



Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Restoring landscapes of fear with wolves in the Scottish Highlands

Adrian D. Manning^{a,*}, Iain J. Gordon^b, William J. Ripple^c^a The Fenner School of Environment and Society, The Australian National University, Canberra, ACT 0200, Australia^b CSIRO Sustainable Ecosystems, Davies Laboratory, PMB PO, Aitkenvale, Qld 4814, Australia^c Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

ARTICLE INFO

Article history:

Received 26 November 2008

Received in revised form 7 May 2009

Accepted 10 May 2009

Available online xxx

Keywords:

Behaviourally-mediated effects

Density-mediated effects

Elk

Landscapes of fear

Lethal effects

Nonconsumptive effects

Nonlethal effects

Predation risk

Red deer

Reintroduction

Scottish Highlands

Wolves

ABSTRACT

The absence of an organism from a landscape for a long time can be a major barrier to the restoration of that species due to factors such as environmental conditions changing since extinction. This can make it difficult to assess the feasibility of reintroduction when an extirpated species cannot, by definition, be observed in the landscape of interest. In such situations, two important options for conservation scientists include: (1) to draw on insights from analogous ecosystems where the organism is extant, or where it has been successfully reintroduced and (2) to undertake research into the reintroduction in the location of interest under controlled experimental conditions.

The idea of reintroducing wolves (*Canis lupus*) to the Scottish Highlands provides an excellent case study of such a situation. A key argument for reintroduction has been that native red deer (*Cervus elaphus*) numbers, considered by many to be ecologically unsustainable, would be reduced through wolf predation. To date, research into the ecological value of reintroduction has focused on this important issue. However, new research, emerging from wolf reintroduction projects in North America, suggests that nonlethal 'behaviourally-mediated' effects of wolves also have a profound effect on deer behaviour and consequently on the ecosystems in which they live. In short, deer avoid places or browse less where there is a high risk of wolf predation, which allows previously inhibited tree regeneration. The implications for wolf reintroduction in Scotland are that changes in deer behaviour could be as important as lethal effects, and that fewer wolves may be needed than indicated by predator–prey modelling to have significant positive impacts on ecosystems in the Scottish Highlands. Understanding the relative likely contributions of both lethal and nonlethal effects in the Scottish context will be challenging because nonlethal impacts result from an interaction between deer behaviour in response to wolf predation and particular landscapes and ecosystem features. While a full reintroduction may be far off, research must begin in the near term. There would be considerable scientific merit in establishing a large, controlled experiment (for example on an island or in a fenced area) in the Scottish Highlands to examine the relative lethal and nonlethal effects of wolves on deer and ecosystem restoration. In this paper, a long-term pathway for scientific research to provide sound ecological evidence to inform future decision-makers is proposed.

© 2009 Elsevier Ltd. All rights reserved.

Conserving biodiversity is often unsuccessful if we concentrate on limited patches. We need to look at the bigger picture: reconnect nature; extend and link up habitats; reduce barriers; and understand the dependencies and needs of different species. We need to think in terms of landscapes and ecosystems, not just in terms of species and habitats. (Scottish Executive, 2004, p. 25).

1. Introduction

Ecosystem restoration is recognized as a critically important response to the ongoing destruction and transformation of ecosys-

tems by human activity (Dobson et al., 1997; Hobbs and Harris, 2001; Millennium Ecosystem Assessment, 2005). An important component of ecosystem restoration is the reintroduction of organisms that have become locally or regionally extinct. Of particular importance are 'keystone species' whose impact on an ecological community is disproportionately large compared to their abundance (Paine, 1969; Power et al., 1996). However, the long-term absence of any organism or ecosystem from a region can be a major barrier to restoration (Manning et al., 2006) because, over generations, human memory of an ecosystem, or the presence of a particular organism diminishes, and expectations of 'good' ecological conditions are gradually lowered (often called 'shifting baselines syndrome', see Pauly, 1995; Miller, 2005). At the same time, ecosystems may have changed considerably since the loss of an organism which can mean that the idea of reintroductions and

* Corresponding author. Tel.: +61 2 6125 5415; fax: +61 2 6125 0757.

