parameters with the highest uncertainty attached, but are also parameters that can to some extent be controlled by management interventions. Other important parameters were the probability that an immigrant wolf from Sweden was male, the probability of establishing a territory and survival rates. When the sensitivity analysis was run with a ±10% change in parameter values, rather than varying them over a feasible range, the results were qualitatively the same, except that the importance of the survival rates increased. As expected, there was no discernable relationship between most of the variables and the functional extinction rate. The relationship between the functional extinction rate and the immigration and unauthorised mortality rates was linear with an r^2 of 0.61 and 0.27 respectively. The total uncertainty in extinction risk that stems from the uncertainty in the initial parameter values can be calculated based on the inherent uncertainty from the three most influential variables (unauthorised mortality levels ± 10%; immigration rate ± 10%; probability of success in establishing a territory ± 5%). From these three dominant sources of model sensitivity the total uncertainty in extinction risk (due to uncertainty in initial parameter values) can be estimated at ± 15%, using the basic error formula:

$$\sigma_y^2 = \sigma_{x_1}^2\left(\frac{\partial y}{\partial x_1}\right)^2 + \sigma_{x_2}^2\left(\frac{\partial y}{\partial x_2}\right)^2 + \sigma_{x_3}^2\left(\frac{\partial y}{\partial x_3}\right)^2 \qquad \text{Eqn 1}$$

(where σ_y = uncertainty in the dependent variable, σ_{xi} = uncertainty in the ith independent variable, y = the dependent variable, x_i = the ith independent variable, i = 1 - 3)

This is a conservative estimate of the experimental uncertainty in the extinction risk, and assuming that the relationship between extinction risk and any independent variable is of constant form as parameter values vary, it was applied to the rest of the results where appropriate.

Validation of overall model behaviour was carried out by applying the model to data from the Yellowstone wolf population (it was not possible to validate the model against data from the Norwegian population, as the relevant time series is too short). The Yellowstone population grew from a small initial population introduced in 1995, in an area of abundant prey, according to available data (taken from the official web-based data stores maintained by the US Centre for Biological Diversity, and Yellowstone National Park, accessed 2006). Hence, the qualitative behaviour of the population in Yellowstone is likely to be similar to that of the Norwegian population in the absence of human interference, particularly given the constancy of wolf biology over a wide geographic range (Mech 1970). Therefore, starting with the known wolf population introduced to Yellowstone in 1995, the model was used to predict the subsequent growth of that population. The official data sources mentioned were used to establish upper and lower bounds of the estimated wolf population in Yellowstone from 1995 onwards, and the model was found to predict a wolf population that was comfortably within these bounds, thus validating general model behaviour. Validation of the estimate for immigration rate was carried out by applying the model to the Scandinavian population as a whole and calculating the net immigration rate across the Swedish-Norwegian border (Scenario 1b; Table 3). The model was then used to explore a number of management scenarios (Table 3).

Results

The baseline model

The baseline parameter values given in Table 1 produced a population that fluctuated dramatically, with a mean number of wolves of 4.2 ± 3.4 (the standard deviation is used throughout), and an average of 67% ± 15% of years having no functional breeding packs (Scenario 2a, Fig. 2a). With these rates, the Norwegian wolf population is sustained by immigration from Sweden, and would otherwise quickly go extinct. If we assume no legal culling, the functional extinction rate is virtually unchanged, at 0.64 ± 0.15 (Scenario 2b). The results are, however, sensitive to parameter values, and the functional extinction rate (Scenario 2a, 2b) is significantly reduced to 0.07 ± 0.15 if the far higher natural/unauthorised survival rates estimated by Liberg et al (2008) are utilised. In the absence of either unauthorised mortality or legal culling, and with constant immigration from Sweden, the model predicts a zero functional extinction rate, and instead rapid growth to an equilibrium population fluctuating around 250 animals (Scenario 2c, Fig 2b). Given that our density dependence and prey dependence assumptions are crude, this result is not intended predicatively, but merely as an exploration of model behaviour. The model assumptions are best suited to exploring dynamics at low population sizes when there is negligible resource limitation.

