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A Population Viability Analysis for Wolves in Norway under Different Management Regimes

by

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Abstract

The report describes a model of the population dynamic of the Norwegian wolf population, and makes recommendations for finding an improved wolf management regime through a combination of modelling, consultation, and a literature review.

The wolf population of the Scandinavian Peninsula, of which the Norwegian wolves are a subset, re-established naturally in the 1980s following extirpation, leading to conflict with livestock farmers and hunters who had become accustomed to the absence of the carnivore. The present approach of the government is to cull the wolves to realise a three pack target demographic, a policy which is expensive and generally unpopular for various reasons, both domestically and internationally.

Due to the small size of the population in question and the suspected possibility of a second extirpation, the model employed was an individual based population viability analysis (PVA). Having built the model, and validated its accuracy through sensitivity analysis and a test against empirical data, potential future management regimes were outlined through consultation with relevant individuals in England and Norway. The model was then used to test these regimes and make predictions about the likely outcomes, both in terms of the extinction risk for the wolves and to a lesser extent socially and economically for the various stakeholders in Norway.

It was confirmed that the present population is seriously threatened with extinction, is sustained mainly through immigration from the neighbouring Swedish population, and is suppressed largely by illegal poaching. Poaching was shown to have a positive, overwhelming and non-linear effect upon extinction probability, to the extent that the actual target number of packs under the government's culling regime was almost irrelevant. The present extinction risk was estimated at 67 % ± 15 % using a metric defined in the report, and the management would not seem to be fulfilling the objectives of important stakeholders. It was concluded that a joint Scandinavian management body should be established, and recommendations based upon modelling work and consultation included allowing a slightly larger target population, encouraging more stable pack units, considering some form of legal wolf hunt as an alternative to culls, and providing government subsidies for those landowners bearing the direct cost of retaining a wolf population.

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1. Introduction

1.1 General Introduction:

The grey wolf (*Canis lupus*) has, for thousands of years, and throughout most of the northern hemisphere, lived in close proximity to mankind, and the relationship between the two species has been ever dynamic, but never less than extreme. In the past the wolf has been revered by a number of societies (Frazer, 1922), and is still biologically very similar to its ubiquitous domestic relative the dog. Conversely, in recent times, the perception of the wolf has increasingly been that it is not only a serious agricultural pest as far as livestock is concerned, and a predator that competes with hunters, but also that it is dangerous and potentially a direct threat to people who live in areas where the wolf is present. Consequently, the wolf has experienced severe persecution, reflected by a sharp decline in global population in recent centuries, and extirpation from much of its former range (see section 1.2).

However, as a consequence of the charismatic nature of the animal and the development and expansion of the environmental movement, a large proportion of conservationists, scientists, policy makers and the public now recognise the value of the wolf as a potent symbol of the wild (and thus a useful 'flagship' species), as a tool for ecological management (in certain habitats it is thought to act as an integral 'keystone' species, and is inextricably intertwined with other animals in often unexpected ways; e.g. Berger 1999, 2001); and as a vulnerable component of global biodiversity (it appears upon the IUCN red list and the appendices associated with the CITES and CBD conventions; see IUCN Red List, 2006; CITES, 2006; CBD, 2006). This recognition has led to serious interest in the preservation and reintroduction of wolves, and as such, it is important for decision makers to understand the survival capabilities of small wolf populations, and the degree to which they are robustly self-sustaining under external pressures, anthropogenic or otherwise. Equally, it is necessary to find viable ways in which wolves can be managed so as to co-exist with people with minimal conflict, and for those people to respect and accept the existence of wolves. This project constitutes an attempt to contribute to this understanding, by modelling the small Norwegian wolf population and exploring its responses to different management regimes. Inevitably, it will involve discussion as to whether the wolf should be conserved from ecological, political, social and legal viewpoints, and if so, how this might be achieved.

1.2 History of wolves:

The grey wolf evolved during the great Ice age around 1 million years ago, and at its peak the range of the wolf was effectively the entire northern hemisphere, encompassing tundra, forests, deserts and everything in between, and possibly making it the land mammal with the most far reaching and diverse natural range in history, excluding mankind (Mech, 1970). It is supremely adaptable and hardy, as one might expect from an animal so successful, and it was only with the development of human society that the wolf began to go into decline. Even though earlier societies often respected or even revered the wolf, the expansion of human agriculture and the competition for game between humans and wolves at the top of the food chain inevitably caused conflict. The fact that wolves can prey upon livestock and game and are perceived to prey upon people (although accounts of the latter are often exaggerated; Linnell *et al*, 2002) meant that wolf hunting became more popular as civilisations evolved, to an ever increasing degree. Gradually, wolves began to disappear in certain areas (for example, in the UK wolves were extirpated around 1600 AD; Wolf Trust, 2006) or even go extinct (the Dire wolf (*Canis dirus)* disappeared towards the end of the Pleistocene era, possibly due to anthropogenic pressure (Stevens, 1997), and more recently so did the two subspecies of wolf in Japan, in 1898 and 1905; Wikipedia, 2006). Today, the wolf is endangered throughout much of its range, despite remaining widespread (it is found in certain states in the US, scattered throughout Europe in Scandinavia, Russia, Iberia, Italy and the East, and in Canada and Asia):

Figure 1: Map of current wolf distribution in solid black, with speckled areas representing the further extent of the historical range. Source: IUCN, 2006.

An instructive report upon the global status of the wolf at the turn of the millennium, detailing its recent decline, present status and conservation requirements for the near future, can be found by Hinrichsen *et al* (2000).

The attitudes and policies that have led to this decline maintain a strong influence today, and show much inertia and reluctance to change despite extensive scientific work that could challenge various misconceptions: the wolf is one of the most well studied wild species in the world today.

1.3 Recent history of Norwegian wolves:

The wolves of the Scandinavian peninsula in particular are an interesting case (it should be noted that throughout this report, 'Scandinavia' will be used as shorthand to mean 'the Scandinavian peninsula', although in reality the former includes Denmark, which has no wolf population). Having faced deliberate persecution for centuries, wolves were considered functionally extinct in the region by the 1960s (Wabakken *et al*, 2001). However, in 1983, a single breeding pack was discovered in South Eastern Norway, close to the Swedish border. Whether the wolves had travelled there from elsewhere or had merely remained undetected until then was debated for some time, but these founding members of the present population are now widely considered to have immigrated from Finland or Russia (Linnell *et al*, 2005; Wabakken *et al*, 2001). The population slowly grew, but faltered under the effects of genetic depression until being sustained by the arrival of a third immigrant in 1991 (Vila *et al*, 2003). Since then, the population expanded rapidly, until culls began in Norway when they numbered around 30 individuals with three main breeding packs. Despite being signatories to various conventions which were established to protect endangered animals and list the grey wolf as being subject to such protection, the Norwegian government was under pressure from a highly vocal anti-carnivore lobby to control or even remove the wolves, and the issue became one of serious domestic importance. Consequently, despite passionate opposition on behalf of national and international public interest groups and NGOs, and to some extent from the Swedish authorities (the Swedish and Norwegian wolf populations are biologically one population, and Sweden hopes to encourage the population to grow), the government issued limited permits to cull specific individuals. The most recent cull, in 2005, targeted 5 wolves out of the 21 individuals in Norway at that time, aiming to preserve three breeding alpha pairs, as the government's official stance is that they want to control numbers, not eliminate the animals altogether (Kirby, 2005). Five were taken, but a highly successful alpha female from one of the packs to be preserved was killed when she wandered into another territory, and as such the future of two of the packs is now in serious jeopardy (Proact Mammal Campaigns, 2006): only the alpha pair in a pack breed, and if one or the other is lost the pack often falls apart and disperses unless they are quickly replaced (Fuller *et al*, 2003). Whilst the wolves thus officially number 16 permanent residents with only one confirmed breeding pair, wolves still immigrate across the border from Sweden, and so there is hope for the population.

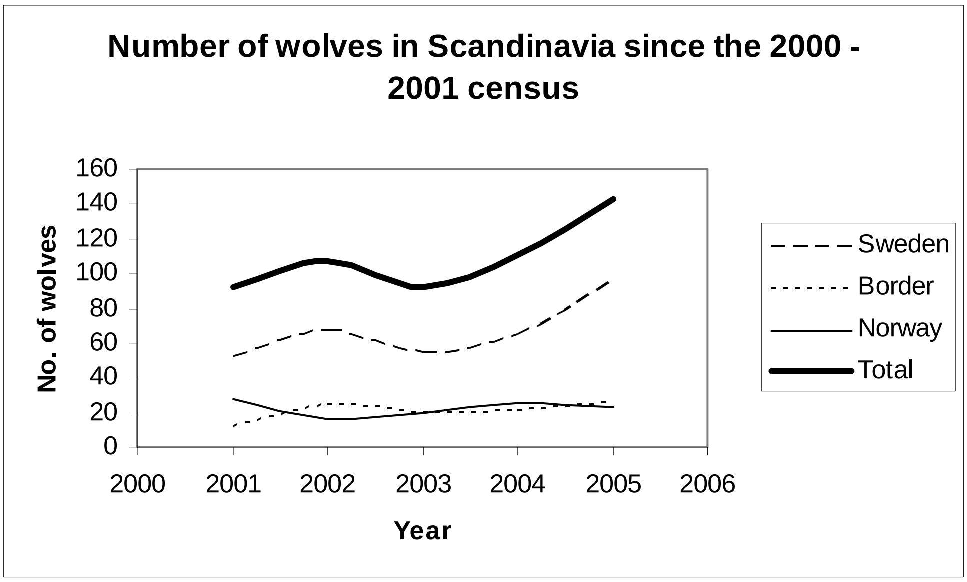

Figure 2: Plot showing wolf population data for Scandinavia since the turn of the millennium (Wabakken et al, 2001b, 2002, 2004a, 2004b, 2005)

Politically, the wolf has become a focus for the more general conflict between rural and urban communities, the former leaning toward eradication of the wolf as a pest, and the latter toward conservation of the wolf. Equally, it bears the brunt of animosity towards large carnivores in general: though the brown bear, lynx, wolverine and golden eagle also take livestock in Norway, and indeed the bear is more of a threat to people's safety and the wolf represents the least prolific of the five carnivores in livestock depredation, anger is nevertheless generally directed toward the wolf for cultural and historical reasons. It is this (at times irrationally) strong feeling directed at the animal, combined with its position as an icon to various groups in greater conflicts, that make the management of the wolf such a sensitive political issue (A. Mysterud, pers. comm.). Any realistic management regime must therefore take into serious account the views of all stakeholders, and must draw upon community feeling as well as general ecological expertise.

1.4 Problem definition, aims and objectives:

In summary of the points raised in section 1, the problem can be stated as follows. Neither the objectives of the anti-carnivore lobby nor conservationists are being met: the former still complain that they suffer economic damage from wolf depredation upon livestock and moose, and the latter believe that the present regime will inevitably result in the extirpation of the wolf.

So far, the government have attempted to act upon farmer's fears and remove the problem by culling some of the wolves, whilst retaining the absolute minimum viable population. This has not generally solved the problem for either side: conservationists believe that the population size is too small and will collapse, and continue to passionately campaign against lethal methods of control, whilst the culling of wolves propagates the farmer's belief that wolves are a serious threat to livestock, and if anything, encourages hatred and fear for wolves. Furthermore, the present approach incurs a heavy financial burden.

There are a number of alternative wolf control or livestock protection methods/techniques that could be implemented as an alternative to the present regime. It was established which are most feasible, and the likely ecological outcome of the different regimes was determined using the PVA model, i.e. if a management option is considered socially and economically acceptable, the project demonstrated whether it would be likely to allow the wolf population to persist.

Therefore, there were two main aims associated with the project: firstly, to develop a model of the population dynamics of the Norwegian wolf population, and secondly, to use this to explore what could happen to the population under different management approaches.

The objectives were thus:

1. To gather together and examine ecological data on the grey wolf, relating to its lifestyle, habits, and particularly its social dynamics.
2. To modify and build upon an existing PVA model, used to explore the effects of reintroducing wolves to Scotland, so as to make it applicable to Norway.
3. To gather existing historical data, and use it to test the likelihood that the new model is accurate, making further corrections if necessary, and possibly comparing the outcomes with those from other models.
4. To use the model to make predictions about the fate of the Norwegian (and Scandinavian) populations under the present management approach.

5. To interview a number of relevant experts in Norway (academics, ecologists, habitat managers, etc), and collate the responses into a list of potential management policies.

6. To further refine the list of potential management regimes through discussion concerning relevant international law, and public attitudes towards the wolf.

7. To use the PVA model to predict the potential ecological outcomes of these different policies.

8. To evaluate these policies taking into account their biological, social, political and economic implications.

9. To complete a report detailing all of the above, and thus comprising of a study into the ecology of the grey wolf and the dynamics of its co-existence with man.

2. Background

2.1 Wolf policy and international law:

Norway is party to a number of international conventions which would seem, at first glance, to conflict directly with its policy of wolf culling. However, the issue is debatable on both sides, and to date Norway is technically acting within its legal obligations (Rees, 2001; K. Mcdonald, pers. comm.).

The convention on the Conservation of Biological Diversity (CBD), for instance, was ratified by Norway in 1993. In article 7 it identifies those species that should be conserved in-situ "as far as possible and where appropriate" as those that are "wild relatives of domestic species", of "social, scientific or cultural" value, and of "importance for research into the sustainable use of biological diversity", arguably descriptions which all apply to the wolf. However, in article 8, the emphasis of the CBD is to (d) ensure "maintenance of a viable population of the species in its natural surroundings", and furthermore, to (i) ensure "compatibility between present uses and conservation of biological diversity". The Norwegian government aims to maintain three breeding pairs within its borders as well as an unlimited number living across the border with Sweden, which it considers viable in the context of the entire Scandinavian population. Furthermore, it needs to ensure compatibility with the rearing of livestock within the region; on the basis of these two points it is acting within the confines of the CBD. Such compromises are a common interpretation of wildlife laws governing returning species, and the importance and debate largely focuses upon definitions, e.g. what exactly is a ‘viable population’ (Rees, 2001). One point that is interesting however, is that in article 3 the CBD reasserts 'principle 21', that Norway's activities shouldn't interfere with the environment of other countries: given that the Swedish government have complained that Norway's actions have meant that Sweden must take most of the responsibility for conserving the Scandinavian wolf population as a whole, it is arguable that they are flouting this article.

Of perhaps greater relevance is the Bern convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention, 2006), which came into force in Norway in 1986, with no reservations made for wolves (Canis Lupus is listed in Appendix II - "strictly protected fauna"). Whilst article 2 demands members "shall take requisite measures to maintain wild fauna at, or adapt it to, a level which corresponds to ecological, scientific, or cultural requirements", which Norway may not quite fulfil (the minimum genetically viable population for Scandinavia has been estimated at as much as 400 individuals; Nilsson, 2003), again it also states that this must only be done "while taking account of economic and recreational requirements", and clearly there is the argument that a bigger wolf population would cause substantial economic damage through livestock losses. Furthermore, whilst article 8 demands Norway "prohibit use of all indiscriminate means of capture and killing" wolves, the exceptions in article 9 allow culling "to prevent serious damage to...livestock" and "in the interest of public health and safety" - there is still a widespread belief that wolves pose a serious threat to people (see section 2.3). What is difficult to ignore, however, is that in appendix IV, the use of "aircraft" and "motor vehicles in motion" is a prohibited means of killing animals, but both were used in the recent culls (Proact Mammal Species Campaigns, 2006; Environment News Service, 2006).

In summary, the fact that the government aims to retain a certain small but viable population of wolves in a prescribed area allows them the discretion of culling wolves in order to minimise conflict local farmers and other people. Hence, the important debate at present is actually whether the target of three breeding pairs is sufficient not only to help preserve the Scandinavian population, but also to take a fair share of the burden for doing so with Sweden.