E-mail address: adrian.manning@anu.edu.au (A.D. Manning).

large-scale ecological restoration seems too intractable, complex, open-ended, confronting, or radical to be feasible (Manning et al., 2006). From an ecological perspective, it can be difficult to assess the feasibility of reintroduction where, by definition, the extinct species cannot be observed in the landscape of interest. In such situations, two important options include: (1) to draw on insights that can be learned from analogous ecosystems where the organism is extant, or where it has successfully been reintroduced and (2) to undertake research into the reintroduction in the location of interest under controlled experimental conditions.

The proposal to reintroduce the wolf (*Canis lupus*) into the Scottish Highlands is a good example of a situation where the species has been absent for at least 250 years (Yalden, 1993; 1999), but where (1) ecologically analogous ecosystems exist elsewhere and (2) where experimental research, under controlled conditions, may be an acceptable forerunner to a full reintroduction. The idea of wolf reintroduction to Scotland has excited considerable media attention in recent years (BBC News, 1999, 2002, 2008; Radford, 1999; Morgan, 2007; O'Connell, 2008); however, there is great uncertainty as to when this might happen on the ground. The cultural, political and practical barriers to reintroduction cannot be underestimated (Yalden, 1993, 1999; Wilson, 2004; Nilsen et al., 2007), but there are valid ecological reasons for reintroducing a keystone species, such as the wolf. These conflicting views will continue to fuel the debate in the media, society and amongst conservationists and ecologists.

Even though the final decision on wolf reintroduction to Scotland would be political, it is nevertheless important that any decision is ecologically-informed. In fact, to be most useful to the broader debate, questions of the ecological viability and potential ecosystem effects of such reintroductions should be evaluated independently of other issues.

A major argument for the reintroduction of wolves to the Scottish Highlands has been their potential to help naturally control deer numbers (Wilson, 2004; Gorman, 2007; Nilsen et al., 2007). Deer populations began to increase to current levels in the late 1700s and 1800s with growing interest in stalking (i.e. 'hunting'; Watson, 1983; Yalden, 1999). Deer densities in Scotland are now high and are thought to be close to food-limited carrying capacity in some areas and much higher than is considered ecologically sustainable (Clutton-Brock et al., 2004). High deer densities are having serious, ongoing consequences for the structure, composition and function of native ecosystems in the Scottish Highlands due to heavy grazing and browsing pressure which affects vegetation, such as native Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) regeneration (Staines et al., 1995) (Fig. 1a and b). The negative effect of high deer abundance on biodiversity is recognized in legislation (the UK Government's Deer (Scotland) Act, 1996 and the Scottish Government's Nature Conservation (Scotland) Act, 2004), and in relevant national Scottish strategies (e.g. Forestry Commission Scotland, 2006; Deer Commission for Scotland, 2008).

To date, research on wolf reintroduction in Scotland has focused on the potential lethal effects of wolves on deer populations (Gorman, 2007; Nilsen et al., 2007). While these effects are important, new research emerging from studies of wolf reintroduction in North America suggests that nonlethal effects of wolves on herbivore behaviour have profound consequences for ecosystems. The North American studies emphasise the need to consider the consequences of conservation action on whole ecosystems, rather than a particular species of interest. This requires scientific understanding of the consequences of the reintroduction for both other extant species and the local ecosystems *before* a release takes place. This is a significant challenge in a country like Scotland, where the wolf, an ecologically important yet controversial species, has been absent for centuries. However, the restoration of 'landscapes of fear' (*sensu* Laundré et al., 2001; see below) for deer, through the rein-