The Norwegian population is only one part of the Scandinavian population, and so the model was run for the Scandinavian population as a whole, for comparative purposes. The following specifications were used (Scenario 1b): there was no immigration (the Scandinavian population as a whole is effectively isolated), no culling (the Norwegian culls act on a small proportion of the population, so were ignored for simplicity), unauthorised mortality levels were set to 0.20 (as estimated by Liberg *et al*, 2008), and the initial population was 15 packs (approximately the 2005 size). The metric of extinction was the proportion of runs in which the population reached zero (because the population is isolated and assumed not re-colonisable). With the baseline set of parameter values, the extinction rate was 0.92. This value was highly dependent on the unauthorised mortality rate (Fig. 3), with a probability of extinction of zero when unauthorised mortality was zero, and a rapid, non-linear increase in probability of extinction between unauthorised mortality rates of 0.10 and 0.20. The extinction probability was also far higher than the 0.05 – 0.29 calculated by Nilsson (2003) for various short term scenarios using an age-structured model rather than an IBM. The discrepancy is likely to be due to a number of differences in the model, including the lower unauthorised mortality rate and higher initial population assumed by Nilsson (2003); and indeed, when rerun using the survival rates estimated by Liberg et al (2008), our model does agree with Nilsson (with a mean functional extinction rate of 0.06).

We used the model of the Scandinavian population as a whole to calculate the net number of dispersers moving from the Swedish to the Norwegian populations, on the assumption that Norway has 3 of the 15 packs. The value was calculated as 4.6 ± 2.7 wolves, not significantly different from the 4 ± 1 animals used in the model, which was based on expert opinion. This gave us further confidence in the validity of the model assumptions.

Management interventions

The current management regime in Norway revolves around a target maximum number of packs (currently 3), with the presumption that any packs formed above this number will be broken up by culling the dominant pair. The other major component of the management regime is the designation of a “wolf zone”, within which wolves are allowed to exist, and outside which animals are culled. We model changes in the size of the wolf zone through the proxy of the probability of establishing a territory, on the assumption that the probability that a dispersing animal is able to establish a territory is linearly related to the area available. This assumption is questionable, but is taken in the absence of empirical evidence about the relationship between the area of the wolf zone and wolf demography. On varying the target maximum number of packs (Scenario 3a) and the probability of territory establishment (Scenario 3b), we see that above a target number of packs of about 5, the probability of functional extinction is unchanged as the target number of packs increases. The total number of wolves in the area (irrespective of whether they are in packs) is also insensitive to the target number of packs after the initial increase to 5 packs, and is very low, between 5 and 7 animals (Fig. 4a). The effect of an increase in the probability of establishment is also minor. It is clear that the limiting factor for Norway’s wolves is neither the size of the wolf zone nor the chosen target number of packs, and hence that varying either aspect of the current management regime will not improve the population’s viability. Increasing the actual number of packs in the initial starting population rather than the maximum number of packs allowed, on the other hand, has a direct linear relationship with functional extinction rate (Scenario 4a, Fig 4b).

The functional extinction rate is highly sensitive to the immigration rate from Sweden, and as the immigration rate increases, the sensitivity of functional extinction rate to the target number of packs also increases (Scenario 3c, Fig. 5, Table 4). This again demonstrates that under the current levels of unauthorised mortality, the main driver of the viability of Norway's wolves is the success of Sweden's management interventions. Similarly, looking at the Scandinavian population as a whole, the existence of immigration from Finland or Russia at the rate of just 2 animals per generation (the level required to ensure that inbreeding is not an issue) reduced overall extinction risk significantly; from 0.92 ± 0.10 to 0.60 ± 0.15 when using the baseline parameter values (Scenario 1c). Starting from a zero population (i.e. after a second extirpation of Norway's wolves), the probability of a viable population re-establishing through immigration from Sweden depends strongly on the unauthorised mortality rate (Scenario 4b, Fig. 6). The number of wolves in the population after 100 years increased to a high level when unauthorised mortality rates fell below 0.30 with other parameters at the baseline values, showing a self-sufficient population not reliant on continued immigration from Sweden. The same quantitative relationship is observed when the higher survival rates reported by Liberg *et al* (2008), but with a higher unauthorised mortality threshold below which the population is relatively secure (0.40 – 0.50).