2.2 Economic perspectives:

An economic analysis would tend to support the conservation of a larger wolf population after applying a cost-benefit evaluation: an example being that carried out by Boman *et al* (2003) for Sweden (a study which is highly relevant to Norway), which found economic gains from a wolf population as much as 500 strong. Such gains arise from the calculation that the benefits of a wolf population (in terms of non-consumptive existence value, recreational hunting value and wolf tourism) outweigh the costs associated with wolves due to depredation on domestic animals and people's fear for their own safety. Furthermore, in a study in the US pertaining to the relationship between money spent on predator control and numbers of sheep owned as livestock, using a model inclusive of market prices and production costs, it was found that these latter economic forces were responsible for most of the correlation with empirical data (77%), and hence that sheep losses were far more closely related to these parameters than to the extent to which depredation was controlled (Berger, 2006).

In reality, however, in the case of Norway, such analyses do not necessarily truly allow an understanding of the situation. Those who farm sheep tend to own small flocks as a complementary source of income, and rely upon government subsidies to sustain such a way of life (who, in turn, provide subsidies largely to retain a significant proportion of the Norwegian population practising agriculture in rural areas). Wolf attacks on sheep tend to be concentrated (i.e. the cost of depredation is not spread over all farmers as general economic analysis implies) and can effectively decimate an entire flock in an attack, thus doing more damage than mere statistics represent, and leading at least partially to the high anti-wolf sentiment in rural communities.

Hence, according to the literature, analyses at a national level tend to support the establishment of a larger wolf population, whereas it is important to note that the cost of the wolf presence is presently made clearly manifest only to a small percentage of the population, and this should be accounted for in searching for a solution.

2.3 People killed by wolves in Scandinavia, and general fear of wolves:

There are differing estimates as to the number of people killed or injured by wolves, and accounts are often anecdotal, or inclusive of attacks by rabid animals which should really be classified as non-predatory, and the latter issue has clearly diminished with the disease itself. However, a good estimate for Scandinavia would be that, during the last 250 years (a period during which rabies has been absent from the region and can thus be discounted), a total of 17 people have been killed in predatory attacks by wolves in the entire region (Linnell *et al*, 2002, Swenson *et al*, 1996, 1999; in Roskaft *et al*, 2003). Of these, 12 were killed in Sweden in the 1820s by a single wolf that had been raised in captivity and then released, and only 1 was killed in Norway, in 1800 (Linnell *et al*, 2002). Of course, there have been very few wolves in Norway during that period, but nevertheless, with such a history it is fair to conclude that public fears for safety in Scandinavia are largely unjustified.

It is questionable as to what extent this could change. According to a number of studies, fear is not always simply related to hard truth when it comes to large carnivores. For example, Roskaft *et al* (2003) found that reported fear increased with age group, and was higher for those living in rural areas in the absence of wolves than for those living in urban areas with wolves nearby; furthermore, fear was lower amongst those who enjoyed outdoors activities (such as small game hunting) than those who didn't. Equally, according to Zimmermann *et al* (2001), fear can also be defined as a function inversely dependent upon distance from wolf territory, and decreases with time and experience of living with wolves. Such findings suggest that the present anti-wolf sentiments could be hard to shift, however, it was also found that fear decreases with education (Zimmermann *et al*, 2001) and that the media potentially has a strong influence (Schofield, 2005; Ericsson and Heberlein, 2003), so it is possible that, especially with the return of wolves, a more realistic perception of the actual costs and benefits of living with wolves might be reached. It should also be noted that, whilst it is a factor, surveys found that fear of wolves does not always necessarily determine acceptance levels (Zimmermann *et al*, 2001).

Specifically in Norway, whilst many in the wolf region display passionate and vocal opposition to the wolf population re-establishing, the country as a whole recognizes the right of the wolf to exist, and leans towards supporting its return (A. Mysterud, pers. comm.; Skogen, 2001).

2.4 Quantitative wolf population data:

2.4.1 Structure of present Norwegian wolf population:

In order to justify the starting population used during modelling, it was useful to understand the present population structure. During the 2004/2005 winter, there were between 22 and 24 wolves living in Norway, consisting of 12 belonging to the "Julassa" and "Graafjel" packs, 3 scent marking pairs, and around 5 other individuals (Wabakken *et al*, 2005). The cull in early 2005 resulted in the deaths of the alpha female from the Graafjel pack and two of the scent marking pairs, with numbers now estimated at 16 (Proact Mammal Species Campaign). Consequently, the population structure in Norway as of 2006 can be estimated as follows: there are 16 wolves, belonging to three 'packs'; the Julassa alpha pair with around four pups, the Graafjel alpha male with around four pups, a third 'pack' consisting of a pair of wolves, and then three dispersing individuals. It should be noted that only the Julassa pair were thought to have any real chance of breeding success during the 2006 season.

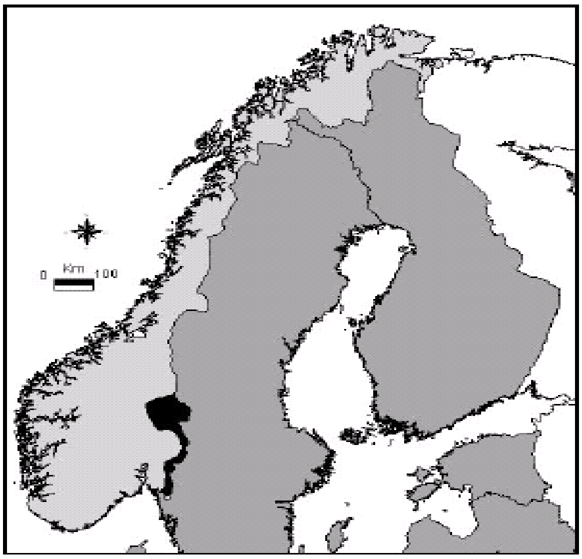

Figure 3: Map showing Norway (light grey), Sweden and Finland, with 2005 wolf distribution (black shaded area). Source: Salvatori and Linnell, 2005.

This structure could have been used for the first time step in the model, however, study of population dynamics in the immediate past (Wabakken *et al*, 2001b, 2002, 2004a, 2004b, 2005) revealed that it actually represents a dip in numbers due to stochastic fluctuation and heavy culling. As such, a more representative starting point was the mean population over the last five years, and present management target, i.e. three packs (a useful wolf pack template is an alpha pair with a litter of four cubs; Mech, 1970).

2.4.2 Recent dynamics of Yellowstone wolf population:

In order to complete the model validation exercise using existing data on wolf dynamics from Yellowstone national park, a detailed exploration of this data was undertaken at the literature review stage (see section 3.3.5).

It is impossible to gain an exact estimate of the Yellowstone population, as there is some debate as to whether wolves had completely disappeared from the region prior to re-introduction (there may have been a few individuals remaining), and additionally, it can be difficult to carry out an accurate census for such a far ranging and restless animal. It was found that estimates originating from official sources were normally relatively high, and those from the voluntary sector relatively low, and so the cynical but justifiable assumption was made that these represented upper and lower limits respectively, and gave a good indication of the range in certainty.

In 1995, three packs (the “Crystal Creek”, “Rose Creek” and “Soda Butte” packs) were introduced, consisting of 14 individuals, and in 1996, a further three (the “Chief Joseph”, “Druid peak”, and “Nez Perce” packs), consisting of 17 individuals, were added to the population (USCBD, 2006; YNP, 2006; Smith *et al*, 2003). In order to simplify the model test, these packs were combined so that the model population began in the first year with 31 wolves, in 6 packs. As any individuals already living in the region would probably only make up a small proportion of this introduced population, and the model does not consider the effects of greater genetic diversity, and finally as there is no reliable means of estimating how many wolves were present if indeed any were, it was assumed that there were no wolves in Yellowstone prior to 1995.

The upper bound estimate for wolf numbers is that in 2002 there were 164 wolves, in 2004 there were 324, and in 2006 the number had dropped to 294 (USCBD, 2006). Conversely, the lower bound estimate gives 171 in 2004, and 113 in 2006 (DoW, 2006), and by inference, around 60 individuals in 2000 (see figure 9). The fact that numbers decrease by all accounts for the period 2004 – 2006 may indicate stabilisation in the wolf population due to its having reached a size subject to some density dependent mechanism. It was thus hoped that the model would predict that the population showed signs of stabilisation at this time, as well as falling within the upper and lower boundaries on absolute population size.

In terms of anthropogenic pressure, the data suggest that this removes about 0.125 % of the population annually, representing about half of the total wolf mortality rate (YNP, 2006).

2.5 Potential alternative management regimes:

The following section outlines a discussion of management regimes and tools that could feasibly be introduced in Norway, and was based upon both literature review and consultation.

An extensive number of potential management tools and approaches exist as far as wolf management and livestock protection are concerned, but that which is realistic in Norway is severely limited by what would prove acceptable to the general public. For example, age old European methods for reducing depredation without resorting to wolf hunting are still used today in some areas, such as shepherding, fencing or the use of livestock guarding dogs (LCIE, 2000). However, in recent years the absence of wolves in Norway has encouraged farmers to change their practices, for example, by allowing sheep to range through the forests outside fences, or by taking secondary employment and thus no longer having time to give over to shepherding. Consequently, any possibility of reinstating such methods has generally diminished, due to both a lack of the necessary expertise and lifestyle structure, and certain inertia on the behalf of modern farmers (Linnell *et al*, 1996). The case in which these methods and others (such as aversive conditioning, in which various chemical and physical techniques are used to instil in wild wolves a predilection against attacking sheep; or livestock switching, in which sheep are exchanged for livestock like cattle or horses, which are less susceptible to depredation) were used was modelled simply by a free expansion of the wolf population subject to density dependence and stochastic wolf mortality as a consequence of the inevitable poaching. It should be re-emphasised that the model makes assumptions that rely on small wolf populations, so in exploring a free expansion it was only really possible to demonstrate how quickly the population might grow initially, and show qualitatively whether or not the population eventually stabilized and extinction became unlikely.

Realistic variations upon the present management regime also exist: firstly it was possible to model the effect of changing the target population size, i.e. the basic number of packs permitted to establish upon Norwegian soil. At present, wolves are generally culled during the winter after littering and the process of new pack formation, normally with a year’s lag from the census data, and this fact can be incorporated into the model along with a variable target number of packs. Having studied this, it would have been of interest to discover if there were any impact upon the stability of the population under differing culling regimes with a constant target if, for example, it were simply the case that all dispersing wolves were shot, or that any new scent marking pair were instantly culled upon discovery, and these approaches could have been modelled by removing individuals at different stages of the annual cycle in the model. However, due to time limitation these possibilities could not be studied, but for further exploration of this idea the reader is referred to Haight *et al* (2002).

Secondly, by increasing the number of immigrants from Sweden in the model, it was possible to reflect the case in which management of the Swedish portion of the Scandinavian population as a whole caused an increase. This is a likely scenario, and was of interest in establishing the degree to which Norway relies on the Swedish wolf population to sustain its own, and to explore any situation in which there was agreement that the Swedes will bear the greater responsibility for Scandinavian wolf conservation.

At present, the officially designated wolf zone is, as mentioned, far larger than that required by the wolves living there; however, it was of interest to model the effect of varying the size of the wolf zone (achieved here by increasing the likelihood that a dispersing wolf will succeed in establishing a new territory: the exact relationship between size of wolf zone and probability of success would be a project in itself to determine, so it had to be assumed for the sake of this experiment that the relationship was simple and linear). Not only could this have affected population dynamics, and been of interest in conjunction with increasing the target population size, but may have acted in indirect ways, such as for example by effectively diluting the effect of poaching upon the population.

A slightly more dramatic departure from the present management approach, but one which has proven successful in the case of the lynx in Norway (A. Mysterud, pers. comm.), would be to allow a free expansion of the wolf population to a larger threshold, and then find a sustainable legal annual wolf harvest. This was modelled by decreasing restrictions upon wolf population growth but keeping some poaching pressure, and then allowing a fixed number, or proportion, of the population to be removed every year. Such an approach might be more acceptable to the various stakeholders, as conservationists (despite regretting the extra wolf mortality) might approve of the increased numbers and hence stability of the population, whilst the anti-carnivore lobby might enjoy the relaxation of hunting law and the opportunity to become more directly involved in wolf management.

In summary, the main management options to be tested were:

- the cessation of lethal control
- the effect of changing the target number of wolf packs
- varying the immigration rate from Sweden, as indicative of changes in management over the entire peninsula
- varying the probability that dispersers will establish a new territory, as proxy for varying the size of the wolf zone
- the exploration as to the effect of a legal hunt
- additional exploration as to the effect of poaching, and the ramifications should the wolf population undergo a second extirpation.

2.6 Relevant wolf biology:

Given that the grey wolf is such a well studied species, and so similar to the domestic dog in terms of its fundamental biological make up, a relatively large amount is known on this subject. A thorough account can be found in Mech (1970), however, this will not be expanded upon here. Of greater interest in the context of a modelling project are both the manner in which wolf populations are structured socially, which is unusually complex, and the interaction dynamics between the wolf and its prey.

Wolf populations are organised in a highly modular way, in that groups of wolves form distinct packs with extremely strong and exclusive bonds, within very clearly defined territories (Mech, 1970). In general, dispersing wolves will attempt to find both a mate and territory, and if they are successful they become a scent marking pair. Wolves bear a litter of pups once a year, and although average size varies, four pups a year would be considered normal (Pedersen *et al*, 2005). These pups stay with the alpha pair for at least a year, when the next litter arrives, and may then begin to disperse, so as to find new territories; those that stay simply remain a part of the pack, and leave at another point. Occasionally wolves that have dispersed but have been unable to establish a new pack elsewhere can return to their natal pack, but it is extremely unlikely for a pack to take in a wolf originating from another pack, and in fact they will normally attempt to kill any such individuals dispersing into their territory.

The wolf pack itself has a very strict hierarchy, with the alpha pair generally leading the pack in travelling and hunting, and dominating the social order, with the various other individuals having diminishing social standing down to the zeta animal. Whilst there are constant power struggles within the pack, the alpha wolves are not generally challenged, and indeed when either or both die the pack will normally break down and all remaining wolves disperse (unless the empty alpha position is rapidly filled). Pack size varies, and whilst most might be expected to number between 5 and 10 individuals (Pedersen *et al*, 2005) occasionally many more are found (for instance two packs of 19 and 26 individuals recorded in Yellowstone National Park in recent years; YNP, 2006). The cohesiveness of the pack is very important not only as far as retaining a territory is concerned, but to effectively hunt prey. Wolves can only bring down animals such as moose, which make up most of their diet, when hunting in packs, and are unable to do so alone. When wolves disperse, either in search of a new territory or following pack disintegration, they are thus forced to change their diet and take 'easier' prey, such as livestock: a point which has clear ramifications as far as this investigation is concerned.

The prey type for wolves in Norway is well documented, consisting largely of moose and supplemented with deer, occasionally smaller animals like beaver, and to some extent domestic livestock (Graham *et al*, 2004), although wild prey is generally preferred (Meriggi and Lovari, 1996). It is often debated, and fundamental to a modelling project of this type, whether the ecological relationship between wolves and their prey can be characterised as 'top-down', 'bottom-up', or as a mixture of both. There is still much research required upon the subject (both for wolves and in general), especially for a difficult situation such as that in Norway where there is a large prey resource and small re-introduced predator population (Eberhardt *et al*, 2003). In general it is often concluded that there is evidence for a 'bottom-up' process, i.e. wolves are generally dependent upon prey density (Testa, 2004), whilst the factors shaping prey populations in situations similar to that in Norway are largely climatic or anthropogenic, and only partly due to wolf predation (for example, Vucetich *et al* (2005) found that of an 8.1% decline in elk numbers in Yellowstone following wolf re-introduction, 7.9% was best explained on the basis of climate and harvest rate). Combined with the fact that there are so few wolves and such a surplus of potential prey in Norway, and that wolf numbers will most probably be suppressed for some time to come, it could be concluded that in this case ‘top-down’ effects are negligible.

3. Research Methods

3.1 PVA and IBM:

Population Viability Analysis (PVA) is a broad term that encompasses any modelling approach that constitutes an extinction risk assessment for a biological population within a given time frame. Common approaches include the use of commercial PVA packages (such as VORTEX) that can be applied to many species, and which involve input of demographic rates and an emphasis upon careful interpretation of results, and Individual Based Models (IBMs) that follow each individual within a population and are often tailor made to a specific scenario. Such analyses have been used extensively in conservation biology, and yet there is still much controversy not only concerning the best approach, but as to how results should be interpreted, or indeed whether they should be trusted at all.