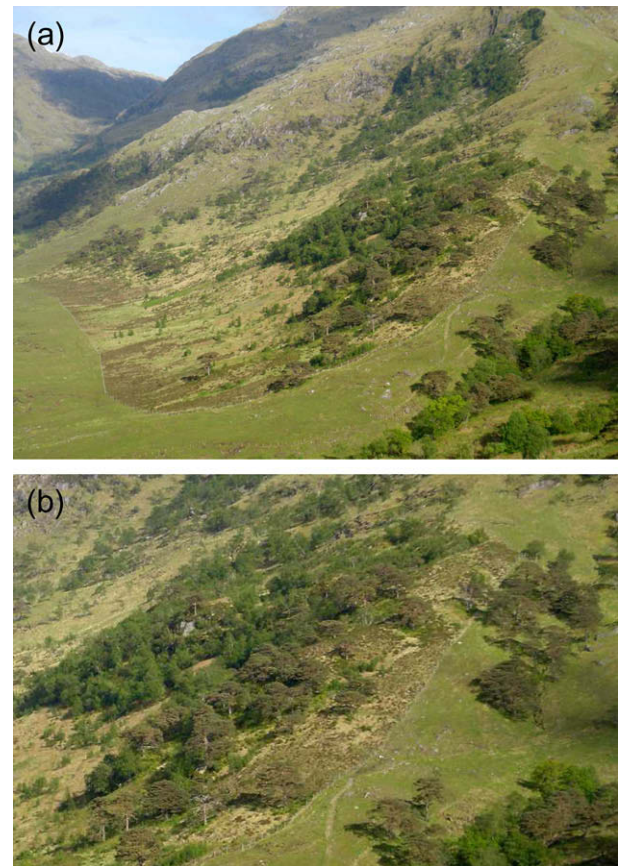


Fig. 1. (a) Photograph from Knoydart, in the Scottish Highlands, of a deer exclusion fence showing tree regeneration where deer browsing is present (bottom and right) and absent (middle and top). (b) Enlargement showing contrast between inside and outside the exclusion fence. Could fear of reintroduced wolves in Scotland have the same effect as exclusion fences on deer browsing in certain areas? (Photo by Alison Hester).

roduction of wolves, could play a vital role in ecosystem restoration in the Scottish Highlands.

In this paper, we (1) outline results emerging from Yellowstone National Park in the USA regarding the ecosystem effects of wolves following reintroduction; (2) discuss the implications from this analogous ecosystem of restoring landscapes of fear in the Scottish Highlands and (3) outline a potential pathway for scientific research, including a large-scale controlled experiment, to inform future consideration of wolf reintroduction in the long-term.

2. The ecosystem effects of wolves: a case study from Yellowstone National Park, USA

There are two main ways in which predators influence ecosystems through their effects on herbivores:

- (1) By lethal (density-mediated) effects, i.e. by killing herbivores and, therefore, reducing grazing pressure.
- (2) By nonlethal (behaviourally-mediated) effects, i.e. by altering foraging patterns and habitat use of herbivores under risk of predation (Ripple and Beschta, 2007) otherwise called 'nonconsumptive effects' (Schmitz et al., 2008). Thus, anti-predator behaviour can affect ecosystem structure, composition and function.

Most analyses of vertebrate predator–prey dynamics do not account for the cost of anti-predator behaviour for prey (Creel et al.,

2007). Studies of predation often implicitly assume that lethal effects are larger than, or positively correlated with, nonlethal effects (Creel and Christianson, 2008). However, while much research has focused on lethal effects, it is possible that nonlethal effects may be just as significant or greater (Schmitz et al., 1997). In fact, even when rates of predation are low, risk effects could still be large (Creel and Christianson, 2008).

2.1. Evidence of the behaviourally-mediated effects of wolves

Nonlethal effects of predation result in herbivores avoiding parts of the landscape where they are more likely to be preyed. This avoidance behaviour can take place on a continuum of scales from broad habitats and terrain to very fine scales of a few meters (Ripple and Beschta, 2006b). Consequently, in a landscape with large predators, patterns of foraging by large herbivores are modified, both in terms of where they feed but also the duration and frequency of anti-predator behaviour, such as vigilance; which affects how long they feed.