Public opinion may dictate that a legal wolf cull is required in order to ensure that wolves are accepted within the wolf zone. Hence we explored the effects of a legal cull on wolf population viability. If the cull is a straight proportion of the population size it leads to increases in functional extinction rate equivalent to the effects of raising the unauthorised mortality rate by the same amount (Scenario 5a, Fig. 3). A decision rule was then tested by which a set number of dispersing wolves could be killed once the number of dispersers had reached a threshold level (Scenario 5b). This policy aims to maintain the stability of the breeding packs, and has negligible effect on extinction probability. However, the cull is only possible in certain years, with the number of years dependent on the level at which the threshold is set. For example, if one wolf can be killed every time there is one or more disperser, 40 ± 5 wolves are killed in 100 years, while if two wolves can be killed when there are 2 or more dispersers, 10 ± 5 wolves are killed in 100 years. Again, this is dependant upon the assumed parameter values, and more wolves are culled if higher natural survival rates are assumed.

Given the low number of wolves actually killed, the feasibility of this strategy depends on whether the mere fact that there is a legal cull in principle is enough to satisfy the public, and upon whether it would be possible to implement such a policy in practice. We tested another variant of the legal hunting quota; a proportional threshold cull, which has been shown previously to be a robust hunting strategy under conditions of uncertainty (Scenario 5c, Engen et al. 1997). Under this strategy, a fixed proportion of the population, with individuals selected at random, is culled once the population size has exceeded a certain threshold. This was explored both under the baseline unauthorised mortality rate and on the assumption that unauthorised mortality levels are at half this level, following Liberg et al. (2008). Under baseline unauthorised mortality levels and for culling thresholds greater than 15 wolves, the population size was so low that hunting virtually never took place, and so the extinction risk was unaffected. However, with an unauthorised mortality rate of 0.2, the overall extinction risk was lower, and there were corresponding changes in the actual hunting rate and the extinction risk. For instance, with baseline parameter values, hunting beginning at a threshold of 9 wolves (i.e. approximately 2 packs) and a proportional hunting rate of 0.18, on average 1 – 3 wolves could be legally culled a year, with a mean functional extinction rate of 0.29. By way of comparison, using the higher survival rates from Liberg *et al* (2008), with a proportional hunting rate of 0.18 but a higher threshold of 15 wolves (approximately 3 packs), as many as 6 - 7 wolves could be culled on average a year, with a mean functional extinction rate of 0.09.

Discussion

Our model of Norway's wolf population estimates a functional extinction rate of 0.67±0.15 under the baseline parameter values based on a literature survey, while it was 0.07 with the current high survival reported by Liberg et al. 2008. The former result is comparable to Vucetich *et al*'s (1997) finding of a 0.70 extinction probability for an isolated population of 50 wolves over 100 years, also using an IBM. The functional extinction rate is completely dominated by the relative values of the immigration rate from Sweden and unauthorised mortality, and the outcome is insensitive to current management policies, such as the size of the wolf zone and the target number of wolf packs. This is a worrying finding, firstly because unauthorised mortality is difficult both to monitor and to control, and secondly because of the precarious state of the Scandinavian population as a whole. The extinction rate is sensitive to both natural and anthropogenic mortality rates. Currently, Norway appears likely to be a sink for the Swedish part of the population, completely reliant on Sweden to meet its management objectives. Norway also has a policy of higher management off-take for other carnivores: Norway has the dominant part of the trans-boundary population of wolverines, and Sæther et al. (2005) modelled that current off-takes on the Norwegian side of the border make the northern population likely to go extinct. Wolves in Norway are not necessarily currently self-sustaining, and if the current situation remains unchanged we would expect to see very low and highly variable population sizes (in line with empirical observations from recent wolf censuses in Norway; Wabakken et al. 2001a, 2002, 2004a, 2004b, 2005), with regular functional extinction of the breeding packs followed by re-colonisation from Sweden. The model does not account for any effects of low genetic variation (see Methods), which is likely to be a characteristic of such a small population. Although a discussion on genetics goes beyond the scope of this paper, it is likely that this would be a further factor contributing to a high probability of functional extinction of the Norwegian wolf population (see Nilsson, 2003, Liberg et al., 2005).