As a tool PVA can be effective and accurate, with acceptable sensitivity to initial parameters and good predictive powers where projections have been subsequently compared to empirical data (Fieberg and Ellner, 2001; Brook *et al*, 2000). However, there are certain generally agreed criteria regarding the population to be modelled which should be fulfilled if PVA is to be effective: available data on the species should be extensive and reliable, and, if using a commercial PVA package, vital rates should remain effectively stationary over time (Coulsen *et al*, 2001). Other commonly made recommendations include that a model used in PVA should be open to external review and that the model structure should be treated as a hypothesis to be tested (Reed *et al*, 2002). Assuming sufficient species data and given enough time, such recommendations clearly support the use of non commercial (i.e. custom built) models, which circumvent certain issues that the commercial packages do not. It is nevertheless important to bear in mind that results should be interpreted carefully, and not accepted prior to external critique of the model used.

A major criticism of the PVA approach is that it is often the occurrence of catastrophes (environmental, demographic, anthropogenic etc) that cause a species to actually go extinct, and it is impossible to evaluate the likelihood of such an event with any certainty (Coulsen *et al*, 2001; Wikipedia). As such, it is often suggested that PVA not be used to make reliable quantitative estimates of extinction risks or minimum viable populations, but more to compare different management regimes, or other pressures upon a species (Reed *et al*, 2002).

The situation is complicated further due to some contention as to how best to evaluate extinction risk. An example of a standard definition would be one in which a probability is calculated as the ratio of the number of simulations in which a population goes extinct to the total number of simulations, but there are a number of potential alternatives, each of which is best suited to different situations. In this investigation, the extinction probability metric is generally as defined in section 3.3.1, and if an alternative is employed this is noted explicitly.

3.2 Existing wolf models:

The literature contains a number of previous modelling investigations pertaining to the grey wolf both in Scandinavia and elsewhere, which it was hoped the model used here would complement. Previous use of custom built IBMs includes Haight *et al* (2002), in which a custom built stochastic IBM was applied to a hypothetical subset wolf population of the western Great Lakes region in the US, using similar performance indicators to distinguish between the effects of hunting at different times of year, for a population in little danger of extirpation. It was concluded that such an approach can provide a robust basis for wolf management, alongside certain more specific conclusions; that hunting at different times of year affects both the number of wolves that can be sustainably taken and the cost of doing so, and that a reactive management regime can ensure conservation; which are directly relevant here. Similarly, Vucetich *et al* (1997) employed an IBM to realise a PVA for small wolf populations, assuming predator-prey interactions as described in section 2.6, which highlighted the importance of including detailed social structure and the giving of due consideration to prey dynamics when modelling a wolf population in this manner. Such previous work encourages the use of a custom built IBM, as not only does it demonstrate the effectiveness of the approach and provide strong recommendations as to the building of such a model, but furthermore comparisons made between results achieved using different custom built PVA models for the same species must ultimately provide insight into the usefulness of PVA and IBMs as conservation tools.

As an alternative technique, Nilsson (2003) employed a commercial PVA package (VORTEX) to study the wolves of the Scandinavian peninsula as a whole, demonstrating the large positive impact of hunting upon extinction risk but also that a large basic population makes possible a limited legal hunt, and highlighting the importance of inbreeding and catastrophic events upon long term survival. Interestingly under such an analysis, the extinction risk for the population was almost negligible over 100 years.

Elsewhere in the literature, there exists much modelling work concerning the impact of wolves upon ungulate prey, which might be expected given the economic and scientific interest in understanding this interaction to a greater extent. The novelty in the model built for this project lies in the shift of emphasis, away from this interaction (but incorporating many of the conclusions drawn on the basis of this work), and towards the reaction of the wolf population to changes in management. The IBM used builds upon suggestions made as a consequence of the work alluded to during this section, but went further in ensuring realism and modelling a variety of management regimes that are directly feasible in the present political environment. As such, besides providing a comparison useful to the ongoing debate about PVA, the model attempts to build upon the literature and provide an improved means of advising policy decisions.

Relative disadvantages in the model built include its specificity to the wolves in Scandinavia and further to only small populations of wolves, but this does ensure that the model is well equipped to contribute towards Norwegian policy making, and nevertheless opportunities exist to draw general conclusions. There is also the relatively simplistic treatment of the wolf-prey interaction (see section 3.3.1), but in being weaker than existing models in this respect, the different emphasis ensures that the results complement, rather than repeat, work already achieved in the literature.

3.3 The PVA Model:

3.3.1 The model:

In order to translate the wolf life cycle and social hierarchy described in section 2.6 into a mathematical model, individuals were first grouped into four social groups (1 to 4) using the following construct:

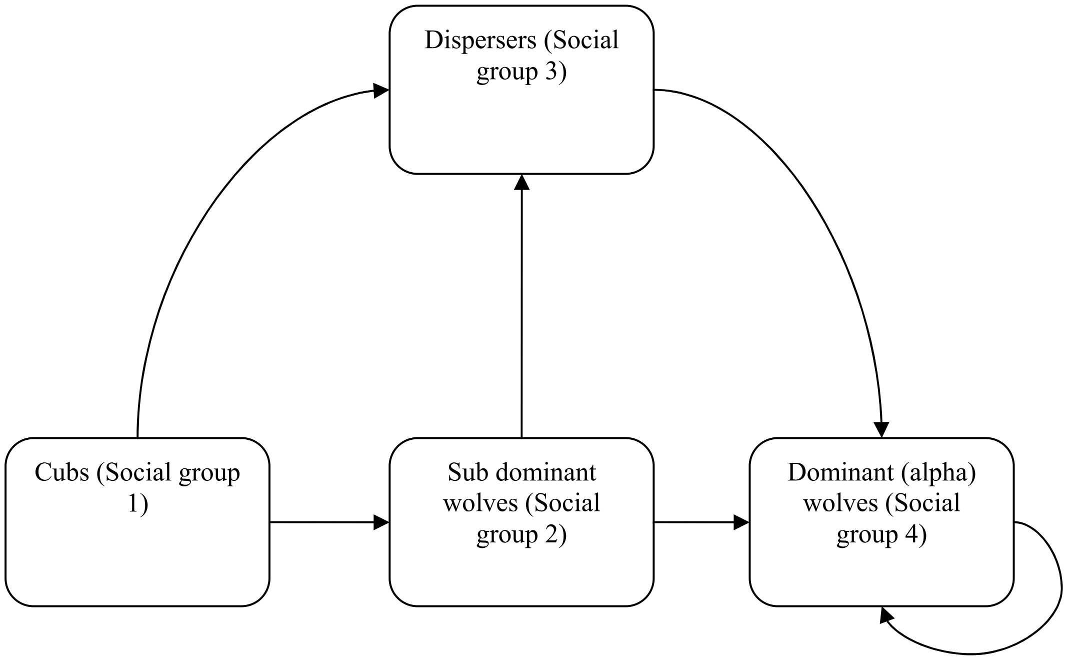

Figure 4: Flow diagram showing how the wolf social hierarchy was represented in the model using four social groups, and direction of transition between groups.

A PVA model constructed by Nilsen *et al* for the theoretical case of anthropogenic wolf re-introduction to Scotland, using this construct, consisted of three sections: encapsulating the dynamic of the predator (wolf) population, prey (deer) population, and the predator-prey relationship (Nilsen *et al*; under review). This programme took four main functions which represented the key biological mechanisms in the wolf life cycle; survival, recruitment, dispersal, and new pack formation (see section 3.3.2); and applied them over 100 time steps (each increment representing one year) to a basic population of twenty individuals, with a randomly generated initial set, and inherent environmental and demographic stochasticity.

Given that there are only a small number of wolves in Norway, and the fact that these wolves have been studied in much detail so data are extensive, this IBM was considered appropriate as a basis for a new model. However, since the prey population in Norway is presently stable, and the number of individuals taken by wolves is less than that generally taken by hunters and hence the wolves are unlikely to be able to disrupt this stability (A. Mysterud, pers. comm.), it was decided that for the purpose of the project, observing the principle of parsimony (Hilborn and Mangel, 1997), the prey could be treated as a relatively stable and self renewing resource that absorbed any effects deriving from wolf predation (see section 2.6). Consequently, there was no need for a separate 'prey' section within the construct of the model, and parameters governing the wolf's success in finding food could be absorbed into the basic wolf survival rate; hence only the section of the original model pertaining to wolf dynamics was retained. Furthermore, instead of initiating calculations with a random theoretical population, a set and realistic three pack population based upon data from recent years was used as a starting point (see section 2.4.1).

The model simulated the fate of the population for a one hundred year period over which the extinction probability was calculated; although Nilsson (2003) warns that certain effects (e.g. inbreeding depression) might be made manifest only over a longer time period, the period used here is standard for PVA. In order to determine the mean likely population trajectory, the model was looped and run 50 times, and the resulting extinction probabilities averaged so as to find the general extinction risk; effectively, a Monte Carlo approach (also standard for PVA). It should be noted that in this case, given the fact that wolves are continually taken into the population from Sweden and that the management goal was to retain breeding wolves in Norway at all times, 'extinction risk' was defined as the number of years in which no breeding packs existed in Norway, as a proportion of the total number of years in each simulation. This can be seen to be appropriate considering that, in the absence of breeding pairs in Norway, the population could be considered functionally extinct were it not for the influx of individuals from Sweden.

The wolf population was defined using a matrix with a row for each individual wolf, and five columns individualizing the wolves (Age, Sex, ID number, Pack number and Social group). The central loop applied the four basic biological functions to the wolves (see section 3.3.2), and so calculated the new population as it changed every year. Additionally, on an annual basis, the model added immigrants to the wolf population from Sweden (as dispersers), took out a random proportion of wolves that had been either 'poached' or random packs that had been 'culled', and varied the prey availability through the 'prey' factor. The latter was simply a multiplier applied to the wolf survival rate that varied randomly but with some continuity every year, to allow for natural fluctuations in the prey population, in accordance with the aforementioned assumption of a bottom up process only:

$$S_1 = S \times P \tag{1}$$

(where S = basic survival rate, P = variable prey factor, S_1 = survival rate inclusive of bottom up effects).

The prey factor 'P' was assumed to contribute a range of ± 20 % to survival rate, a conservative estimate based upon the literature. This was applied equally to wolves of all age and social classes (see section 3.3.3).

The core function of the model was thus:

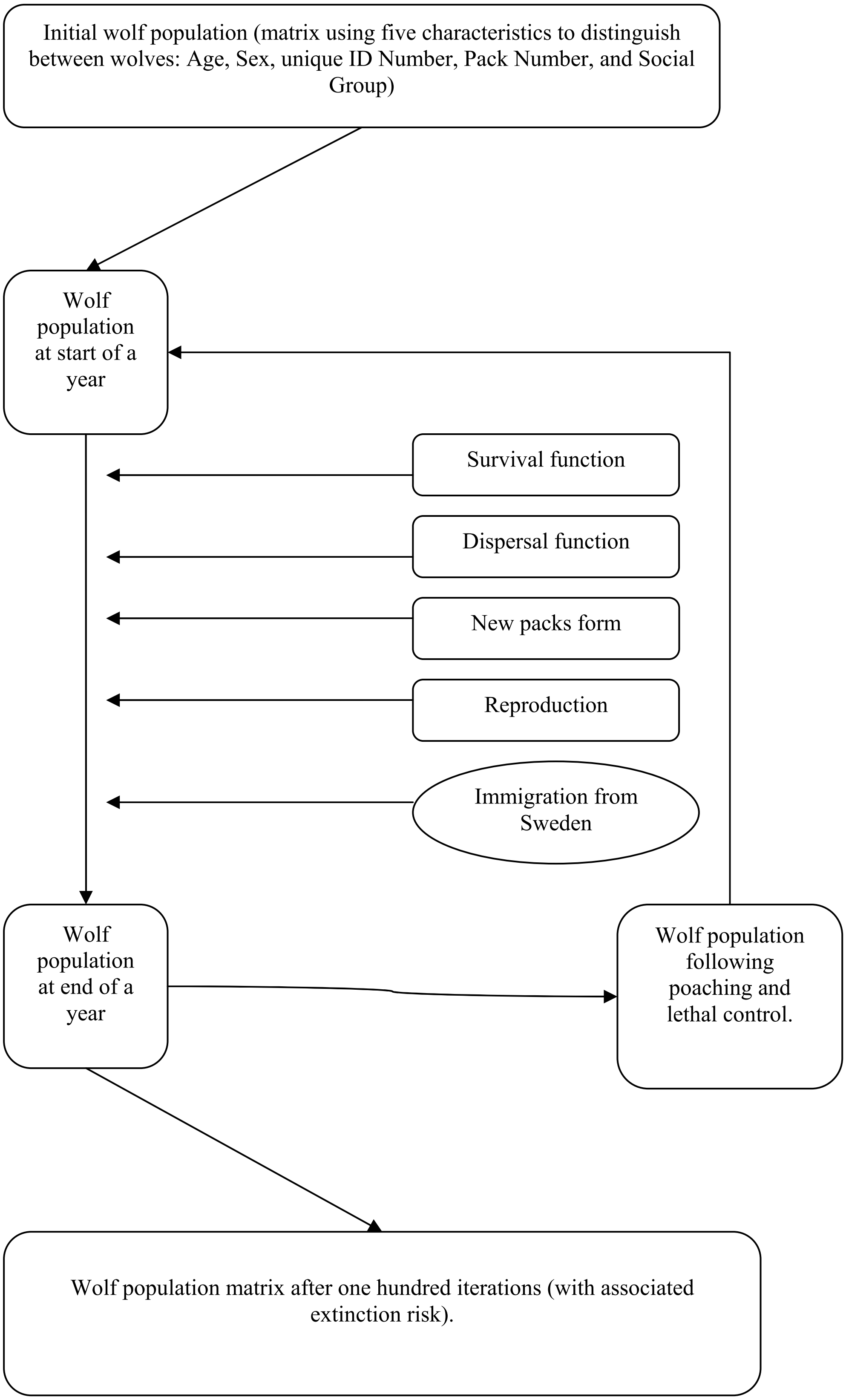

Figure 5: Flow diagram representing core aspect of model.

In the absence of a predator-prey interaction component to the model, it was necessary to introduce some kind of density dependence factor, as this would have the effect of stabilizing the population and ensuring that, in the event of rapid growth, the population did not expand exponentially. The assumption was made that this could be modelled again by a simple factor of survival rate, using a ratio dependent metric as suggested in the literature (Eberhardt *et al*, 2003), and hence the model was modified so that as the total population increased, mean survival rate was steadily reduced. In reality, the population could grow quite large before this would begin to have a significant effect, as the designated wolf zone in Norway presently vastly exceeds that required by the population (B. Zimmermann, pers. comm.), so for simplicity the survival rate in the model was increasingly diminished as the population grew, but only beyond a population of 100 wolves. This figure represents the number that could, without serious competition or detriment to each other, establish within the present wolf zone (Pedersen *et al*, 2005; T. Stromseth, pers. comm.):

$$S_2 = S_1 \times \left(\frac{W_n}{W_t} \right) \qquad (W_n \geq 100)$$

$$S_2 = S_1 \qquad (W_n < 100) \tag{2}$$

(where S_1 = product survival rate in Equation (1), W_n = number of wolves, W_t = a threshold number of wolves at which intra-specific competition ceases to be negligible, S_2 = compound wolf survival rate).

