

Restoring ecological balance to the British mammal fauna

MARTYN L. GORMAN

Department of Zoology, School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

ABSTRACT

1. The mammal fauna of the British Isles has seen major perturbations since the end of the last ice age, some natural and some anthropogenic. Today, 61 species of terrestrial mammals breed in the British Isles, but only 39 of them are native species, the rest have been introduced. Furthermore, 19 native species have disappeared from the fauna including all the large predators, lynx *Lynx lynx*, wolf *Canis lupus* and brown bear *Ursus arctos*.

2. Inevitably, these changes in species composition have been accompanied by major changes in community function including changes in patterns of energy flow through the mammalian community. For example, a high percentage of all the energy now flows through the introduced rabbit *Oryctolagus cuniculus* population and red deer *Cervus elaphus*, which, in the absence of natural predators, are living at extremely high densities.

3. Could the reintroduction of species help to reverse such changes in community structure and function? The successful return to the wild of species such as the Arabian oryx *Oryx leucoryx* and beaver *Castor fiber* has shown that reintroductions are certainly possible. However, the impact on community function of returned species is more difficult to evaluate.

4. This question is addressed in relation to the consequences for deer populations of any possible reintroduction of the wolf to Scotland. Based on what we know of wolves elsewhere, predictions are made about the likely demography and patterns of killing behaviour of introduced wolves. These values are then used to parameterize a Leslie matrix simulation of the impact of wolves on contemporary populations of red deer in Scotland. The simulations suggest very strongly that wolves are very unlikely to have any significant impact on the high-density populations of deer now living in the Scottish landscape.

Keywords: British mammal fauna, community function, energy flow, predation, red deer, reintroduction, wolves

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THE BRITISH MAMMAL FAUNA, MISSING SPECIES AND CHANGES IN PATTERNS OF ENERGY FLOW

Ecosystems have always been in a state of constant change as a result of natural processes. In relatively recent times, however, these natural changes in plant and animal populations and communities have been compounded by relatively major and rapid changes due to humans causing species extinctions, changes in population sizes and species' distributions. In the popular press, at least, these changes are often described in terms of a disturbance of the ecological 'balance'.

Correspondence: M. L. Gorman. E-mail: m.gorman@abdn.ac.uk

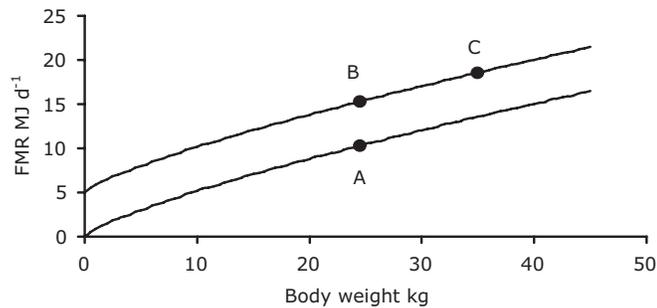


Fig. 1. The lower curve is the relationship between field metabolic rate (FMR) and body size described by an allometric equation (Nagy, Girard & Brown, 1999). Point A is the predicted value for a 25 kg African wild dog and point B the average value for a series of field measurements of the species. The upper curve is that described by the allometric equation but with the intercept adjusted to take into account the difference between predicted and actual values for the wild dog. Point C is the predicted value for a free-living 35 kg wolf.

As an example of the kinds of changes that have taken place within communities, in this paper I consider the British mammal fauna, which has seen major perturbations since the end of the last ice age, some natural and some anthropogenic. I also address the question of whether the reintroduction of missing species can help restore the ecological balance to a previous and perhaps more natural value, using the exemplar of the wolf *Canis lupus* which is native to Britain but currently absent.

Today, there are 61 species of terrestrial mammals breeding in the British Isles, but only 39 of them are native species, and man has introduced the rest (Yalden, 1999). Furthermore, a number of native species have disappeared from the fauna since the end of the last glaciations. Twelve of them, mammoth *Mammuthus primigenius*, Saiga antelope *Saiga tatarica*, Arctic fox *Alopex lagopus*, lemming *Lemmus lemmus*, Arctic lemming *Dicrostonyx torquatus*, narrow headed vole *Microtus gregalis*, northern vole *Microtus oeconomus*, pika *Ochotona pusilla*, wild horse *Equus ferus*, giant elk *Megaloceros giganteus*, reindeer *Rangifer tarandus* and wolverine *Gulo gulo*, have been lost due to natural climatic change. Seven others, beaver *Castor fiber*, wild boar *Sus scrofa*, moose *Alces alces*, aurochs *Bos primigenius*, lynx *Lynx lynx*, brown bear *Ursus arctos* and wolf, have been hunted to regional or global extinction by man.