Some of the key evidence for the nonlethal effects of wolves is emerging from Yellowstone National Park and surrounding areas in the USA; where wolves have been reintroduced. Laundré et al. (2001) found that female elk (*Cervus elaphus*) and bison (*Bison bison*) were more vigilant in areas with wolves as compared to those without wolves. They also found that vigilance increased in female elk over a five year period as wolves expanded into an area. This led to the authors coining the term “landscape of fear”, that is:

“...prey individuals live in a second landscape, one with differing levels of risk or fear of predation: a “landscape of fear.” The topographic “hills” and “valleys” of this landscape represent the differing base levels of predation risk, e.g., edges versus open areas” (p. 1402).

In another study, Fortin et al. (2005) found that as the risk of wolf encounters increased, the selection of elk for aspen (*Populus tremuloides*) stands decreased. Similarly, Ripple and Beschta (2007) found reduced browsing by elk and increased heights of young aspen in places with high predation risk (riparian areas with

downed logs). Since elk numbers decreased significantly after wolf reintroduction, they attributed the patchy aspen recruitment to a likely combination of lethal and nonlethal effects. These same authors found similar effects on willow (*Salix* spp.) growth in some valley-bottom riparian sites where browsing was reduced by increased predation risk (Ripple and Beschta, 2006b, Fig. 2). Bergman et al. (2006) found greater elk vulnerability to wolf predation when the elk were close to hard edges such as structures (i.e. streams, burned forest edges) that could impede their movement by affecting speed, maneuverability and escape potential around these structural impediments. Halofsky and Ripple (2008) found that elk vigilance was significantly higher near escape impediments (<30 m) than at locations away from impediments. In an additional study, researchers hypothesized that an interaction between the effect of fire and the risk of wolf predation on elk distribution facilitated aspen growth, with more escape impediments, through an increase in downed wood and dense aspen thickets after fire (Halofsky et al., 2008).

Creel et al. (2005) also found that elk reduced their use of preferred grassland foraging habitats that had high predation risk. Both the change in habitat use and the increase in vigilance in the presence of wolves could lead to a decline in the nutrition and condition of prey. This led the authors to suggest that wolves may have greater effects on elk dynamics, through altering diets and energy budgets, than by predation alone.

Nonlethal effects on herbivore condition resulting from anti-predator behaviour could also affect susceptibility to other factors that affect population size (e.g. food, predation, weather) through mortality or lowered fecundity. For example, research in Yellowstone has shown that female elk experiencing heavier predation pressure have lower progesterone values, which are correlated with lower calf production in the following year (Creel et al., 2007). If nonlethal effects are not explicitly considered, population changes could be incorrectly attributed to lethal factors alone (Creel and Christianson, 2008).

Both nonlethal and lethal effects of wolves (and other large carnivores) can have broader cascading effects on organisms beyond large herbivores. For example, wolf and grizzly bear (*Ursus arctos*)



Fig. 2. Comparison photographs taken in 1997 (left) and 2001 (right) near the confluence of two streams in northern Yellowstone National Park showing the height of willow plants during suppression (left photo) from long-term browsing by elk and their release (right photo) following wolf reintroductions that began in 1995 and 1996. This site appears to be high in predation risk because of significant escape impediments for elk due to topographic and stream barriers. Source: Ripple and Beschta (2003).

have been shown to have a positive effect on migratory birds that use riparian vegetation through reducing moose (*Alces alces*) density (Berger et al., 2001). Wolves kills also the provide carrion for other species to consume (e.g. Wilmers et al., 2003) and suppress of medium-sized predators (e.g. Berger and Conner, 2008) which could in turn affect other prey species. These broader effects should also be considered when evaluating the likely consequences of reintroduction.