The literature contains accurate measurements of Scandinavian and global wolf parameters, such as fecundity, death rate, likelihood of dispersal, and so forth. These basic values, confirmed through extensive consultation, were as follows:

Parameter	Baseline value (probabilities unless stated)	Uncertainty
Cub dispersal rate	0.35	± 0.15
Yearling dispersal rate	0.5	± 0.25
Adult dispersal rate	0.9	± 0.2
Mean net annual immigration rate	4 (individuals/yr)	± 1 *
Probability that an immigrant is male	0.7	± 0.1
Probability of success in establishing territory	0.8	± 0.1
Probability of having a large litter (distributed around 5 cubs), as opposed to a small litter (distributed around 2)	0.73	± 0.03
Cub survival rate	0.73	± 0.03
Survival rate for wolves aged 2 – 8	0.83	± 0.03
Survival rate for wolves aged 9	0.4	± 0.04
Survival rate for wolves aged 10	0.25	± 0.05
Probability of any one wolf surviving poaching	0.6	± 0.1 *

*Table 1: baseline parameter values used in model. Uncertainties in parameter values were also taken from the literature, except * which were conservative estimates reached during consultation.*

3.3.2 Biological functions:

The four basic biological functions were applied annually (see figure 5), and incorporated into the model as follows. Firstly, dispersal: the function isolated all non-alpha individuals and, on the basis of their age and dispersal likelihood, randomly decided whether they leave the pack on an individual basis. Furthermore, for packs in which both alpha individuals had died, all wolves dispersed (see section 2.6).

Similarly, for the new pack formation function, dispersing wolves were randomly successful in establishing new territory dependent upon the probability of success in doing so, and then either filled existing empty territories (with no alpha individuals, or one alpha individual of the opposite sex), or if all available territories were occupied, created a new territory.

The recruitment function again isolated all alpha pairs in the population, and then created a random new pup matrix based upon the average litter size, and with the corresponding number of litters. This new matrix was then incorporated into the main population matrix.

Finally, survival was applied to all wolves, with certain individuals being removed from the population randomly and upon the basis of the survival rate (which was itself composed of the basic survival rate and the factors corresponding to prey availability and density dependence arising from intra specific competition).

3.3.3 Model assumptions:

A number of key assumptions were made when constructing the model which would effect the outcome, and determine the range of applicability and how best to interpret the results. Fundamentally it was assumed that net immigration was from Sweden into Norway, and that this took the value in table 1. This was justifiable given that the greater part of the population resides in Sweden and assuming random dispersal; as for the absolute value of the parameter, this was established logically on the basis of the number of dispersers one might expect throughout Scandinavia in any given year and simple calculation, and validated through consultation, as no information on this matter exists in the literature. Clearly this value had to be ascertained as accurately as possible, and so further validation was obtained using the model itself, as described in section 4.1.1. Other key biological values, where not available specifically for Norway, were taken from wolves elsewhere assuming a degree of conformity across their enormous range, as suggested in Mech (1970).

Poaching, the effects of density dependence and those due to prey fluctuations were all applied equally across the entire demographic range. In the case of poaching this was most probably fair, as poachers do not generally distinguish between wolves of different social classes. Regarding prey fluctuations, it is generally the case that when a pack has a successful hunt, all individuals will be able to feed (Mech, 1970), and since wolves cannot bring down moose alone (see section 2.6), all wolves should hence be equally affected by prey shortage or overabundance. Similarly, once a pack has established a territory the wolves will tend to tolerate a larger pack size and hence high density, so for simplicity the assumption about density dependence can also be made.

Official culls were applied annually in the model, and following recruitment. In reality culls take place every few years, but it was assumed that annual culls would be a fair approximation. Haight *et al* (2002) found that culling at different times of year affected the number of wolves culled (as pack size varied with recruitment) and the cost of doing so, but not the extinction probability, and hence time of year could be neglected in this investigation.

In order to examine variation in the size of the wolf zone as a management technique, it was assumed that this could be tested using the probability of success in dispersers establishing a territory as proxy. The relationship between the two is unknown and establishing this would possibly constitute a project in itself, but for the purposes of this project the assumption is justifiable logically and on the basis of basic ecological theory.

Finally, bottom up effects were assumed and top down effects ignored in the predator-prey interaction, as explained in section 3.3.1.

3.3.4 Sensitivity Analysis:

It was necessary to find how sensitive the outcome of the population model was to the fundamental biological parameters, so that particularly influential ones could be ascertained to greater accuracy if necessary, and so that a suitable margin of error was allowed for whilst exploring different management regimes (for more discussion, see Saltelli *et al*, 2000).

The twelve parameters in table 1 were subject to the analysis, with the uncertainty indicated in table 1 providing the range over which to test for model sensitivity. This represents a relatively high number of biological parameters, which is a reflection of the relatively complex social structure of the wolf. It should be noted that two of the parameters (poaching survival, and immigration rate from Sweden) were not fundamental biological rates, one deriving from anthropogenic pressure and the other merely a consequence of a geo-political boundary: but since both could be considered inherent to the system over the timescale in question, they were treated alongside biological rates in the model. The sensitivity analysis had to account for not only the effect of varying different parameters upon the model outcome, but also the effect of varying different *combinations* of parameters. To experiment with all possible combinations would have been prohibitively computationally intensive, and as such, the model was run a number of times with a random set of parameter values (i.e. within the range of uncertainty), and analysed statistically using a general linear model with a binomial link (see McCarthy *et al* (1995) for theory and validation). The number of runs required in order to provide a statistically meaningful result was estimated at around 500 (McCarthy *et al*, 1995; Nilsen *et al*, in review; E. Nilsen, pers. comm.), and given that each set of parameters was used to run the population model 50 times (see section 3.3.1), this amounted to 25,000 simulations of the hundred year period. The sensitivity analysis and empirical test described in section 3.3.5 were both carried out in order to validate the PVA model, prior to taking the main body of results.

It is important to note that in this investigation it was not necessary to determine the exact relationship between parameters and extinction probability. The main purpose was to find the parameters to which the model is significantly sensitive, so that the final results could be interpreted in light of model sensitivity to these parameters.

3.3.5 Testing the model with empirical data:

It is often recommended with PVA that models be validated both by using sensitivity analyses as above, and furthermore, through an iterative process of comparison between predictions made and existing data (McCarthy and Broome, 2000; McCarthy *et al*, 2000). In the case of the wolves in Norway, previous data are not useful in this respect, as not only have there been an insufficient population in recent years to make comparisons statistically meaningful, but the decline of the wolf previously in the same region took place under a vastly different management regime, and hence would require a different model.

However, in the last decade wolves have been successfully re-introduced into Yellowstone National Park: the abundance of prey and territory, the small initial population, and the unavoidable pressure from poaching make these two scenarios comparable in most respects, as does the previously indicated fact that the relevant biological parameters tend to remain relatively constant over a vast geographical range (Mech, 1970). Hence, empirical data was obtained from the literature concerning the population dynamics of the Yellowstone wolves over the last decade, and with a similar initial population the PVA model was applied, in order to evaluate any major discrepancies between reality and prediction.

3.4 Consultation:

Consultation was carried out in the form of unstructured interviews with a number of relevant and knowledgeable individuals on Norway, over a one month period spent working at Blindern university in Oslo, and Hedmark University College at Evenstad (a region in central Norway that borders Sweden, and which is inside the established wolf zone). As well as covering the demographic rates and potential management regimes, these consultations were employed to get a general feel for attitudes towards wolves in Norway amongst different groups, and to talk around the topic on wider issues such as the use of PVA in general, European management of large carnivores, general ecological dynamics in predator-prey systems, and so forth. Whilst points raised during consultation are generally quoted in this report without direct reference, a full list of those consulted can be found in Appendix I.

4. Results

It should be re-iterated at this juncture that, throughout the results section (unless otherwise stated), the terms "extinction probability" and "extinction risk" refer to a definition of this variable, whereby the number of years for which no established and territorial alpha pairs exist in Norway, as a proportion of the total number of years in the simulation.

4.1 Application of model to present situation:

4.1.1 Application to Scandinavian wolf population as a whole:

It was constructive to run the model for the entire Scandinavian population, as the size of the present population is small enough that the assumptions made in setting up the model remained valid, and not only could an extinction probability be estimated for the entire population, but importantly an attempt could be made to validate the value used for immigration rate to Norway, through consideration of the number of wolves dispersing in any one year over the peninsula as a whole.

The model was used with the following specifications: 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), poaching levels were halved (to account for lower poaching levels in Sweden), and the initial population was taken to consist of 15 packs (the present size).

The extinction probability was defined differently during this test, as the definition used elsewhere in the results section was defunct in the absence of immigration. Instead, another common definition was used: the proportion of runs in which the population died out during the 100 years of the simulation. Using this metric, the model was predicted a very high extinction probability = 92 % ± 10 % over a hundred years (see section 4.3.1(ii) for uncertainty calculation. Although the uncertainty in this result is different the method employed to estimate it was the same). This value is higher than might be expected, which, it was felt, was probably attributable to overly heavy or randomized poaching: a supposition which was tested by repeating the experiment and varying the poaching levels:

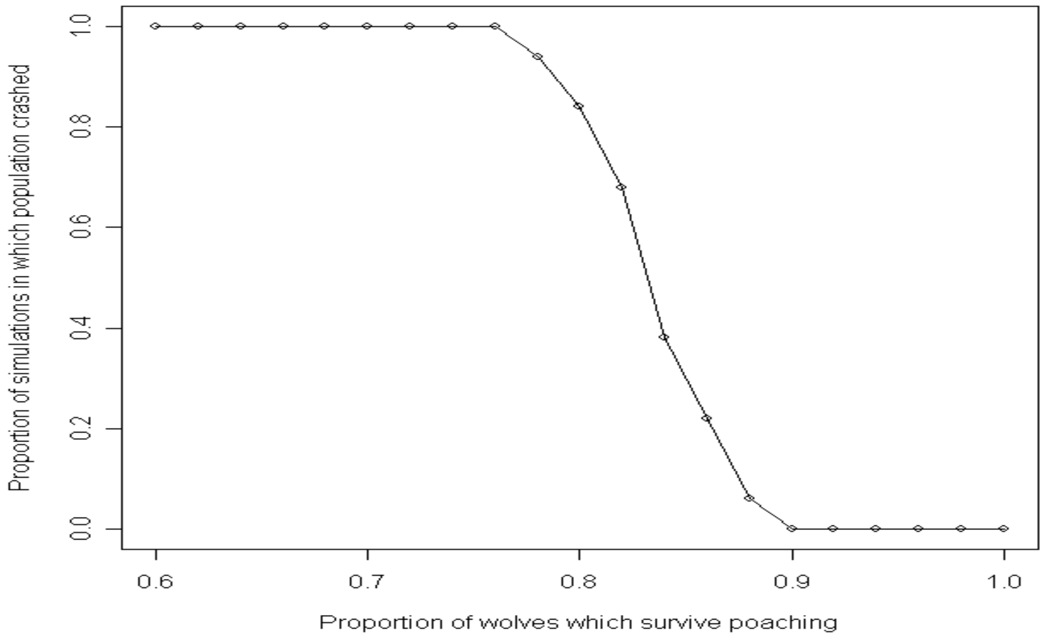

Figure 6: Plot of the proportion of simulations in which the wolf population had reached zero after 100 years (as proxy for extinction risk) against the proportion of wolves which survive poaching, for the entire Scandinavian population.

As can be seen, poaching does demonstrate a strong and non–linear influence over extinction probability, indeed to a surprising extent: it is probably partly the case that this is a consequence of the manner in which the population has been constructed in the IBM, but it is interesting to see how the application of the poaching function to this structure has such an important non-linear effect around an unstable 'tipping point' (here when the poaching survival ≈ 0.83). Given the large uncertainty in mean poaching levels for Scandinavia as a whole, it is clear that work beyond the scope of this project would be required in order to determine more exactly the actual extinction risk for the greater population. In any case, this does show that if the Scandinavian population remains isolated and subject to heavy anthropogenic pressure, its future would seem uncertain.

During this run of the model, the average number of dispersers a year was found, and then a value for the Sweden-Norway immigration rate was calculated given that Norway's proportion of the population is 3/15 packs. This gave an annual net immigration rate of 4.6 ± 2.7 wolves. Although this is slightly higher than the value used, the difference is not significant, and the baseline value was retained.

4.1.2 Population dynamics under the present Norwegian management regime:

Under the present management regime, the extinction risk for Norway was estimated to be 67 % ± 15 %, a value in agreement with similar studies; for instance, Vucetich *et al* (1997) showed a 70 % extinction probability for an isolated population of 50 wolves over 100 years using an IBM; and which should be considered unacceptably high. Also of relevance was the extent to which the population fluctuated (figure 7, which is characteristic of the results obtained); this not only represents a reasonably realistic dynamic given the wolf censuses of recent years (Wabakken *et al*, 2001, 2002, 2004a, 2004b, 2005), but highlights the instability in the population arising from the present regime:

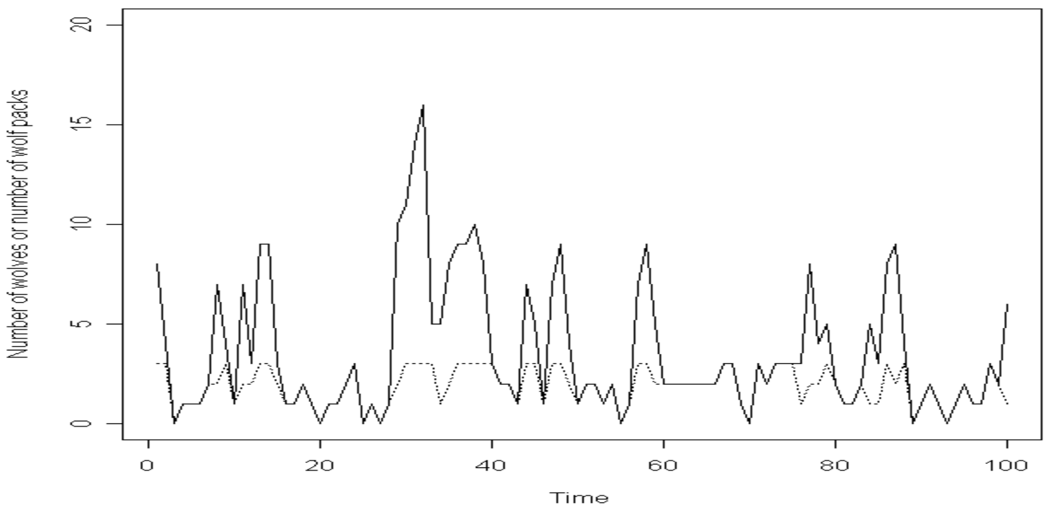

Figure 7: Example plot of wolf population and number of packs, in solid and dashed lines respectively, against time in years, under the present management regime. In this particular run, there were 73 years in which no breeding packs existed in Norway (i.e. extinction probability = 73%).

4.2 Model validation:

4.2.1 Sensitivity analysis:

The sensitivity analysis was performed, and the relationship between the extinction probability and the independent variables described by a general linear model with coefficients β_i:

Parameter	**Standardised β_i**	p **- value**
Cub dispersal rate	0.003	0.23
Yearling dispersal rate	0.003	0.40
Adult dispersal rate	0.002	0.82
Mean net annual immigration	-0.213 *	< 2e-16
Probability that an immigrant is male	0.095 *	< 2e-16
Probability of success in establishing a new territory	-0.043 *	< 2e-16
Litter size	-0.004	0.33
Cub survival rate	-0.003	0.002
Adult survival rate	-0.030 *	< 2e-16
Survival rate at age 9	-0.002	0.11
Survival rate at age 10	0.003	0.65
Survival rate after poaching	-0.172 * #	< 2e-16
(Important interactions)		
Poaching survival-Adult survival	-0.02 *	5.21e-09
Poaching survival-Immigration rate	-0.08 *	< 2e-16
Adult survival-Immigration rate	-0.01 *	0.0002
Poaching survival-probability immigrant is male	0.02 *	0.003
Immigration rate-Probability immigrant is male	0.05 *	< 2e-16
Poaching survival-Probability of establishing territory	-0.02 *	5.69e-10
Immigration rate-Probability of establishing territory	-0.02 *	4.20e-16
Poaching survival-Probability immigrant is male-Probability establishing territory	-0.03 *	0.02
Poaching survival-Probability immigrant is male-Probability establishing territory-Adult survival	-0.06 *	0.002

*Table 2: parameters in model with calculations of coefficients when fitted to a general linear model. * the parameters (and interactions between parameters) to which the model demonstrates significant sensitivity. # for clarity it should be noted that the poaching parameter corresponded to the proportion of the population surviving the poachers, hence the negative sign in this coefficient (i.e. as this parameter increases, extinction risk drops).*

As can be seen, the model was most sensitive by far to immigration rate and poaching levels, which were two of the hardest parameters to accurately quantify. It was interesting to note, however, that these were also two parameters that might change through the adoption of different management regimes. The model was also significantly sensitive to the probability of a dispersing wolf establishing or being male, and also to the survival rate for wolves between the ages of 2 and 8; although far less so than to the former two parameters. All other parameters were relatively insignificant under this analysis, although certain interactions between the parameters, which are specified in table 2, were important.