Inevitably, associated with changes in the species composition of the mammal fauna, there have also been major changes in community function. For example, all the large native predators are missing from Scotland and, partly as a consequence, red deer *Cervus elaphus* are now living at exceptionally high densities of up to 30 animals/km². Such broad-brush changes in community function can be described rather more rigorously by quantifying patterns of energy flow through the mammalian fauna. The average amount of energy used each day (the field metabolic rate or FMR) by any free-living mammal can be estimated from its body mass by using an allometric equation from Nagy, Girard & Brown (1999):

$$\text{FMR} = 4.21 \times \text{body mass}^{0.772}$$

where FMR is measured in kJ/day and body mass in grams (Fig. 1).

The total amount of energy flowing daily through the mammal fauna can be calculated by multiplying the measurements of the FMR of each species by the estimated number of individuals of that species that are present in Great Britain (Harris *et al.*, 1995). The calculations are of course, relatively approximate, given the uncertainty of existing population estimates for many species.

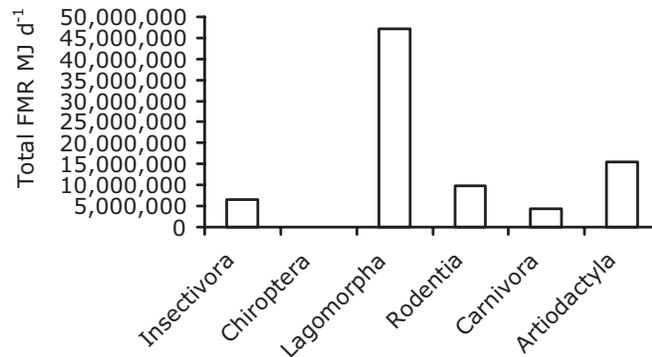


Fig. 2. The total field metabolic rate (FMR) of the major terrestrial taxonomic groups of the British wild mammal fauna.

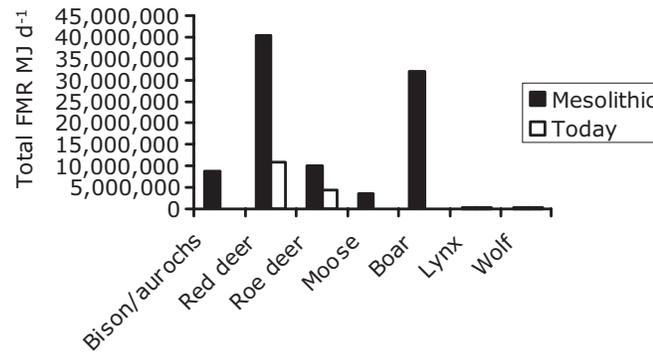


Fig. 3. The total field metabolic rate (FMR) of selected species in the modern British mammal fauna compared to that predicted in Mesolithic times.

A calculation of the total FMR of the major taxonomic groups (Fig. 2) reveals that a very large percentage of the total energy flow through wild mammals is passing through the Lagomorpha, and the great majority of that through the rabbit *Oryctolagus cuniculus*, which is, of course, an alien introduced species. This is ecological imbalance on the grand scale.

The native large carnivores, wolf and lynx are, of course, now extinct in Britain. It is possible, however, to get some idea of the amount of energy that would have flowed through these species before humans had a large impact on the environment. There are good measurements of population densities in the primeval forest of Białowieża in Poland (Jedrzejewski *et al.*, 1993) and these can be used to calculate likely population sizes, and values for FMR, back in the Mesolithic at a time when Britain was largely forested. The differences between the Mesolithic and contemporary faunas are dramatic (Fig. 3).

Clearly, there have been major changes in the structure and function of the mammalian community with a high proportion of the energy flowing through an alien species and with all the large native carnivores now absent. On this basis, it could be said that the British mammal fauna is indeed now in a state of ecological 'imbalance' and we might address the question of whether reintroductions of missing species might help restore ecological

'balance'? There are two obvious aspects to this question; is it possible to reintroduce missing species of mammals, and if so will the reintroduction lead to changes in community structure on the scale desired?