However, our analysis has also revealed some potential ways forward. We show that if unauthorised mortality were brought under control, Norway's population could grow to a self-sustaining level within the current wolf zone, assuming they can utilise this area to the full. With only a few additional immigrants per year from Finland or Russia, and with reduced unauthorised mortality, the Scandinavian population is potentially viable both ecologically and genetically. If Liberg's (2008) estimates of unauthorised and natural mortality in Scandinavia as a whole are also applicable to the Norwegian subpopulation, this would be enough to reduce the functional extinction rate to a low level. Research to reduce uncertainty surrounding estimates of mortality rates in Norway, and action to reduce these mortality rates, are key priorities for scientists and managers aiming to ensure a viable, self-sustaining wolf population in Norway, as envisaged in Government policy.

A permit-based legal cull, of the proportional threshold type recommended by Engen et al. (1997), could provide a means of control by providing a mechanism for legal wolf hunts. By its precautionary nature, it would allow Norway to fulfil its conservation objectives and support a more robust wolf population; potentially also reducing reliance upon the ‘wolf zone’ approach to conservation, which can lead to social conflict. Given that many Norwegians are in favour of a continued wolf presence in Norway, and that the Swedish wolf population is currently indirectly supporting Norway’s wolf population through cross-border movements, there is a case for increased cooperation between the two governments. This might take the form of a joint wolf management agreement, in which Sweden was recognised as the partner maintaining the majority of the wolf population and acting as a source for Norway’s population, while Norway took the role of ensuring immigration from Finland or Russia to safeguard the genetic viability of the joint population. The economics of management of joint stocks has been explored for other species (e.g. Skonkoft, 2005), and this body of theory could form the basis for an equitable agreement.

Our study is a useful contribution to the wolf management literature partly because we have been explicit about testing the implications of the Norwegian government’s stated management objectives. We have shown which parameters impact most strongly on the government’s ability to fulfil these objectives, and which are most in need of improved monitoring in order to reduce uncertainty about outcomes. We have also been able to demonstrate the relative effectiveness of current and potential management interventions. It is important that governments state their objectives and management strategies in the transparent way that the Norwegian government has done, as this enables evaluations of this sort to be carried out.

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Table 1. Parameter values used in the model. “Symbol” refers to symbols used in Figure 1a. Baseline values are probabilities unless otherwise stated; square brackets give the values recently published by Liberg *et al*, 2008. The standard deviations for the distributions around the mean values used in the sensitivity analyses are shown in the “Standard Deviation” column. Parameter values were taken from the literature, except those marked “Expert” which were conservative estimates reached during consultation with wolf experts in Norway.

Parameter	**Symbol**	**Baseline value**	**Standard Deviation**	**Source**
Cub dispersal rate	d_c	0.35	0.15	Gese and Mech 1991
Sub-adult dispersal rate	d_s	0.50	0.25	Gese and Mech 1991
Adult dispersal rate	d_a	0.90	0.20	Gese and Mech 1991
Mean net annual immigration rate (individuals/yr)	m	4.0	2.7	Expert (see acknowledgements), confirmed through modelling
Probability that an immigrant is male	p_m	0.7	0.1	Study bu Pullianen quoted in Mech (1970).
Probability of establishing a territory	p_t	0.8	0.1	Pedersen et al, 2005
“Small” litter size (# cubs)	f_S	2	1	Mech (1970)