Since the sensitivity analysis was carried out using parameter ranges based upon initial uncertainty, it was weighted towards biological sensitivity, which explains for example why wolf survival rate was important (adult survival is generally relatively stable in wild mammal populations; Gaillard *et al*, 1998); equally so for the sex ratio in immigrants, as clearly the higher the bias in immigrating sex ratio in a small population, the more drastic the effect upon the number of scent marking pairs that can establish (especially given the importance of immigration to the Norwegian population, see below). It is also arguable that the large initial uncertainty in the 'anthropogenic' parameters contributes towards their high sensitivity in this analysis. In order to examine the parameters that gave model (as opposed to biological) sensitivity, the analysis was repeated using simple 10% ranges in all parameters. The results supported the results obtained above, with the exception that the parameters concerning litter size and cub survival rate became more important: however, since these parameters were known with relative accuracy from the literature, it was felt that further results could be based upon the original sensitivity analysis.

It was necessary to check the extent to which the important parameters demonstrated a linear relationship to extinction risk, so as to ensure the application of a general linear model was valid. This was achieved by plotting the 'logit' of the extinction risk against each standardized parameter in turn, and then finding the r^2 value of a straight line relationship between the two (if a relationship is linear, plotting the logit of the dependent variable should give a straight line graph; McCarthy *et al*, 1995):

$$\text{logit}(E) \;=\; \ln\left[\frac{E}{1-E}\right] \tag{3}$$

(where E = extinction risk)

For most of the parameters, there was no discernable relationship with extinction probability (which would be expected, given the relative lack of model sensitivity to those parameters), but the two most influential parameters (immigration rate and poaching levels) did in fact prove sufficiently approximate to a linear relationship:

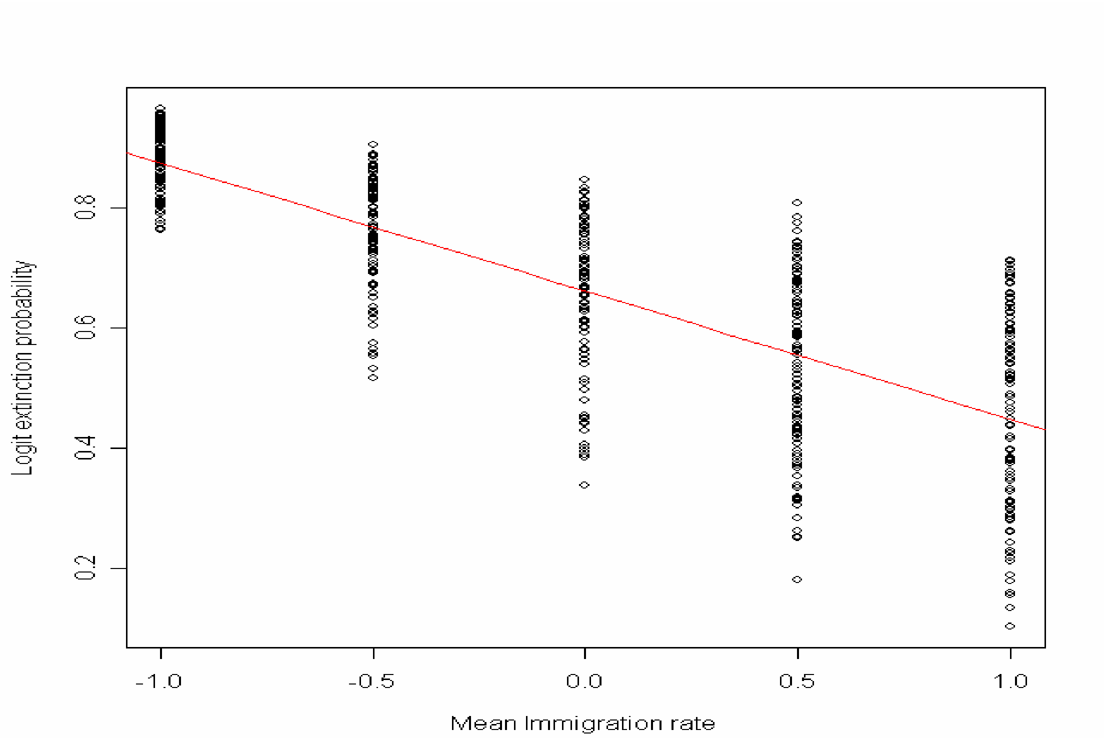

Figure 8a: Plot of logit extinction probability against standardized mean immigration rate, following sensitivity analysis. Linear fit gives adjusted r^2 = 0.61.

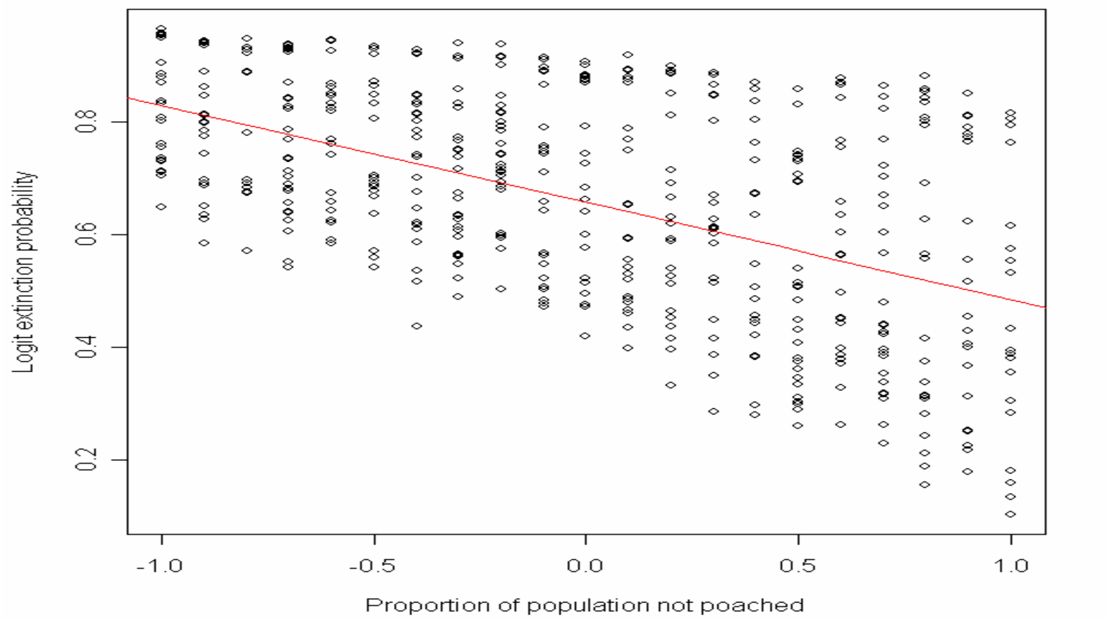

Figure 8b: Plot of logit extinction probability against standardized proportion of population not poached, following sensitivity analysis. Linear fit gives adjusted $r^2 = 0.27$.

4.2.2 Model test with Yellowstone data:

The empirical data (upper and lower bounds) were plotted in two ways: firstly as straightforward time series, and secondly, by plotting the lines of best linear fit to the raw data. The latter was felt instructive, since it was only in the last year for which data was available that wolf numbers did not increase, and as such, it did not necessarily follow that the wolf population was stabilizing at this point. The (upper and lower bound) lines of best fit thus crudely indicate the growth rate over the last decade:

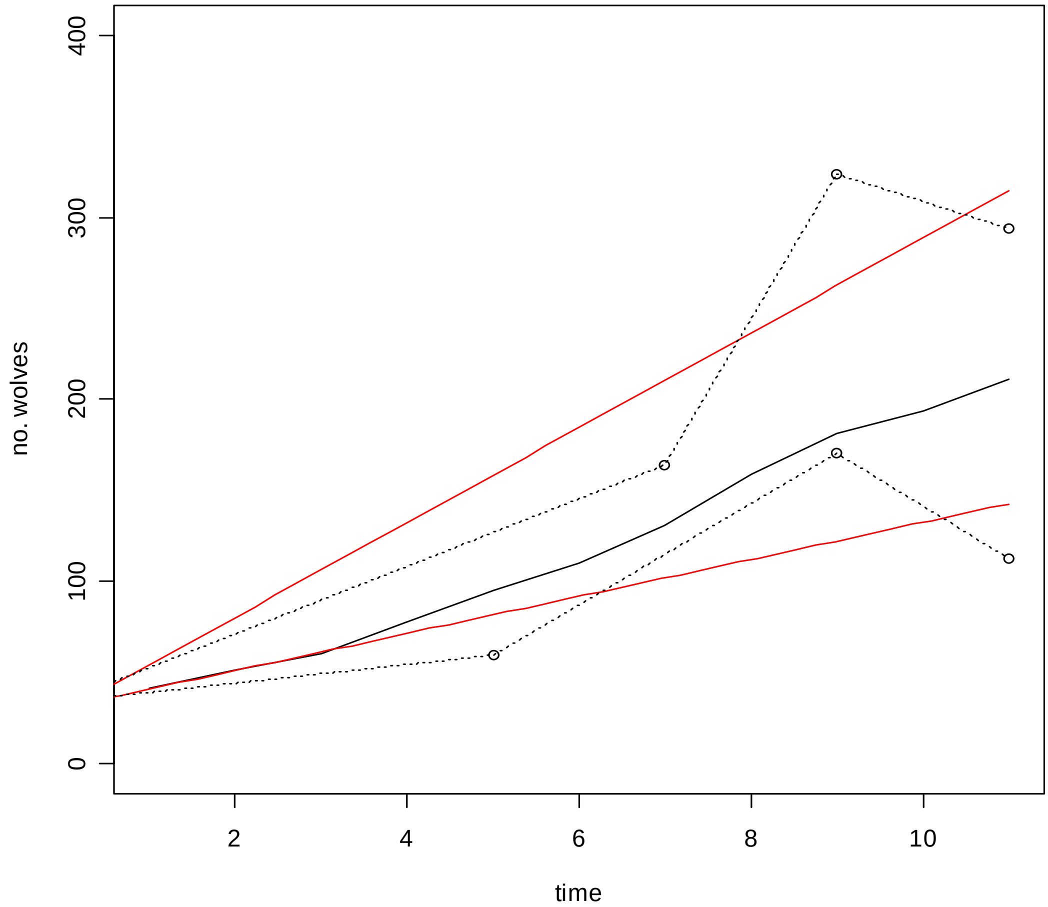

Figure 9: Plot of the number of wolves in Yellowstone Park, USA, against time in years, from 1995 onwards. Dotted lines represent the upper and lower bounds of empirical data for the region, straight lines represent the linear best fit for these data, and the solid curved line represents prediction of population trend made by the PVA model, using the empirical initial population and mortality rates.

As can be seen, the growth trend predicted by the model clearly lies within the bounds formed by the empirical data. It should be noted that, though empirical data only exist for the 11 year period as shown here; i.e., up until the present day; the model predicted imminent stabilization of the Yellowstone population, thus supporting suspicions that the recorded drop in numbers for Yellowstone wolves from 2004 – 2006 was as a result of stabilization of the population there. On the whole, this empirical test would appear to provide further validation of the model.

4.3 Experimentation using different management regimes:

4.3.1 Basic changes in management:

(i) Population dynamics with no lethal management:

With no anthropogenic intervention, that is, without culling or poaching but with the wolf zone as presently defined, and otherwise constant biological values and net annual immigration from Sweden, the extinction probability effectively drops to zero in the model. A typical run sees the population level out (whilst remaining subject to random fluctuations) at around 250 individuals, which is a consequence of the assumption that density dependence begins to have some effect when the population reaches around 100 - 150 individuals. This value can of course not be taken as a numerical result due to initial assumptions, which only remain valid at a smaller population size than that reached here, but it is useful to show the dynamic; that is, that the population would initially grows rapidly and eventually stabilizes, with a low likelihood of crashing:

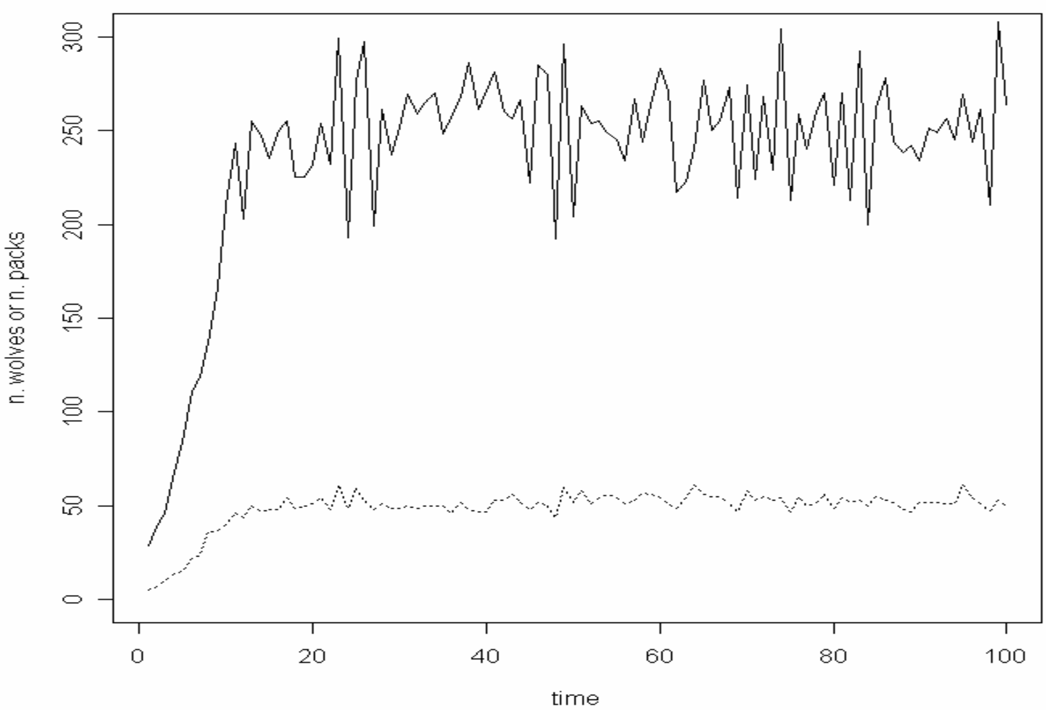

Figure 10: Example plot of wolf population and number of packs, in solid and dashed lines respectively, against time in years, with no anthropogenic intervention except the preservation of the existing wolf zone. Note that absolute values should not be given too much weight; this graph mainly demonstrates qualitative behaviour.