3. Implications of restoring landscapes of fear in the Scottish Highlands

The research on landscapes of fear emerging from Yellowstone is particularly relevant to understanding the ecological consequences of wolf reintroduction in Scotland, because a number of the key species are the same, or closely related, to those of interest e.g. the wolf (*C. lupus*), elk and red deer (*C. elaphus*) and aspen (*P. tremuloides* in Yellowstone and *Populus tremula* in Scotland). Landscapes of fear already exist in Scotland for all animals that are predated by other animals. This is because prey will assess and use different parts of their environment according to the perceived risk of predation (Lima, 1998; Brown et al., 1999; Laundré et al., 2001; Searle et al., 2008). Currently, deer in Scotland are not routinely predated by natural predators (though they are hunted by humans), and their feeding strategy involves maximising nutrient intake i.e. they eat where and when they want (Illius and Gordon, 1987; Gordon, 1989). This has major localised and landscape-scale effects on vegetation structure, and on efforts towards large-scale ecosystem restoration (Albon et al., 2007). Hunting by humans in Scotland does affect deer behaviour (Jayakody et al., 2008) and probably also elicits a type of landscape of fear for the deer. However, it is not clear that human hunting can replicate that which is created by wolf predation, and unfortunately the appropriate research to determine this unequivocally has yet to be undertaken (see Berger, 2005). This is because some characteristics of human and wolf hunting differ. For example, shooting occurs from a distance, whereas large carnivores, like wolves, engage in close pursuit and chase prey (Berger, 2005), which will interact more with local fine-scale landscape structures and topography. Also, hunting by humans occurs seasonally (Jayakody et al., 2008) and generally occurs during daylight hours, whereas wolf hunting occurs all year and 24 hours a day (Theuerkauf et al., 2003; Berger, 2005). Thus the landscapes of fear created by wolves are more continuous, cover a larger area, and exist at a finer-scale than those created by human hunting and consequently will have a greater cascading effect on different trophic levels within any ecosystem.

In Scotland there is now increasing recognition of the need for conservation management and restoration at the landscape and ecosystem level in both the government (Scottish Executive, 2004; Forestry Commission Scotland, 2006) and nongovernment sectors (Watson Featherstone, 1997, 2004a,b; Amphlett 2002; Scottish Wildlife Trust, 2009); and this includes the management of deer (Deer Commission for Scotland, 2008). There is also growing interest in the concept of 'wildland' (National Trust for Scotland, 2002; McMorran et al., 2006; John Muir Trust, 2004) and 're-wilding' (Taylor 2005; Watson Featherstone, 1997, 2004a,b). Wolves are relevant in this context because they have strong interactive effects at the ecosystem level (as demonstrated in Yellowstone), and operate at a landscape scale, i.e. their home ranges can encompass many ownership, land use and ecological boundaries.

Table 1 outlines the components, spatial patterns and processes that structure natural boreal forest, which could act as a guide for ecosystem-level restoration in the Scottish Highlands (Summers et al., 2008). In addition, we have also added herbivores, predators and their interactions. This is because: (1) large mammalian herbi-

Table 1

Important structural components, spatial patterns and processes for biodiversity in natural boreal forest in Fennoscandia (adapted from Esseen et al., 1997). One item under spatial patterns has been added to structural components, and processes in bold indicate additional important ecosystem processes. All these features would also be key components of forests in the Scottish Highlands where 'natural' character is the ultimate goal.

Structural components

Very old pine and spruce
Old broad-leaved trees, particularly *Populus tremula* and *Salix caprea*
A developed understory of tree saplings and shrubs
Trees with abundant growth of epiphytic lichens
Broken, stag-headed and leaning trees
Trees with holes and cavities
Dead standing trees (snags)
Fire-scarred trees, snags and stumps
Large downed logs in various stages of decomposition

Spatial patterns

A developed understory of tree saplings and shrubs
Mixed stands, with both conifers and broad-leaves
Uneven-aged stand structure
Multi-layered tree canopies
Patchy distribution of trees

Processes

Post-fire succession
Succession with tree-species replacement
Self-thinning
Gap formation
Snag and log formation
Decomposition of coarse woody debris