“Large” litter size (# cubs)	f_L	5	1	Nilsson, 2003
Probability of a large rather than a small litter	F	0.73	0.15	Calculated based on Pederson et al, 2005
Cub survival rate	s_c	0.73 [0.903 Liberg *et al*, 2008]	0.15	Nilsson, 2003; Mech 1970
Survival rate for wolves aged 2 – 8 years	s_a	0.83 [0.903 Liberg *et al*, 2008]	0.17	Nilsson, 2003; Mech 1970
Survival rate for wolves aged 9 years	s_9	0.40	0.08	Mech, 1970
Survival rate for wolves aged 10 years	s_{10}	0.25	0.05	Mech, 1970
Unauthorised mortality	H	0.4 [0.203 Liberg *et al*, 2008)	0.25	Expert (various sources; see Acknowledgements)
Prey availability multiplier		0.2		Expert (various sources; see Acknowledgements)
Density dependent threshold		100		Expert (various

				sources; see Acknowledgements)
Legal cull level		3 breeding pairs		Government target

1

Table 2. Results of a sensitivity analysis in which a generalised linear model was fitted with a binomial link, and the functional extinction rate as the dependent variable. The table shows the coefficients of all the parameters in the full model, and the significant interactions. Significance is coded as: P<0.001 ***, P < 0.01 **, P < 0.05 *, P > 0.05 NS.

Parameter	**Standardised β_i**	**Significance**
Mean net annual immigration	0.076	***
Unauthorised mortality	0.050	***
Probability that an immigrant is male	0.013	***
Probability of success in establishing a new territory	0.045	***
Adult survival rate	0.073	***
Cub survival rate	0.040	*
Cub dispersal rate	0.001	NS
Yearling dispersal rate	0.001	NS
Adult dispersal rate	0.001	NS
Litter size	0.003	NS
Survival rate at age 9	0.002	NS
Survival rate at age 10	0.001	NS
Unauthorised mortality x Adult survival	0.013	***
Unauthorised mortality x Immigration	0.010	***

rate		
Adult survival x Immigration rate	0.004	***
Immigration rate x Probability immigrant is male	0.005	***
Unauthorised mortality x Probability of establishing territory	0.001	***
Immigration rate x Probability of establishing territory	0.005	**

Table 3. The different management scenarios explored using the model. Scenarios 2 – 5 model the Norwegian population.

Number	Scenario	Explanation
1	a	Yellowstone wolf population (model validation)
	b	Scandinavian population as a whole, in isolation
	c	Scandinavian population as a whole, with immigration from Russia/Finland
2	a	Baseline (i.e. present management regime, Norwegian population)
	b	Baseline without legal culls
	c	Baseline without legal culls or unauthorised mortality
3	a	Baseline; vary target number of packs
	b	Baseline; vary size of wolf zone
	c	Baseline; vary immigration rate
	d	Baseline; vary unauthorised mortality rate
4	a	Present management regime, but vary no. packs in initial Norwegian population
	b	Present management regime, zero wolves in initial Norwegian population
5	a	Legal cull; fixed proportion of wolf population annually
	b	Legal cull; fixed number of dispersers given a threshold population
	c	Legal cull; proportional cull of population given a threshold

		population

Table 4. The threshold target number of packs at which the extinction probability levels out, and the value at which it levels out, for different immigration rates.

Immigration rate (# wolves)	Target number of packs threshold	Functional extinction rate
0	-	0.97
1	-	0.88
2	3	0.76
3	4 - 5	0.65
6	6 - 7	0.39
9	8 – 9	0.35
12	8 – 9	0.16
14	10 - 11	0.11

Figure Legends

Figure 1. Schematic representations of the model. a) The wolf life cycle. The symbols for the vital rates refer to the parameters listed in Table 1. Note that the transition in italics (from sub-dominant to dominant) is not automatic, but depends on the death of an alpha animal. The processes represented here are movements between stage-classes. Survival rates are age-specific, hence there can be several different survival rates operating in one stage. b) The order of implementation of demographic processes in the model, on an annual cycle.