Alternatively, in the situation in which the above experiment is repeated but with poaching at the present levels, the dynamic is altered significantly:

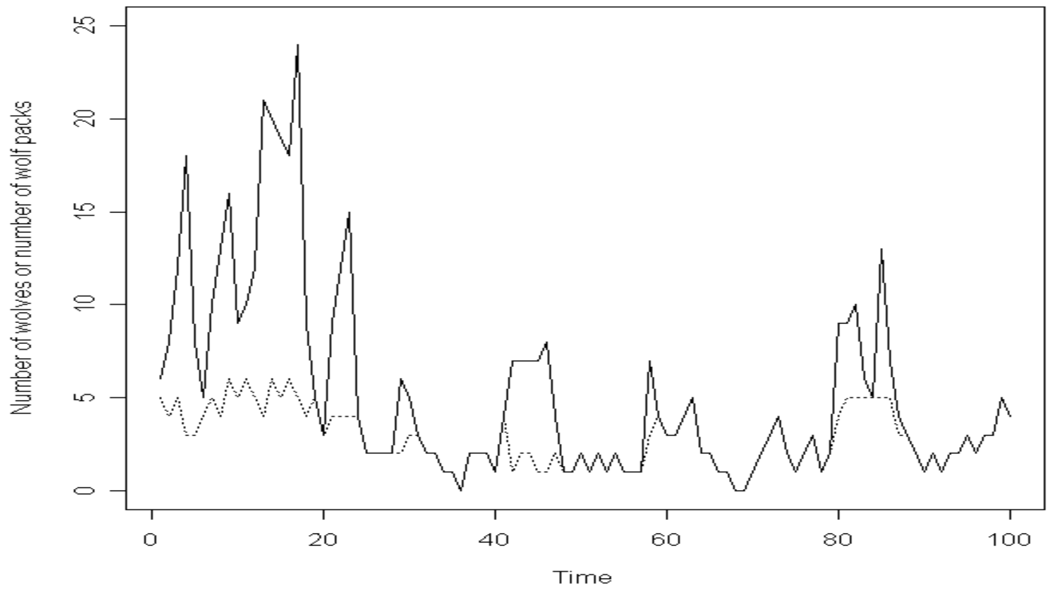

Figure 11: Example plot of wolf population and number of packs, in solid and dashed lines respectively, against time in years, with no culls, but poaching at present levels and with the preservation of the existing wolf zone. Extinction probability = 68 ± 15 %.

This example clearly demonstrates the profound influence of poaching on the Norwegian wolf demographic: in this particular run, the extinction probability was estimated at 68 % ± 15 %, which is slightly higher than the average under this regime (64 % ± 15 %) but which is nevertheless comparable to the extinction risk when the model is inclusive of government culls. Furthermore, it demonstrates how, as a result of poaching, the wolf population might not expand to a politically unacceptable level (which it probably would do in the free expansion case seen in figure 10) even if non-lethal methods of conflict avoidance were employed. However, this does not represent any kind of solution, as it would effectively rely upon an illegal and unpredictable activity to control numbers.

(ii) Variation in the number of wolf packs permitted to establish on Norwegian soil, calculation of uncertainty, and analysis of pack dynamics:

Variation in target number of packs

As would be expected, a target minimum of anything less than three packs would lead to a substantially higher extinction probability, even allowing immigration from Sweden and ignoring genetic effects: hence the risk rose from 66 % ± 15 % with a three pack target to 71 % ± 15 % with two and almost 80 % ± 15 % with only one.

However, and perhaps surprisingly, an increase in the target number of packs did not have an enormous effect upon the extinction probability; once the target number was raised beyond 4 – 5 packs, the risk remained at 66 % ± 15 %:

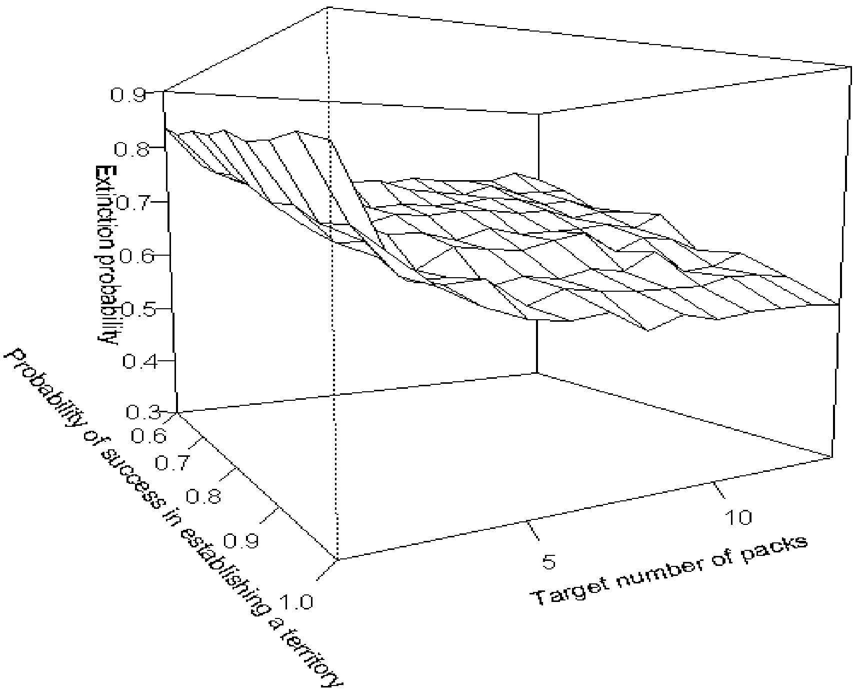

Figure 12: Plot of extinction probability against target number of packs, with all other parameters fixed but showing the effect of uncertainty in the value for probability of success in establishing territory.

Figure 9 not only demonstrates this, but shows how even given the margin of uncertainty in sensitive initial parameters (in this case, probability of success in establishing a territory) this statement remains qualitatively valid. Although there is some difference in the rate of change in extinction probability below a 5 pack target if this influential parameter is varied, and also in the value of the extinction probability, the qualitative relationship as initially stated is the same.

Calculation of uncertainty

Variation in the value used for the other two parameters to which the model is statistically most sensitive (see table 2) would give a similar form of uncertainty in the extinction probability. The inherent uncertainty in poaching levels (± 0.1) gives a similar degree of uncertainty in extinction risk as that inherent in immigration rate (± 10 %), whilst the uncertainty in probability of success in establishing territory (± 0.1) is less influential (± 5 %). However, the qualitative relationship between extinction risk and the independent variable (target number of packs) remains the same. 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:

$$\sigma_y^2 = \sigma_{x_1}^2\left(\frac{\partial y}{\partial x_1}\right)^2 + \sigma_{x_2}^2\left(\frac{\partial y}{\partial x_2}\right)^2 + \sigma_{x_3}^2\left(\frac{\partial y}{\partial x_3}\right)^2 \tag{4}$$

(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 with variation in the baseline value for the latter, it was applied to the rest of the results where appropriate.

Analysis of pack dynamics

It was felt necessary to test whether the relationship between target number of packs and extinction probability was indeed as shown above, or instead a consequence of the definition of extinction risk: that is, was it the case that although in each simulation there was a constant number of years without breeding pairs, in fact a greater target number of packs gave greater long term stability? To check this, the experiment was repeated using the total wolf population after 100 years as proxy for inverse extinction risk, giving the following results:

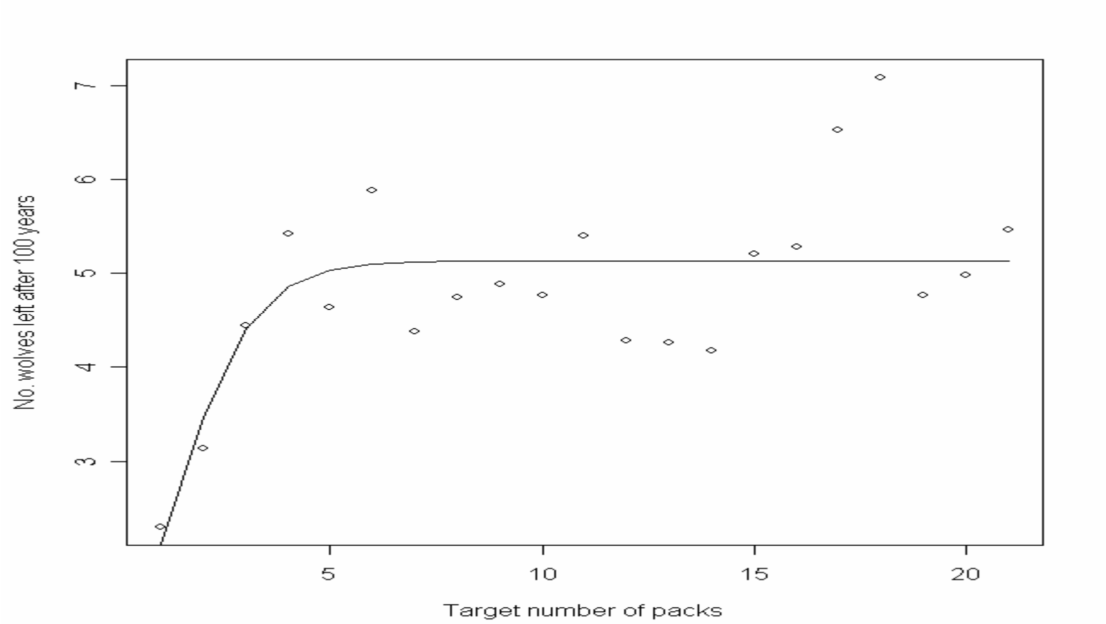

Figure 13: Plot of average number of wolves in population after 100 years (as proxy for inverse extinction risk) against target number of packs.

As can be seen, extinction risk does tend to drop as target number of packs increase, but there is still a leveling out at around a 5 pack target. Equally, there is very little absolute difference in final wolf numbers (the range plotted is only between 2 and 7 individuals), which again supports the previous results, and suggests that they are due to the population dynamics and not simply the extinction metric. In fact, the reason for this leveling out of extinction risk at a 4 - 5 pack 'threshold' can be explained on the basis of the immigration rate:

Mean net annual immigration rate of wolves in to Norway	**Target no. packs at which extinction probability levels out ("threshold")**	**Extinction probability**
0	-	97 %
1	-	88 %
2	3	76 %
3	4 - 5	65 %
6	6 - 7	39 %
9	8 – 9	35 %
12	8 – 9	16 %
14	10 - 11	11 %

Table 3: threshold target number of packs at which extinction probability levels out for different immigration rates.

Although it would be difficult to establish the exact relationship between the two, it can clearly be seen that as the immigration rate increases, this ‘threshold’ number of packs also increases. As such, it seems possible to conclude that the model demonstrates a ‘rolling pack’ dynamic, whereby packs that are formed are quickly broken up (presumably, largely through poaching) and replaced by new packs (as a result of high immigration and dispersal rates). This explains why increases in the target number of packs have little effect over a certain threshold: it is only the number of immigrants arriving that supports a proportionate number of packs, and reducing culls once this threshold has been crossed does nothing, as the packs are still effectively removed (in that they are caused to break up) by the poachers.

Further tests showed confirmed this conclusion, as it was demonstrated that neither poaching survival nor probability of success in establishing new territory affected this ‘threshold’ target pack value.

(iii) Variation in the number of immigrants arriving from Sweden, as reflective of changes in management in that country:

The mean net number of immigrants arriving from Sweden each year was varied between zero (no immigrants) and thirty individuals. It was found that, if no wolves entered Norway from Sweden, the risk of extinction rose to almost 100%, apparently indicative of the fact that the Norwegian wolf population is almost entirely sustained by the existence of the Swedish portion of the Scandinavian population. As the number of immigrants increased, the extinction risk for the Norwegian population dropped dramatically, approaching an extinction probability of 30 % ± 15 % as the net number of immigrants increased beyond 15 – 20:

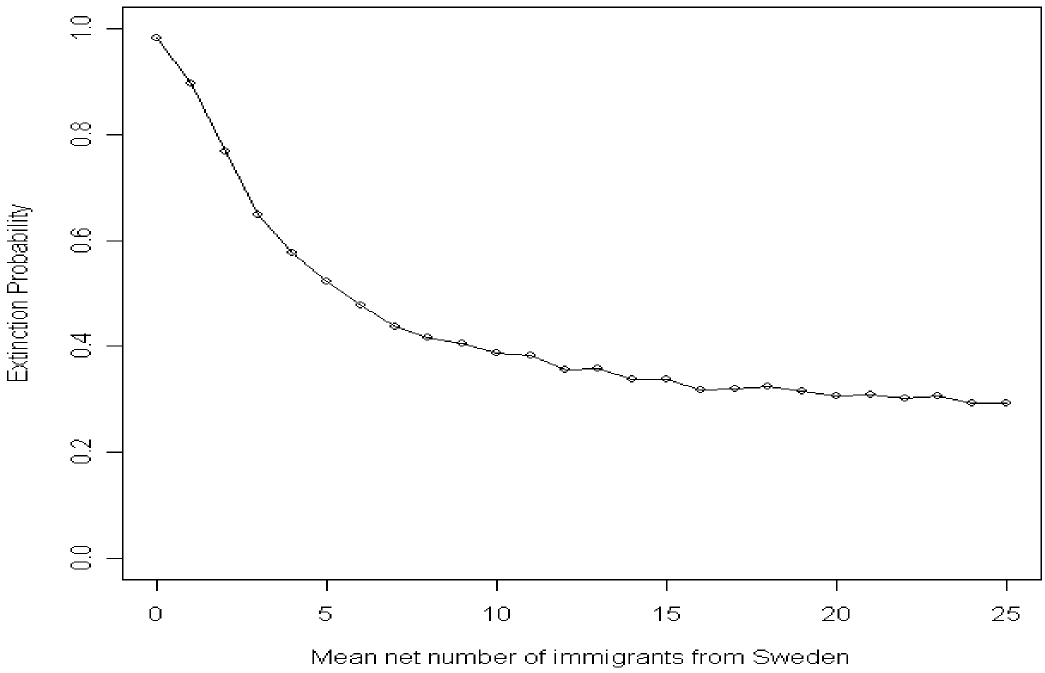

Figure 14: plot of extinction probability against mean number of immigrants, holding all other parameters constant.

This result would appear logical: given the definition of the extinction probability, the more immigrants there are in a given year the less likely that there will not be any breeding pairs established the next year, and so the lower the extinction risk. Furthermore, as immigration rate increases further one might expect its influence upon extinction risk to weaken, as not all the immigrants can establish territories given a finite wolf zone, and this is observed. Apparently though, any form of management that led to a slight increase in net immigration rate from its present value (~ 3 wolves/year) would dramatically reduce the extinction probability, given the gradient of the curve in figure 14.

(iv) Variation in the probability that a dispersing wolf will establish a new territory, as reflective of changing the area of the wolf zone:

At present, and on the basis of consultation with field biologists in Norway, there is approximately a 0.8 probability that a wolf will establish a new territory, if it survives dispersal. By increasing or decreasing the size of the wolf zone, one might expect a corresponding increase or decrease in this likelihood (see section 3.3.3): this parameter was varied in the model so as to explore this as a potential management strategy. It was found that there was a positive linear relationship between extinction probability and probability of success, with an adjusted r^2 value of 0.98.

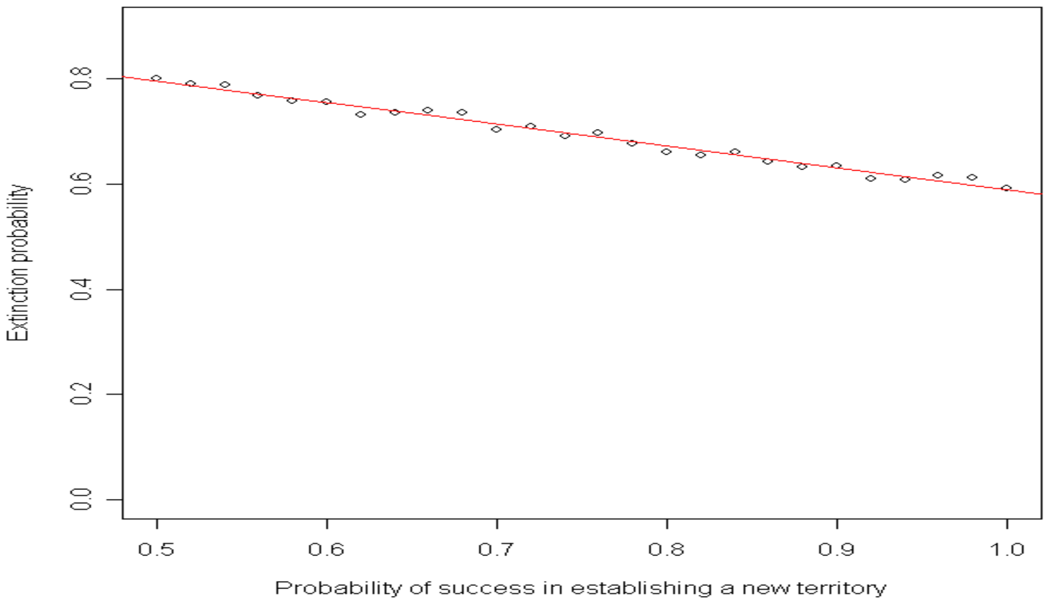

Figure 15: plot of extinction probability against probability of success in establishing territory, with linear line of best fit (adjusted r^2 = 0.98)

Again, one might expect such a result, given the metric used for extinction probability, and the simple fact that the wolf population will be more easily sustained the more easily dispersers are able to settle. The strength of this relationship suggests that it is to some extent an artefact of the model: note, for instance, that there is no real spatial or diffusive element to the model and that the emphasis is thus purely upon this parameter to determine whether dispersers settle successfully, and furthermore that immigration is so integral to the persistence of the population; see section 4.3.1(iii). It might be thus proposed that whilst the extinction probability consequently seems strongly dependent upon this parameter, it is really indirectly a further testament to the importance of immigration for the Norwegian population.