Grazing and herbivory – affecting spatial patterns

Predation of herbivores – lethal and nonlethal effects affecting spatial patterns

vores have been shown to profoundly influence the structure and dynamics of forest ecosystem throughout Europe; including effects on key tree species found in the Scottish Highlands (Scots pine, Birch species, *Betula pendula* and *Betula pubescens*, Rowan, *Sorbus aucuparia* and Pedunculate Oak *Quercus robur*; Hester et al., 2000) and (2) evidence from North America presented above, indicates a high probability that large carnivores, such as wolves, have a significant effect on spatial patterns and processes that structure forests with 'natural' characteristics by impacting large mammalian herbivores. It is likely that original forest in the Highlands lacked the modern homogenization of tree species and age class (McVean, 1963). McVean (1963) wrote: "The terrain that now carries pure pine probably grew a mixed pine, birch forest with abundant alder, rowan, willow, aspen, bird cherry and juniper, with scattered oaks and with a good mixed-age composition in the various constituents" (p. 684). This sort of mixed age, mixed species structure and composition would be a target outcome of managing for 'natural character' (*sensu* Amphlett, 2002).

Modelling the potential nonlethal effects of wolf reintroduction in Scotland on deer habitat use and feeding behaviour will be more difficult than predicting the lethal impacts of wolves on deer population dynamics because it involves interactions between animal behaviour and particular landscapes. With nonlethal trophic cascades, there are typically both winners and losers concerning foraging impacts on plants (Schmitz et al., 2000). Restoring landscapes of fear in the Scottish Highlands could help achieve the vision of forests with 'natural character' through creating a more heterogeneous spatial pattern of deer herbivory. In general, it can be expected that foraging would decrease in some places where escape from wolves may be impeded, such as some riparian areas or other areas with escape obstructions (e.g. Ripple and Beschta, 2007), but might increase where deer can find better protection from wolf predation, such as wooded areas (e.g. Creel et al., 2005) and upland habitats (Ripple and Beschta, 2006b). For example, elk in Yellowstone have been shown to avoid wolf dens and

rendezvous sites, generally in lower elevation areas, during the summer (Mao et al., 2005). The overlapping edges between pack territories, which are generally avoided by wolves, have also been shown to have higher deer densities (Mech, 1977). This would have implications for the regeneration, structure and composition of vegetation, possibly leading to increases in woodland extent at high risk sites. As has been found in Yellowstone, a restored landscape of fear could allow riparian browse species to increase in extent and assist stream restoration by increasing biomass on stream banks and reducing bank erosion resulting in changes in channel morphology (Ripple and Beschta, 2006a; Beschta and Ripple, 2008). Furthermore, red deer in Scotland are known to exhibit more vigilance during the hunting season (Jayakody et al., 2008). Therefore, after wolf reintroduction, deer would have to trade off risks associated with human hunting versus the threat of wolf predation – with consequent effects on habitat use. Another consequence of wolves returning to the Scottish Highlands could be that deer move closer to human settlements to avoid wolves, as shown at various locations in the North America (Hebblewhite et al., 2005; Beschta and Ripple, 2007), resulting in some deer management issues.

The overall effect of predation risk on deer behaviour may not be at the population level, but rather at a local level where deer interact at landscape and topographic feature scales. As such, the fear of wolf predation may affect population levels across Scotland by reducing hind fecundity (*sensu* Creel et al., 2007) or by increasing body condition related mortality (see above).

Although the predicted effect of wolf reintroduction on absolute deer numbers in Scotland varies (Gorman, 2007; Nilsen et al., 2007), results from Yellowstone suggest that relatively few wolves in the Scottish Highlands could have profound effects on the resources deer use by altering their behaviour, with cascading ecosystem effects over a large area. Consequently, potentially fewer wolves might be needed than predicted in modelling of lethal effects to result in significant ecosystem effects. The status of ecosystem recovery could be monitored by collecting field data on key plant species (woody browse species) and wolf numbers with the management goal of maintaining a wolf population sufficiently abundant to sustain these plant communities.