SUCCESSFUL REINTRODUCTIONS OF MAMMALS

Given the political will and adequate funding and given that the reasons for the original loss of a species no longer operate, it is certainly possible to reintroduce species to areas where they have become locally extinct. Exemplars of what can be achieved are the reintroduction of the Arabian oryx *Oryx leucoryx* to the Sultanate of Oman and later to other areas in Arabia, and the return of beavers to most European countries.

In the early 1960s, it was clear that the Arabian oryx was being hunted to extinction and so a small number were captured to establish breeding herds in the USA and Arabia (Spalton, Lawrence & Brend, 1999). The last wild animals were killed in the deserts of Oman in 1972. Ten years later, reintroductions began with the release of 10 animals into Oman's central desert just 75 km from where the last wild oryx had been shot. A second release followed in 1984 and the population grew slowly despite a 3-year drought. Years of good rainfall followed and by October 1995, there were over 280 oryx in the wild ranging over 16 000/km² of the desert.

In early 1996, poaching became a problem once again with oryx being taken on a large scale for sale as live animals outside Oman. Nevertheless, the population continued to increase, reaching a peak of 400 before increasing poaching pressure through 1997 and into 1998 reduced the wild population to an estimated 138 animals, of which just 28 were females. At that point, the wild population was considered to be no longer viable and 40 animals were taken back into captivity. By January 1999, just 11 females and 85 males remained in the wild (Gorman, 1999). The wild population is being rebuilt and in 2002 there were over 150 oryx in the wild. Local and regional measures are being taken to prevent further poaching, including the establishment of the Committee for Conservation of the Arabian Oryx to oversee conservation of the species in the whole region.

The Eurasian beaver is a further example of what can be achieved. Beavers have long been hunted for their fur, for their meat and for their scent or castoreum for use in mediaeval medicine. As a result of over-exploitation, they became extinct in many parts of Europe but since the 1920s reintroduction and translocation programmes across Europe have been extremely successful. The species is now well established in almost all European nations and has been considered for reintroduction to the British Isles (Table 1).

RESTORING COMMUNITY FUNCTION; THE PROBLEM OF THE SCOTTISH RED DEER

Clearly, it is possible to successfully reintroduce mammals but little is known about whether this has any impact on community function, for example on patterns of energy flow. Here, this question is addressed in relation to the consequences of any possible reintroduction of the wolf to Scotland. Those who support the return of the wolf often bolster their arguments by claiming that wolves would help reduce the unnaturally high densities of red deer that currently exist in the Scottish Highlands. There may be other good reasons for reintroducing the wolf, but is it really likely that they will reduce deer numbers?

The red deer *Cervus elaphus* is primarily a woodland species and was abundant throughout mainland Britain when extensive woodlands covered most of the land (Callander & Mackenzie, 1991; Scottish Natural Heritage, 1994). In Scotland, the range of the red deer began to

Table 1. Dates of reintroductions and current populations sizes of European beavers

Country	Reintroduction and/or translocations	Present population size
Austria	1970–90	>1300
Belarus	–	24 000
Belgium	1998–90	100–130
Bulgaria	2001–02	0
Croatia	1996–98	150
Czech Republic	1991–92, 1996	300
Denmark	1999	18
Estonia	1957	11 000
Finland	1935–37, 1995	1 500
France	1959–95	10 000
Germany	1936–40, 1966–89, 1999–2000	10 000
Hungary	1980–2000	70
Latvia	1927–52, 1975–84, 1947–59	>100 000
Lithuania	1947–59	50 000
Luxembourg	2000	4
Netherlands	1988–2000	140
Norway	1925–32, 1952–65	>50 000
Poland	1943–49, 1975–86	17 000
Romania	1998–99	>28
Russia	1927–33, 1934–41, 1946–64	300 000
Serbia	2004	30
Slovenia	1999	<6
Slovakia	1995	>500
Spain	2003	18
Sweden	1922–39	>100 000
Switzerland	1956–77	>350

After Halley & Rosell (2002).

contract some 500 years ago as man started to clear the forests for agriculture. The decline was exacerbated by hunting and by the introduction of sheep onto hill-grazings and the species probably reached a low point in the late 1700s. By that time, the wolf and lynx had been persecuted to extinction.

In the 19th century, deer stalking became a fashionable pursuit in Scotland and huge areas of open hill (so-called deer forests) were managed for the sport, reaching a peak of around 1.5 million ha at the turn of the 20th century. Since the early 1960s, the population of deer has more than doubled in size to over 300 000 occupying almost half of the land area of Scotland. This phenomenal growth has probably resulted from relatively mild winters and dry summers, a reduction in numbers of competing sheep, the lack of natural predators and insufficient culling of hinds (Clutton-Brock & Albon, 1989).