In any case, there is some hint as to the importance of this parameter, and this is referred to in the discussion.

4.3.2 Exploration of legal hunt as a management tool:

(i) Variation in the proportion of wolves hunted as part of a non-adaptive legal hunt, with different target population size:

It was established during consultation that it would be extremely hard too substantially reduce poaching levels, so these were generally taken as an unavoidable background mortality rate. As mentioned in section 2.5 however, it was thought feasible that the wolf might gain greater acceptance if the public had a larger role in controlling numbers, for example by allowing a legal hunt given a bigger target population. It was found that not only would allowing a proportional non adaptive legal hunt substantially increase the extinction probability, as one might expect, but this seems to be almost independent of the target population, so that even with a target of ten or twelve packs, the effect of adding on a proportional legal hunt would be similar, and dramatic.

Presumably, this is due to the fact that the hunt in this case is proportional, randomized and non-adaptive, and is thus functionally equivalent to an increase in poaching, which as was seen in section 4.3.1(i) dramatically increases extinction risk.

(ii) Variation in the number of wolves hunted as part of an adaptive legal hunt quota:

The 'legal hunt' experiment was repeated using a rudimentary adaptive management function, whereby a constant number of wolves were taken out of those dispersing in any one year (on top of poaching), representing a legal hunt, but only if the number of wolves dispersing was greater than a set quota (i.e., if the quota was 10, and there were 5 dispersers in one year, none could be killed, but if there were 15 dispersers in a subsequent year then 10 of them would be killed). The variation in extinction probability was found as a function of both the size of the legal quota and the target population size was varied. It was found that a legal hunt of this nature seemed to have little effect upon the extinction risk. This is slightly misleading, as since the wolves were only hunted in those years in which the number of dispersers was greater than the quota, a higher quota meant that there were fewer years in which wolves were killed (with a quota of one wolf/yr, 40 ± 5 wolves were actually killed legally over the 100 years, with a 2 wolves/yr quota only 10 ± 5 were killed, and none could be hunted with a higher quota). Nevertheless, from a policy perspective the simple act of establishing a legal hunt (irrespective of the number of years in which wolves could actually be shot) might have its benefits, which is explored further in the discussion.

(iii) Combination of preceding methods for allowing a legal hunt:

The above experiment was repeated a further time to analyze the potential outcome from employing a hunt which was proportional and randomized, but only allowed each year if the population exceeded a certain threshold: a combination of the preceding hunt techniques (i.e. if the threshold was 15 wolves and the population was 10, no wolves could be killed, but if it was 20, a set proportion of the population as a whole could be killed). Such an approach has performed well under previous analyses (e.g. Engen *et al*, 1997). Additionally, the hunt was explored for the situation in which poaching levels remained at the baseline, and another in which poaching levels halved (it is clearly feasible that such a phenomenon might occur if a legal hunt were set up). A range in both the population threshold for hunting and the actual proportion of wolves taken in the hunts was explored.

It was found that neither the actual proportion of wolves taken nor the threshold value had any effect upon extinction risk; again, this was due to the fact that there were often not enough wolves to allow a hunt in any one year, in fact, there were almost no years in which hunts were possible. As expected, with lower poaching pressure the extinction probability for the population fell, but this also made possible the emergence of a weak relationship between hunting threshold and extinction risk (at a lower threshold the risk was slightly increased).

Hence, using this model, the constant adaptive hunt in section 4.3.2(ii) outperformed the proportionate adaptive hunt (this section), given that it similarly did not increase extinction risk, but allowed for a greater wolf harvest.

4.3.3 The case of a second extirpation of wolves in Norway:

(i) Application of model to Norway post-extirpation of wolf population:

The model was applied to Norway in the scenario in which the wolves were extirpated, in order to determine whether they could re-establish through immigration from Sweden alone. In this scenario, the net annual immigration rate was raised to 5 individuals (to reflect the fact that no wolves were diffusing back into Sweden from Norway), and it was assumed that the Norwegian management would stop culling wolves, at least at first, following a second extirpation. The poaching levels were varied to find the effect that this would have upon a second natural re-introduction, and the number of wolves left after the 100 years in the simulation was used as the dependent variable (it was felt that this would provide a better indication of recovery of the population in this instance, as the population would always start with no breeding packs for at least a few years):

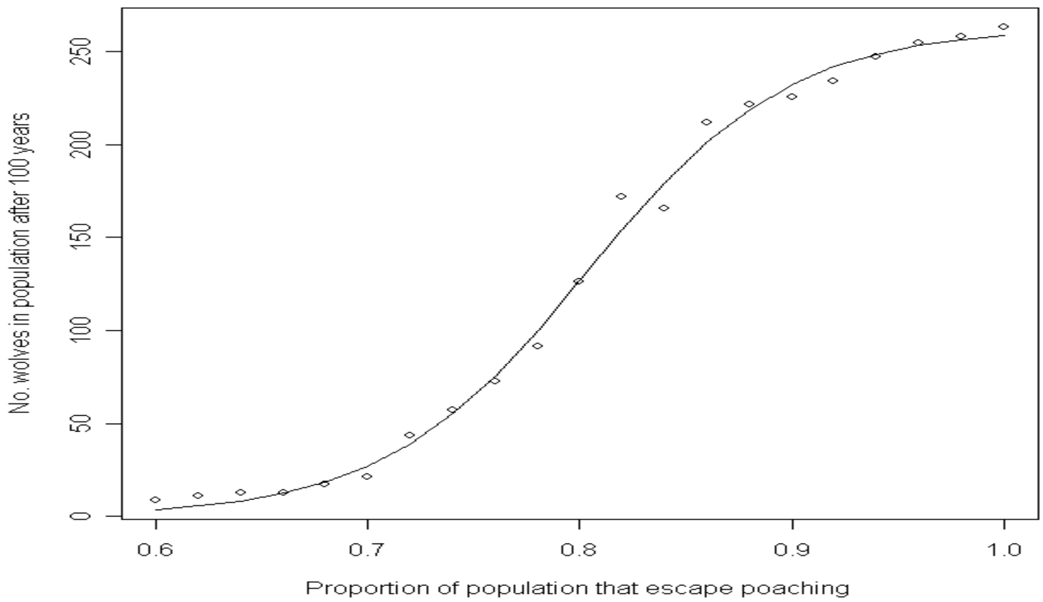

Figure 16: Plot of no. wolves left after 100 years, as proxy for extinction risk, against proportion of population that survive poaching annually. Initial population zero, no official culls.

First and foremost, it is clear that in the absence of culls, the population could re-establish assuming immigration from Sweden. Once again though, the results demonstrate the influence of poaching: at today's levels at the far left of the curve in figure 16, the wolves would struggle to re-establish (and in fact it could be that those wolves remaining after 100 years are just dispersers and not an established wolf population), and it is only as poaching levels drop that the wolf population becomes significant. Even so, this is an optimistic estimation of wolf numbers, given the higher immigration rate and lack of culling assumed in the experiment, both of which would almost certainly change in an unforeseeable way as the population grew again.

(ii) Effect of present regime upon future chances of wolf recovery/population expansion:

A brief experiment was carried out to determine the effect of initial population size on extinction risk. The number of wolves in the population after 20 years was taken as proxy for success in re-establishing, and the initial number of packs at year zero was varied; it was assumed that culls were discontinued so that the wolf population could grow into the present wolf zone, but poaching remained constant:

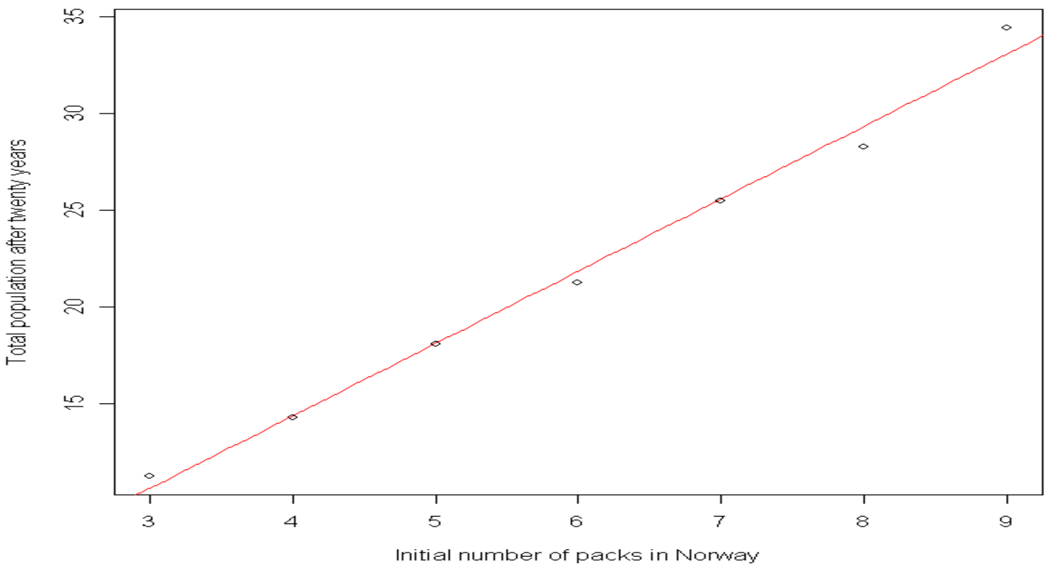

Figure 17: Plot of total population after twenty years, as proxy for success in re-establishing, against starting number of packs as reflective of the present regime. Line shown is linear best fit.

It can be seen that there is a direct relationship between the two variables, such that retaining a higher number of packs under the present regime would allow a more robust expansion of the wolf population in the future, should that become a policy goal. This is a logical outcome, and despite the variables demonstrating such strong correlation it is not immediately clear how this could be explained as an artefact of the model: as such it provides a further argument for preserving a slightly higher wolf population, as greater flexibility in potentially allowing the wolf population to expand in the future would be both biologically and politically advantageous.

(iii) Effect upon Scandinavian population of allowing immigration from Finland/Russia:

During consultation, the subject of genetic depression often arose. Details are included in the discussion, but include the recommendation that there is some constant immigration to Scandinavia (from Finland/Russia), of at least two individuals every generation (~ 5 years), in order to maintain genetic viability. The experiment in section 4.1.1 was repeated with such an immigration rate, so as to determine what the demographic effect would be (clearly this model could not include genetic considerations). It was found that, genetic issues aside, allowing even such a small amount of immigration into Scandinavia would cut the extinction probability for the peninsula (as defined in the previous experiment, i.e. the percentage of simulations for which the wolves survived the 100 year test period) from 92 % ± 10 % to 60 % ± 15 %. This would most probably drop even more dramatically if the model did take genetics into account, making a persuasive case in favour of either Norway or Sweden, or both, encouraging immigration from Finland/Russia.

4.3.4 Use of model to run basic cost benefit analyses:

(i) Incorporation of rudimentary CBA into model, for present regime:

Clearly, the results obtained above and during the consultation exercise imply potential changes to the present management regime, which are explored further in the discussion. Given the importance of economic considerations in this situation however, it was felt that it would be illuminating to use the model to generate some rough idea as to how a new management regime might compare financially to the present one. This was achieved by evaluating the important direct costs and benefits associated with the wolves, and then using the model to perform a very basic cost-benefit analysis (CBA) every year, so as to find the mean annual cost associated with the wolf population.

The experiment was first applied to the present regime, with the following statistics: wolf packs kill 62 – 90 moose a year, normally consist of around 6 – 8 individuals, and in Norway moose constitute around 90 – 95 % of the wolf diet (Pedersen *et al*, 2005). The kill rate was assumed to be constant at 75 moose/yr for the purposes of the CBA, not only to simplify the investigation but because there are no basic models that convincingly explain observed variation in kill rate (Vucetich *et al*, 2002). Going by weight and allowing for the fact that wolves don't eat the whole sheep when they kill one, this means that each wolf would eat around 3 – 6 sheep a year at most. The worth of a single moose and sheep can be estimated at around $2,000 (to landowners selling hunting permits) and $125 (to farmers) respectively (Mysterud, 2006; Nilsen, 2006; Asheim and Mysterud, 2006). Finally, based upon the recent culls, a wolf costs around $36,000 to track and kill (BBC news).

With these figures, incidentally all acting as costs to the economy, the mean annual cost of the wolf population was estimated at around $78,000 ± 3,000. Clearly this only considers direct economic factors, and so ignores indirect effects such as non-economic costs/benefits to farmers of livestock (see Montag, 2003), and benefits such as existence value, as such effects are very difficult to quantify. Equally, costs such as those incurred in monitoring wolves and research grants are ignored for simplicity. However, for the sake of a simple comparison between different regimes the inclusion of these extra effects was felt unnecessary, as they would to some extent cancel out.

(ii) Incorporation of rudimentary CBA into model, for regime in which a higher target wolf population is kept in check through legal hunt and culls:

The above experiment was repeated, with the same unit costs, but with the total mean cost being at least partially offset by any mean economic benefits reaped as a consequence of allowing hunters to pay for the rights to shoot a controlled number of wolves, over and beyond the culls. The hunt was a constant number per year but was only permitted over and above a set threshold in any one year. The market price for a wolf was taken to be $2,000 based upon prices given on various hunting websites (Yukon Hunting, 2006; Gondola, 2006; Sentinel Mountain Safaris, 2006). It was found that size of the wolf quota which could be taken provided there were enough dispersers proved irrelevant to costs, and furthermore, at low target pack numbers the mean costs would prove higher than in the present scenario, but as the target population grew the mean cost dropped just below \$76,000 ± 3,000 and leveled out.

It is interesting to note that the model predicts that increasing the population size and allowing a controlled legal hunt would reduce costs to the economy, in this simplistic analysis. It should be noted that the leveling out of total costs with increasing wolf population here would be expected, again due to immigration levels and the phenomenon explored in section 4.3.1(ii); hence one might reasonably expect that if this restriction were to be removed, the cost would continue to drop with increasing wolf population size to a certain extent.