Figure 2. a) A single run of the baseline model (parameter values in Table 1; Scenario 2a in Table 3), showing the number of individual wolves and of packs in Norway over a 100 year period. In this run the functional extinction rate (number of years with no breeding packs) was 0.66, and the mean size of the wolf population was 4.16. b) A run of the baseline model with no culling or unauthorised mortality (Scenario 2c), showing the population stabilising at a mean size of 263 wolves in 47 packs.

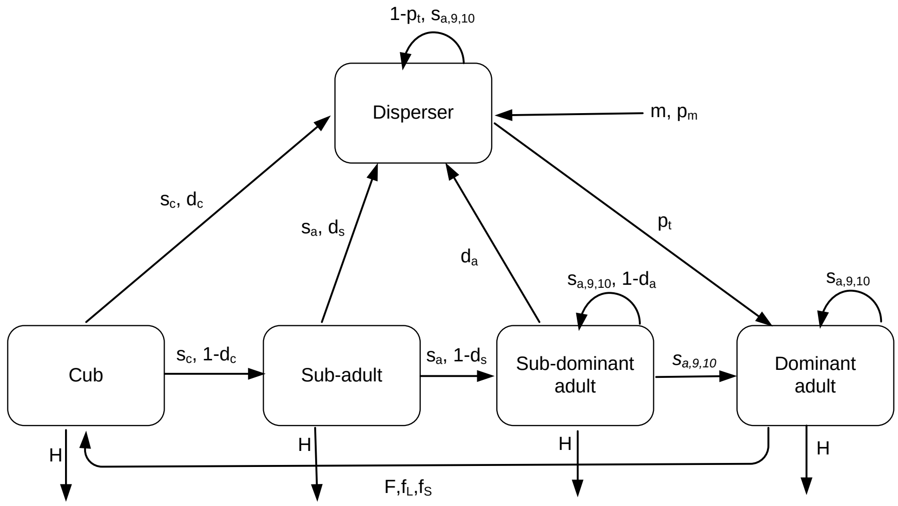
Figure 3. The proportion of runs in which the Scandinavian population as a whole is extirpated (Probability of Extinction), shown as a function of the unauthorised mortality rate (baseline value – 0.20; Scenario 3d).

Figure 4. a) The average number of wolves in the population after 100 years as a function of the target number of packs, with the line of best fit (Scenario 3a, baseline value - 3). b) The total size of the Norwegian population, as a proxy for re-

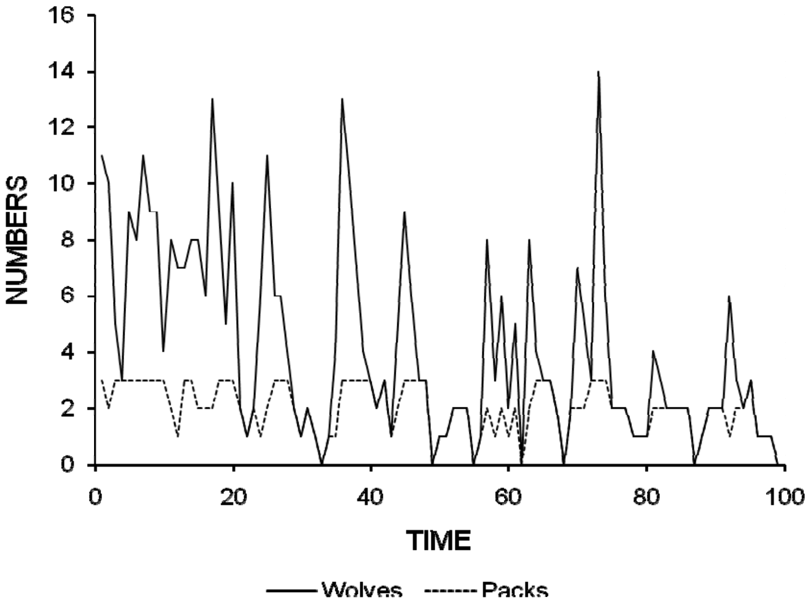
establishment success, plotted against the number of packs in the starting population (Scenario 4a, baseline value – 3).