This population growth of red deer is now causing major concern to foresters and conservationists, the reason being that above a winter density of about five deer/km² grazing pressure prevents the regeneration of such native trees as birch *Betula pendula* and Scots pine *Pinus sylvestris* (Nixon & Cameron, 1994). Contemporary deer densities can be as high as 30/km² and are now incompatible with tree regeneration in 80% of the counting blocks used by the Deer Commission for Scotland.

Clearly, there is an urgent need to reduce deer densities by increasing patterns of mortality. One way to do this is to increase the rate of culling, particularly of hinds. However, those who advocate the reintroduction of the wolf, argue that they would help reduce deer numbers and

in this way restore the ecological balance. In the absence of wolves in Scotland, the best that can be done is to model the likely impact of wolves on contemporary densities of deer.

The potential impact of wolves on red deer was modelled using HillDeer (Partridge *et al.*, 1998), a population model developed jointly by the Macaulay Land Use Research Institute and Biomathematics and Statistics Scotland in Aberdeen. HillDeer is a Leslie matrix population model that accurately predicts changes in the size and structure of a red deer population on the open hill in Scotland on the basis of known rates of age specific natality, natural mortality and culling. The model also incorporates realistic density-dependent functions for mortality and natality and is calibrated with data from real deer populations. The model was designed to act as a decision support system for estate managers, allowing them to investigate the effects on red deer populations of a range of different culling strategies. The approach in this study has been to substitute wolf predation for human culling.

In order to parameterize the model for the simulation of the effect of wolf predation on deer populations it was necessary to know likely wolf densities in Scotland and the rate at which wolves are likely to kill prey. These are complex questions but predictions can be made on the basis of studies carried out elsewhere.

It would seem obvious to quantify food requirements using data on killing rates measured in the wild, but this is far from straightforward. Captive wolves will eat over 3 kg of meat per day and many studies of kill rates in the wild reflect this. However, reported kill rates are very variable in time and space ranging from 0.5 to 24.8 kg per wolf per day. In 18 studies in North America, wolves obtained an average of about 5 kg of prey per wolf per day from kills (Fuller, Mech & Cochrane, 2003) and measurements from Poland are similar at 5.6 kg (Jedrzejewski *et al.*, 1993). However, this value relates not to edible meat but to the whole carcass and inevitably part will be lost to scavengers or wasted and therefore it is difficult to estimate rates of food consumption from these figures.

There are also major differences in the kill rates of wolves hunting prey of different sizes. Thus, the kill rates of wolves preying on deer, 3 kg per wolf per day, are generally up to five times lower than those of wolves preying on large prey such as moose or bison which average out at 25 kg per wolf per day. These differences are unrelated to the body sizes of the wolves concerned and have yet to be convincingly explained. A further complication is that studies are made over different time spans, making generalization difficult. To further confound these difficulties, almost all studies of rates of killing have been made in winter and there are very few data for the summer months.

There are therefore serious difficulties in determining year-round food requirements from measurements of killing rates in the wild. A more fruitful approach is probably to consider the estimated energy requirements of free-living wolves. The allometric equation set out earlier predicts that a 35 kg free-living wolf will have an average daily energy expenditure of 13.6 MJ (Fig. 1). However, this prediction is probably an underestimate. The same equation predicts an FMR of 10.3 MJ for a 25 kg African wild dog *Lycyaon pictus* but field measurements using doubly labelled water result in an average of 15.3 MJ with some dogs using as much as 19 MJ per day (Gorman *et al.*, 1998). These measured values accord well with observed kill rates by wild dogs in the wild.