(ii) Incorporation of CBA, for regime in which there are legal hunts and no culling:

The experiment above was repeated for the case in which government culls were stopped but hunting allowed: in this case the form of hunt in which a proportion of the wolf population is hunted, but again only when a certain population threshold was reached. It was found that again the magnitude of this threshold made little difference to annual costs, but that the higher the proportion of wolves included in the hunt, the lower the direct costs:

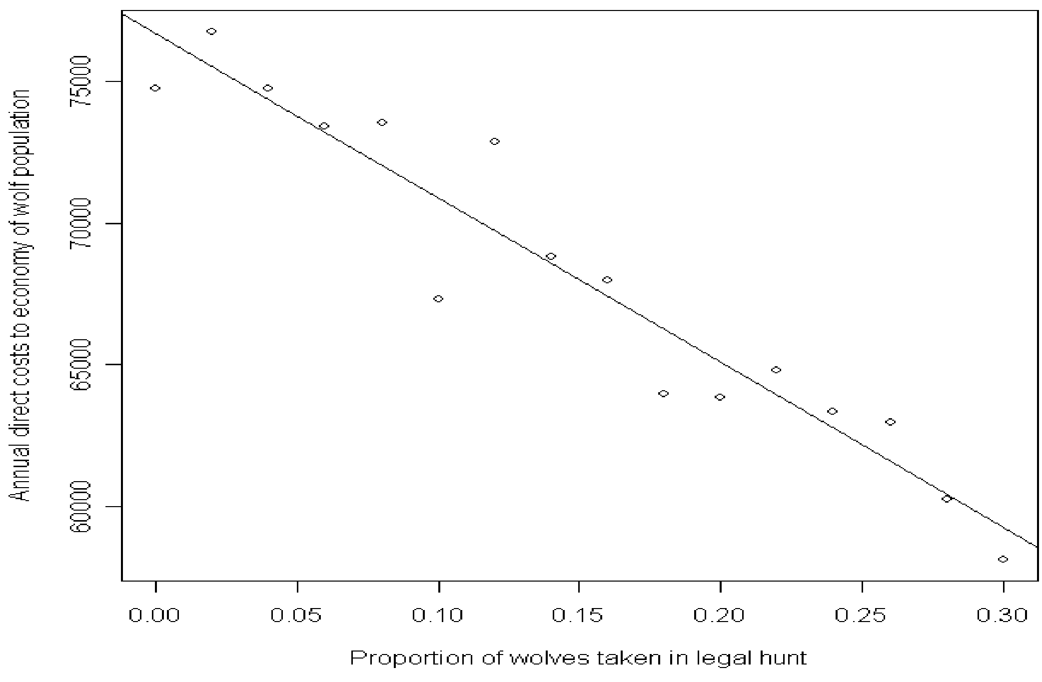

Figure 18: Plot of direct costs against proportion of wolves taken in an adaptive legal hunt, with a threshold population set at 15 individuals. Straight line fit gives adjusted r^2 = 0.9.

These results would tend too support the finding from the rest of this section, and it is therefore clear that by exchanging culls for a legal hunt, the retention of a wolf population could potentially be made more viable economically. Although this area does not represent the main thrust of the project, it is informative that management alternatives, even those that engender a higher target wolf population, could prove more viable economically than the present regime.

5. Discussion

It is beyond doubt that there are a huge number of issues to attempt to bring together in searching for a solution to the controversy surrounding wolves in Scandinavia today. If the situation is ever to be resolved it is likely that most if not all stakeholders will be forced to compromise to some degree. However, to some extent analysis of the results of the consultation, literature review and modelling does suggest certain policy reforms. In the following section, the results from the modelling exercise are discussed in the light of the important points raised during consultation: note that whilst those consulted are not directly referenced below, a list detailing relevant sources can be found in Appendix I.

5.1 Modelling results:

Firstly, to re-iterate the main findings arising from the modelling experiments: the extinction risk for the present population (both in terms of the Norwegian and Scandinavian populations) is very high. The Norwegian population is sustained almost entirely through the immigration of wolves from Sweden, and the main contributing factor to the high extinction risk is poaching, both in that it affects a high proportion of the population and is distributed randomly across the full demographic range. At present, the wolf dynamic seems to follow a 'rolling pack' system whereby there is rapid turnover of packs, so that packs break up quickly but are quickly replaced due to high immigration and dispersal. Management regimes that increase the size of the wolf zone, the immigration rate from Sweden, but only to a limited extent the target number of packs, would decrease the extinction risk for the population. A proportionate legal hunt, even with a larger population, would add to the extinction risk, whereas a legal hunt with a threshold would not, thought the latter would not allow that much actual hunting of wolves; a simple CBA suggests that a legal hunt could also reduce the direct costs of a resident wolf population. Finally, if the population was extirpated for a second time, it could feasibly recover assuming that immigration from Sweden continued, but only if there was a substantial reduction in pressure from poachers.

5.2 Modelling results in light of consultation:

The results suggest that the extinction probability is high (67 ± 15 %) under the present regime. Given that a majority of Norwegians want the wolf to be conserved, and that whilst Norway is acting within the confines of international treaties at present it will probably be in violation if the wolf population drops too much further, it might be categorically stated that the Norwegian government should improve upon its present management strategy. Of the options explored, it is abundantly clear that an increase in immigration from Sweden would reduce the extinction risk most effectively, corresponding to an increase in the Swedish wolf population. Whilst in some sense this is out of Norwegian hands, it does highlight the fact that the Swedes are encouraging their wolf population to expand, so whatever they do, Norway will have a wolf issue for the foreseeable future. One possibility, that this result would support, is that the two countries establish a joint wolf management body, as this would allow immigration to be dealt with more practically.

Equally, it was shown that, by increasing success in territorial establishment, the extinction probability was dramatically reduced. However, for one thing, the relationship between this and an actual management regime (that of increasing the size of the wolf zone) was based upon an assumption that would require clarification through further study before being used to make recommendations. Additionally, it is unlikely that in the present political climate it would be realistic to expand the wolf zone, and since there is space within the existing zone for a higher and/or more stable population, probably unnecessary. Similarly, a management regime which didn’t involve lethal control was shown to be politically unlikely: either the population would expand rapidly to fierce opposition on behalf of the rural community, or poaching would keep numbers depressed, leading to an unstable and consequently unsustainable wolf population.

It was interesting to note that the magnitude of the target number of packs had relatively little effect upon the extinction risk, depending upon immigration levels. At present, a small increase might give some improvement (say to 4 or 5 packs, which would be feasible within the existing wolf zone), but not beyond that, whilst going far beyond such a target would certainly not be popular amongst the rural population. However, an approach that allowed the population to increase whilst implementing an adaptive legal hunt system might be effective in placating the anti-wolf lobby even though it wouldn't necessarily always allow wolf hunts: such a regime would also potentially go some way towards countering poaching, a major threat to the wolves, and would thus seem to show some promise. However, a more detailed theoretical exploration than that undertaken here would be required, if this were to be implemented, as well as a more thorough consideration of different harvesting strategies (see Lande *et al*, 1995, 1997; Engen *et al*, 1997; Milner-Gulland *et al*, 2001).

It might additionally be the case that, as regards lethal control, it is not a question of the extent to which it is carried out, but the manner in which this is done. At present it is often the case that alpha couples are culled, and that at any one time there exist large areas of unoccupied territory along the length of the border. Since alpha losses cause pack break up and dispersal, and Swedish wolves will disperse into territories unoccupied by Norwegian wolves, this means that there are a disproportionate number of dispersers in Norway: which is highly relevant, as it is these dispersers which cause almost all of the problems with depredation upon livestock (as a solitary wolf is generally unable to bring down moose). As such, a more effective approach would involve culls that carefully caught wolves dispersing outside the wolf zone and maybe newly established scent marking pairs, but which placed high emphasis upon preserving the stability of existing packs (instead of allowing a high pack turnover), and in leaving established packs along the border to act as a 'natural barrier' to dispersers from Sweden.

In such a scenario, there would then of course remain the problem, for those within the wolf territories, of economic loss due to livestock depredation, hunting losses and fear of injury. It is arguable that, since the wolf holds economic existence value for the whole country, that it should be the country that pays for any financial losses incurred too, and as such extra subsidies should be paid to those living within wolf territories (note the emphasis upon actual wolf 'territory' as opposed to the greater wolf 'zone'). This measure, definitely an option given Norway's wealth, would not only have the benefit of satisfying those landowners providing habitat for the wolf, but could even soften rural opinion towards the wolf. As a final note upon subsidies, it is further arguable that, where possible, the government might benefit from offering support more in the form of assistance in permanent livestock guarding (e.g. lambing pens, electric fencing, livestock guarding dogs) as opposed to financial support;

however this change would necessarily be a slow process given a general attitude within the rural community against returning to older agricultural practises.

A matter of fundamental importance to this issue and thus one which requires some mention, which was not explored by the model but was alluded to constantly during consultation, is that of genetic depression (see also Liberg *et al*, 2005). It is the opinion of geneticists and a number of wolf biologists that the gene pool in Scandinavia as a whole is far too small at present, and in fact the discovery of an unusual concentration of sterile males in recent years may be the first sign that this is true. If genetic input from Finland or Russia was encouraged, then the population would be viable in the long term if it numbered 150 – 200 individuals, with a constant fresh genetic input provided by 1 – 2 new wolves every generation. If, on the other hand, the Scandinavian population were completely isolated, it would have to number ~ 600 – 800 individuals in order to guarantee long term stability (Liberg, 2006). There is the possibility of wolves immigrating from Finland/Russia through Lapland (as the founders of the present population did), but at present wolves dispersing into this region are effectively all driven away or killed by the Sami. An interesting policy route to explore would be one in which, under a joint Scandinavian management regime, Sweden made use of its less densely populated rural areas to support the bulk of the Scandinavian wolves, whereas Norway used its economic resources and geographic position to assume the burden of providing fresh genetic input (using a wolf 'corridor' from the North). In any case, it was shown in the results section that, irrespective of genetic considerations, this would drastically reduce the extinction probability for the Scandinavian wolf from a purely demographic perspective. Whether or not this would be possible was not agreed upon by the various experts questioned, but if something like it was feasible, it would mean the minimum viable population in Scandinavia being as small as possible: and in any case a population as high as 600 is out of the question in the near future. Although the issue of gene flow as a whole rests slightly outside the scope of this project, the results should be understood within that context.

Finally, although it was a conclusion reached through very basic calculation, it was interesting to note that whilst the wolves presently present a direct net cost to the economy, this cost might feasibly be reduced through changes in the management regime, even if these involved a larger wolf population (the cost of which could be offset by legal hunts as modelled here, or alternatives such as eco-tourism, which is feasible despite receiving little attention in this project). Furthermore, the conclusion that a larger wolf population could force a lesser strain upon the economy than a smaller one has been reached during other, more extensive CBAs (see for example Boman *et al*, 2003, concerning the Swedish wolf population). This is a further argument for changing the present regime, and again illustrates that it may be possible to find a solution more amenable to all parties.

5.3 Broader context:

It is possible to draw conclusions in a broader context as a result of the work carried out here, especially since wolf conservation can be regarded as a global issue due to the species enormous natural range. In particular, there has been much debate in recent years over the act of re-introducing wolves into areas from which they have been extirpated: as has been successfully achieved in Yellowstone and Idaho in the US, and is hotly debated as a potential solution to overgrazing by cervids in Europe. This investigation would tend to support re-introduction in many respects, but only given certain conditions. For example, it can be seen that some of the most important barriers to the establishment of a wolf population are socio-political: hence a population is unlikely to thrive unless there exists the necessary political will to provide suitable conditions (space, conflict resolution mechanisms, provisions for enriching the gene pool, etc), and enough social acceptance that other anthropogenic influences, particularly poaching, do not weigh too heavily upon the wolves. Having met these requirements, it is conversely important that there exists an effective form of control upon the newly introduced population: the model demonstrated (as has been seen empirically in Norway and elsewhere) how a nascent wolf population can increase rapidly, which would not only likely prove problematic for people but counter productive for the wolves themselves who might undermine their own resource base if confined. The model demonstrated how certain such forms of management might prove sustainable, and in the case of a legal hunt, go towards offsetting the economic costs of supporting a wolf population.

In biological terms, and beyond poaching pressure, it was shown how the size of the zone available and the immigration rate had a profound effect upon the extinction risk, and so again, these are probably key to wolf re-introduction. Such requirements might make re-introduction to a country such as Scotland problematic, both in that space is limited and there is insurmountable isolation from the nearest population in Europe. Incidentally, this is not to say that the re-introduction of carnivores in general should be ruled out: the Eurasian lynx, for example, might be a more feasible choice for the UK and provide similar ecological benefits, and, like the grey wolf, is considered near-threatened globally (Wilson, 2004; Wikipedia, 2006).

Finally, concerning the use of PVA in general, the project would seem to add to both sides of the debate. On one hand, the IBM used predicted the known evolution of the Yellowstone wolf population accurately, and calculated a value for the immigration rate from Sweden that was statistically equivalent to the value estimated through consultation. Furthermore, there was confirmation of results achieved using different PVA approaches, such as the extinction probability for an isolated wolf population (in Vucetich *et al*, 1997) and the fact that limited hunting represents a feasible management option (Nilsson, 2003). Conversely, there was some disagreement with results in the literature: Vucetich *et al* (1997) found demographic stochasticity to be the greatest threat (as opposed to poaching), and Nilsson (2003) predicted a far lower extinction risk over 100 years. However, to some extent such disagreement merely re-emphasizes the point that PVA should be transparent and open to external review, and that results should be compared carefully, without necessarily undermining its trustworthiness as a tool in conservation biology.

5.4 Further work:

This project suggests a number of routes for further investigation. For instance, it would be illuminating to use a similar model and extend it, through modification and by taking different basic assumptions (such as incorporating some ‘top-down’ effects, or a more realistic and detailed density dependence function) so as to examine the dynamic of the Norwegian or Scandinavian population at higher numbers and densities, as this could help inform future management decisions. Equally, this could be carried out for a similar model in which genetic effects are taken into account, or to explore to greater depth the potential consequences of complex variations in immigration rate as one of the key parameters, especially as this is likely to change in the near future as the Swedish population is encouraged to grow. In terms of model theory and the validation (or otherwise) of the modelling technique employed here, it might be illuminating to undertake to compare the results with those obtained using different versions of the model, and indeed different models such as commercial PVA packages. Such a comparison, using for example the Akaike information criterion, could contribute further towards the ongoing debate as to the robustness of PVA and IBMs.

In terms of leads to be followed, it would be interesting to further examine (through a similar process of population modelling) the idea of establishing the legal hunt so as to determine whether this would satisfy its aims, or to explore theoretically ideas that would encourage similar social and economic outcomes, such as wolf eco-tourism. On the note of the economy, the basic CBA work employed here could be carried out more thoroughly, as this might help distinguish between different management regimes.

Less technical work of equal relevance might be, importantly, to understand and attempt to resolve the social issues that lead to high poaching levels; alternatively, there is certainly the opportunity if not the need to explore politically the feasibility of establishing a joint Scandinavian wolf management body, or even one responsible for all large carnivores in the region.

Finally, in a broader context and given the importance of the predator-prey interaction issue for wolf re-introduction (both biologically and politically), natural or otherwise, it would be useful to explore this interaction using a similar modelling technique as employed here; this would not be the first time such work has been suggested (Eberhardt *et al*, 2003; Fieberg and Jenkins, 2005).

6. Summary and Conclusions

In summary, the present management regime would appear inadequate, not only as it seems likely that it will eventually prove unsustainable and is thus morally and legally questionable, but also as it seems to provide a mechanism by which the conflict between wolves and the rural population is sustained. The present population is upheld almost entirely by immigration from Sweden, and the main factor keeping the extinction risk high is illegal poaching. Not only the Norwegian population, but that of the entire Scandinavian Peninsula is at high risk of extirpation.

Furthermore, there potentially exist ways in which the situation might be improved, most probably beginning with the establishment of a joint Swedish-Norwegian wolf management body, and involving continued but slightly diminished lethal control with an emphasis on preserving pack stability, compensation for those who bear the financial burden for the wolf presence in Norway, and efforts to decrease indiscriminate poaching and ensure new and regular genetic input from Finland/Russia. The political and economic cost of retaining a larger population could potentially be offset through some form of legal hunt as shown here, or through other methods such as ecotourism. In short, it is very likely that there exist alternatives to the present regime which would satisfy, to a far greater extent, the objectives of the important stakeholders, nationally and internationally.

As mentioned in the introduction, there are a number of strong arguments for the conservation of the grey wolf beyond those that are simply moral, and this project has demonstrated that Norway could improve upon its present management of the species in a number of ways, with the capacity to eventually provide an important safe haven for an animal that has, for hundreds of years, been persecuted across the planet.

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Appendix I.

List of individuals consulted in Norway

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Nilsen, Erlend (University of Oslo and Hedmark University College)
Pedersen, Christian (University of Oslo)
Storaas, Torstein (Hedmark University College)
Stromseth, Thomas (Hedmark University College)
Wabakken, Petter (Hedmark University College)
Zimmermann, Barbara (Hedmark University College)