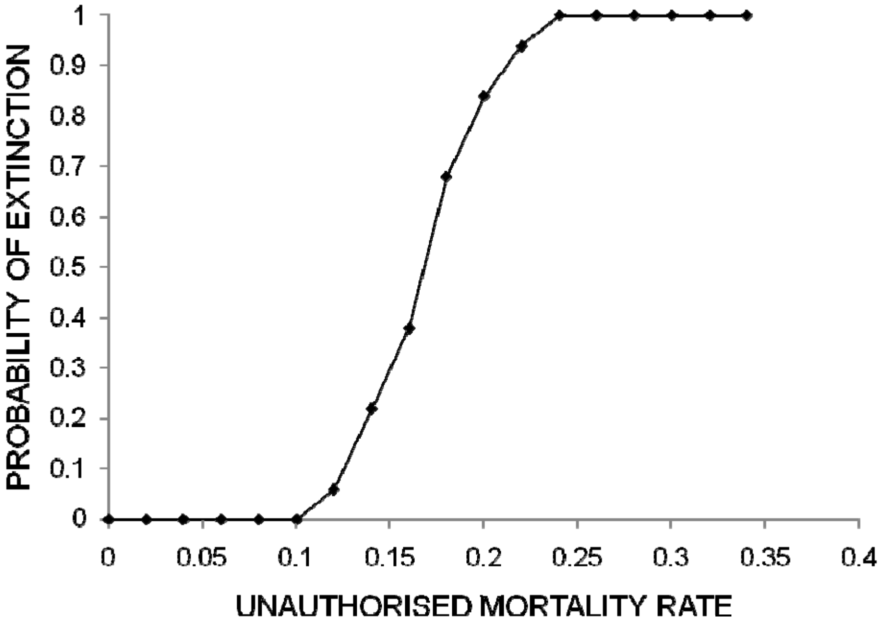
Figure 5. The functional extinction rate of the Norwegian population plotted against the mean number of immigrants entering the population annually from Sweden (Scenario 3c, baseline value – 4).

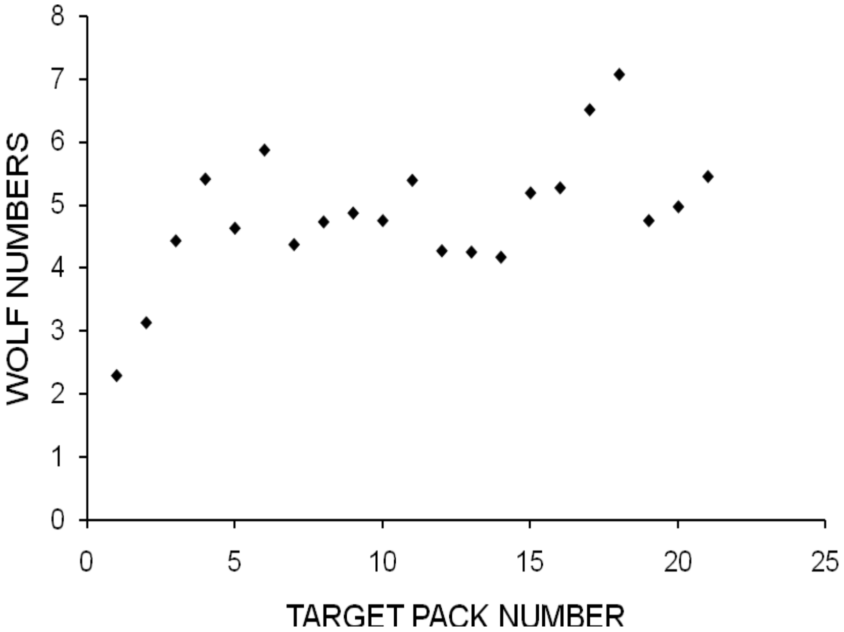
Figure 6. The number of wolves left after 100 years, as a proxy for extinction risk, plotted against the unauthorised mortality rate. The initial population size is assumed to be zero and no culling takes place (Scenario 4b).