The difference between predicted and measured FMRs for wild dogs is about 5 MJ per day and probably reflects the unusually high energy costs that are incurred by cursorial hunters. The basal metabolic rate of a wild dog is in no way unusual and the high FMR is due entirely to the high costs incurred whilst the dogs are actively hunting. The lifestyles of wild dogs and wolves are essentially similar, both are group living cooperative hunters. It is reasonable therefore to adjust the intercept value in the allometric equation to take into account the high

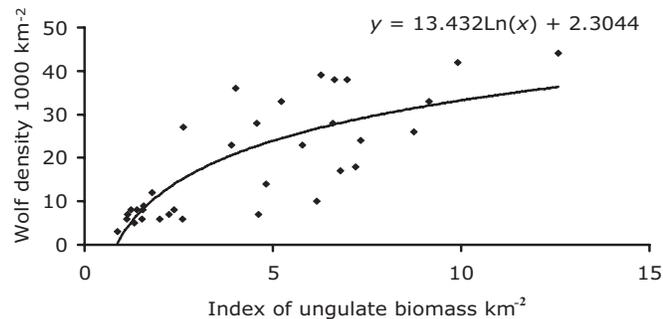


Fig. 4. The relationship between the density of ungulate biomass and wolf density in a number of North American studies. Relative biomasses were assigned as: white-tailed deer 1; mule deer 1; mountain goat 1; Dall sheep 1; bighorn sheep 1; caribou 2; elk 3; moose 6; bison 8 (based on data in Keith, 1983 and in Fuller, 1989).

costs of hunting. The adjusted equation predicts an FMR of 18.5 MJ for a 35 kg wolf (Fig. 1). This is equivalent to a food intake of 4.25 kg of ungulate meat per day, assuming an energy content of 5.2 MJ per kg wet weight, a digestive efficiency of 93% and a 10% loss of energy in the urine. Since an average red deer provides about 50 kg of meat, the predicted kill rate for wolves preying on Scottish red deer is 30 deer per wolf per year.

In order to estimate the numbers of deer likely to be killed each year by introduced Scottish wolves, it is necessary to know not only the *per capita* killing rate but also the likely density of the wolf population.

Wolves live at very different densities in different parts of the world but very rarely exceed 50 per 1000 km² (Pimlott, 1967; Mech, 1973; White & Garrott, 2005). The factors setting this upper limit to density are not completely understood but variation in the available biomass of prey is a major determinant. An analysis of data (Fig. 4) from over 30 intensive field studies from North America (Keith, 1983; Fuller, 1989; Fuller, Mech & Cochrane, 2003) shows that differences in the density of ungulate biomass account for around 64% of the variation in wolf density. In this analysis, relative biomasses were assigned as follows: white-tailed deer 1; mule deer *Odocoileus hemionus* 1; mountain goat *Oreamnos americanus* 1; Dall sheep *Ovis dalli* 1; bighorn sheep *Ovis canadensis* 1; caribou *Rangifer tarandus* 2; elk *Cervus canadensis* 3; moose *Alces alces* 6; bison *Bison bison* 8. On this scale, Scottish red deer have a biomass index of 1. This relationship, shown in Fig. 4, can be used, with circumspect, to predict likely wolf densities in Scotland, for example, a density of 24 wolves per 1000 km² at a deer density of 5/km², the density at which native trees are likely to show successful regeneration.

A 'study area' of 1000 km² calibrated with deer data from the east of Scotland was used for the simulations. The model predicts that in such an area a population of deer will reach a density-dependent asymptote of just over 23 000 individuals, a population density of some 23/km² (Fig. 5). A wolf density of around 43/1000 km² is predicted for this density of deer (Fig. 4). These values of 23 deer/km² and 43 wolves per 1000 km² and the corresponding kill rate of 1300 deer per annum were used in the simulation of the effects of wolf predation on deer.

In all simulations, the initial population was set at 9000 stags, 11 000 hinds and 3000 calves. The wolves were assumed to kill each year a fixed number of deer, 650 stags, 600 yield hinds, 50 milk hinds (and their dependent calves). In addition, it was assumed that a variable percentage of the remaining calves were also predated. Wolves do not kill prey randomly but

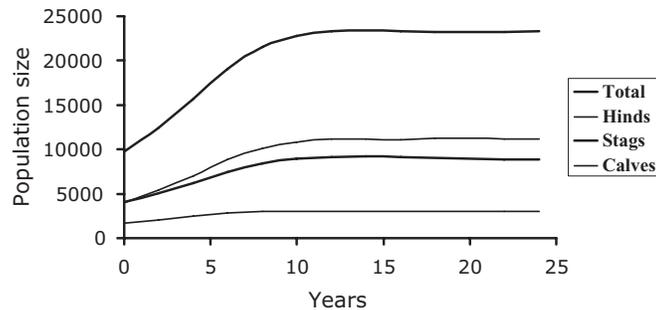


Fig. 5. The pattern of growth in a population of 10 000 deer, living in an area of 1000 km² predicted by the population model HillDeer.