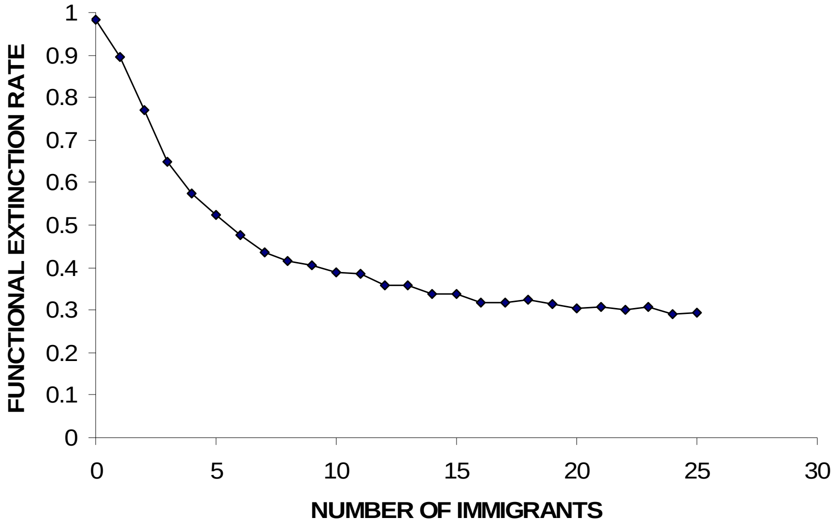
$1-p_t$, $s_{a,9,10}$
Disperser
m, p_m
s_c, d_c
s_a, d_s
d_a
p_t
$s_{a,9,10}$, $1-d_a$
$s_{a,9,10}$
Cub
s_c, $1-d_c$
Sub-adult
s_a, $1-d_s$
Sub-dominant adult
$s_{a,9,10}$
Dominant adult
H
H
H
H
F,f_L,f_S

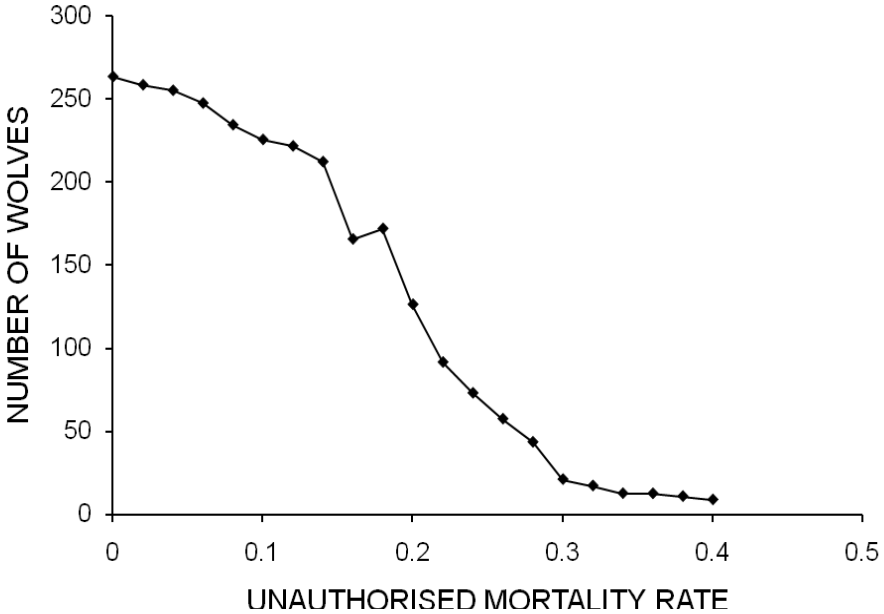

NUMBERS
16
14
12
10
8
6
4
2
0
0
20
40
60
80
100
TIME
Wolves
Packs


PROBABILITY OF EXTINCTION
UNAUTHORISED MORTALITY RATE
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4



1


FUNCTIONAL EXTINCTION RATE
NUMBER OF IMMIGRANTS
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
30


NUMBER OF WOLVES
300
250
200
150
100
50
0
0
0.1
0.2
0.3
0.4
0.5
UNAUTHORISED MORTALITY RATE

1