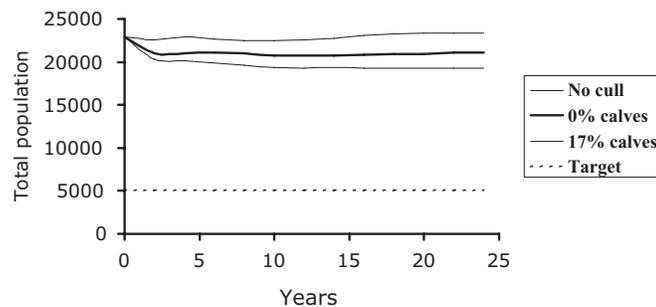


Fig. 6. Changes in total numbers in populations of red deer starting at carrying capacity under different predation scenarios modelled using HillDeer. In each case the initial population consisted of 9000 stags, 11 000 hinds and 3000 calves. When wolves were present the annual kill rate remained constant at 650 stags, 600 yield hinds, 50 milk hinds and their calves. In one scenario 17% of the remaining calves were also predated. The dotted line is the target population for tree regeneration to take place.

concentrate their attacks on particular age groups. This was incorporated into the model by making predation rates age-dependent with 25% of kills being assigned to deer aged 1–4 years, 50% to those aged 5–10 and 25% to those aged 11 or more.

Example population trajectories from the model over a period of 25 years are shown in Fig. 6. In the first there was no wolf mortality, in the second deer were killed in the way described above but with no predation of calves other than those associated with the milk hinds, and in the third 17% of the remaining calves were also killed. This latter rate of predation on calves is probably the maximum that would be expected in the real world. The target population of 5000 deer, the density of 5/km² at which tree regeneration would be possible, is also shown. The population simulations suggest very strongly that wolves are unlikely to have any significant impact on the high-density populations of deer now living in the contemporary Scottish landscape.

In order to investigate under what circumstances wolves might be expected to have an impact on deer densities, simulations were carried out with populations of different initial densities. One, a starting population of 20 000 deer per 1000 km², was already near the carrying capacity predicted by the model, a second started with 10 000 deer and a third with 5000. For each of the three scenarios, wolf numbers were at the levels predicted by the appropriate deer density (Fig. 4) and kill rates were set appropriately for the wolf numbers.

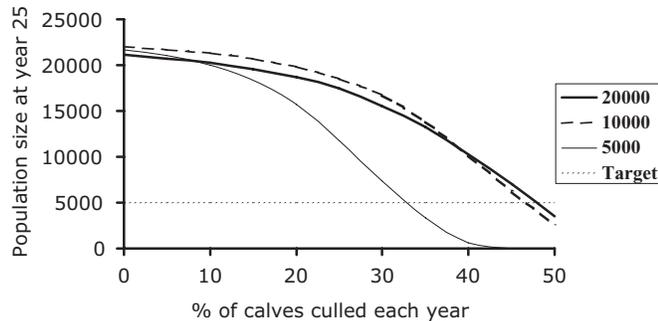


Fig. 7. The effect of different rates of calf predation on the size of deer populations of different initial size after 25 years of wolf predation. See text for further details. The initial populations were 20 000, 10 000 and 5000 deer. The dotted line is again the target population for tree regeneration to take place.

For each of the three scenarios, simulations were run using a range of calf mortality rates, each over a period of 25 years. The results (Fig. 7) are presented as the predicted population size after 25 years, as a function of the percentage of calves killed each year.

The results show that with no calf predation, other than those associated with milk hinds, each of the populations had reached, or remained at, carrying capacity by year 25. Furthermore, the populations were brought down to the target density of 5/km², within 25 years, only when calf-killing rates were extremely and unrealistically high. In the case of the initial population of 5000 deer per 1000 km², a calf mortality of over 32% was needed to keep it at that level, and in the case of the larger initial populations, a calf mortality of almost 50% was required to reduce them to the target population. Such high rates of calf mortality are unknown in the real world (Mech & Boitani, 2003).

It is clear then that the productivity of the contemporary high-density populations of deer in Scotland is such that wolves are unlikely in the extreme to make any inroads into deer populations. It could be argued that at very high deer densities, wolves would increase in numbers and in that way impact on the deer numbers. However, given that wolves are highly territorial and that breeding within packs is restricted to the alpha pair, this is unlikely to happen. Furthermore, in reality wolves would, of course, exploit other wild and domestic prey species in addition to deer with a corresponding lessening of the population dynamics of the deer.

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