In a recent review of nonlethal predator effects, Schmitz et al. (2008) concluded, based on research emerging from Yellowstone, that “the consequences of predator-induced changes in elk behavior on ecosystem properties are qualitatively similar to those observed between open areas and exclosures” (p. 2441). It is therefore plausible that wolf reintroduction to the Scottish Highlands could have similar effects to deer exclosures (Fig. 1a and b) (e.g. Scott et al., 2000). However, unlike fences this effect could occur at a landscape-scale and have fine-scale effects without associated negatives such as the high costs of construction and maintenance, accidental deaths of protected species that fly into fences (e.g. capercaillie *Tetrao urogallus*) and effects on landscape aesthetics (Gordon et al., 2004). Thus, if society finds it acceptable to reintroduce wolves, evidence suggests they could play a critical role in ecosystem restoration in the Scottish Highlands by reinstating their important role in affecting deer behaviour, distribution and density at a landscape scale.

4. What next?

Research findings from North America demonstrate the value of insights from analogous ecosystems, when assessing reintroduction feasibility. In particular, they highlight unforeseen, yet important, ecological ramifications of wolf reintroduction that have, to date, not been considered in depth in Scotland (but see Hetherington, 2006 regarding reintroduction of Eurasian lynx *Lynx lynx*). Due to the interaction between nonlethal effects with specific landscapes and ecosystems, empirical data from the intended area of

reintroduction would be highly valuable. However, the idea of wolf reintroduction highlights some challenging questions for ecologists and conservation biologists in Scotland. How can the relative magnitude of lethal and nonlethal effects of predators on herbivores be assessed before the wolf is reintroduced? How can the nonlethal effects of wolves on deer, which are landscape- and ecosystem-specific, be determined?

A full reintroduction of the wolf to the Scottish Highlands appears unlikely in the near future. However, it is possible to see a trend in conservation values towards larger-scale ecological restoration and ecosystem approaches (see above), and to predict that wolf reintroduction may be supported by Scottish society in the future. Conservation scientists need to anticipate now the likely need for Scotland-specific ecological knowledge because of the long lead-in time to elicit the requisite results. One way to anticipate this future need would be to establish a large-scale controlled experiment to examine lethal and nonlethal effects of wolves on ecosystem restoration in the Scottish Highlands.

4.1. A large-scale controlled experiment in Scotland?

There would be considerable scientific merit in experimentally investigating the ecological effects of wolf reintroduction under controlled conditions; for example on islands (either large offshore islands or large fenced areas on the mainland), reinstating the predator–prey interactions and consequent changes to ecosystem structure and function. Hester et al. (2000) highlighted the lack of understanding regarding the interactions between herbivores and forests, and concluded that the potential of controlled experiments had not been fully-utilised. Controlled (i.e. with fences or other barriers), large-scale, long-term ecological experiments can be an effective way of understanding ecosystems and species interactions that would otherwise be impossible. For example, the Starkey Project in Oregon, USA is a long-term fenced experiment, (40 mi²/104 km²) designed to investigate habitat use by elk and mule deer (*Odocoileus hemionus*) and their response to forest management. The project includes an automated telemetry system that allows elk and deer movements to be intensively tracked in relation to landscape and habitat features (see Wisdom, 2005). This would provide a valuable model for a controlled experiment in Scotland. In addition, the proposed Scottish experiment would also include detailed, automated tracking of wolves and their interactions with deer and the landscape. This would provide a unique opportunity to study multiple, interacting trophic levels as part of the ecosystem restoration process. The project would also provide a unique opportunity to map the landscape of fear of deer before and after wolf release and would allow comparisons to be drawn regarding changes in deer habitat use and vegetation responses (*sensu* Laundré et al., 2001; Searle et al., 2008). The experiment would also allow comparative studies with other adjoining areas to examine the differences between humans hunting and wolf hunting on the deers’ landscapes of fear (*sensu* Berger, 2005). Although wolves would undoubtedly attract considerable media attention, the project would in fact be a whole-of-ecosystem restoration experiment, producing key insights into the restoration process in the Scottish context. A well-designed experiment, with comprehensive baseline surveys of key trophic levels, could provide a strong inferential framework for understanding causal relationships in the restoration process. This would have international significance because it could produce insights into some general ecological principles.

4.2. A research pathway

Fig. 3 outlines a scientific research pathway to inform future decisions on whether or not to reintroduce wolves. Due to the

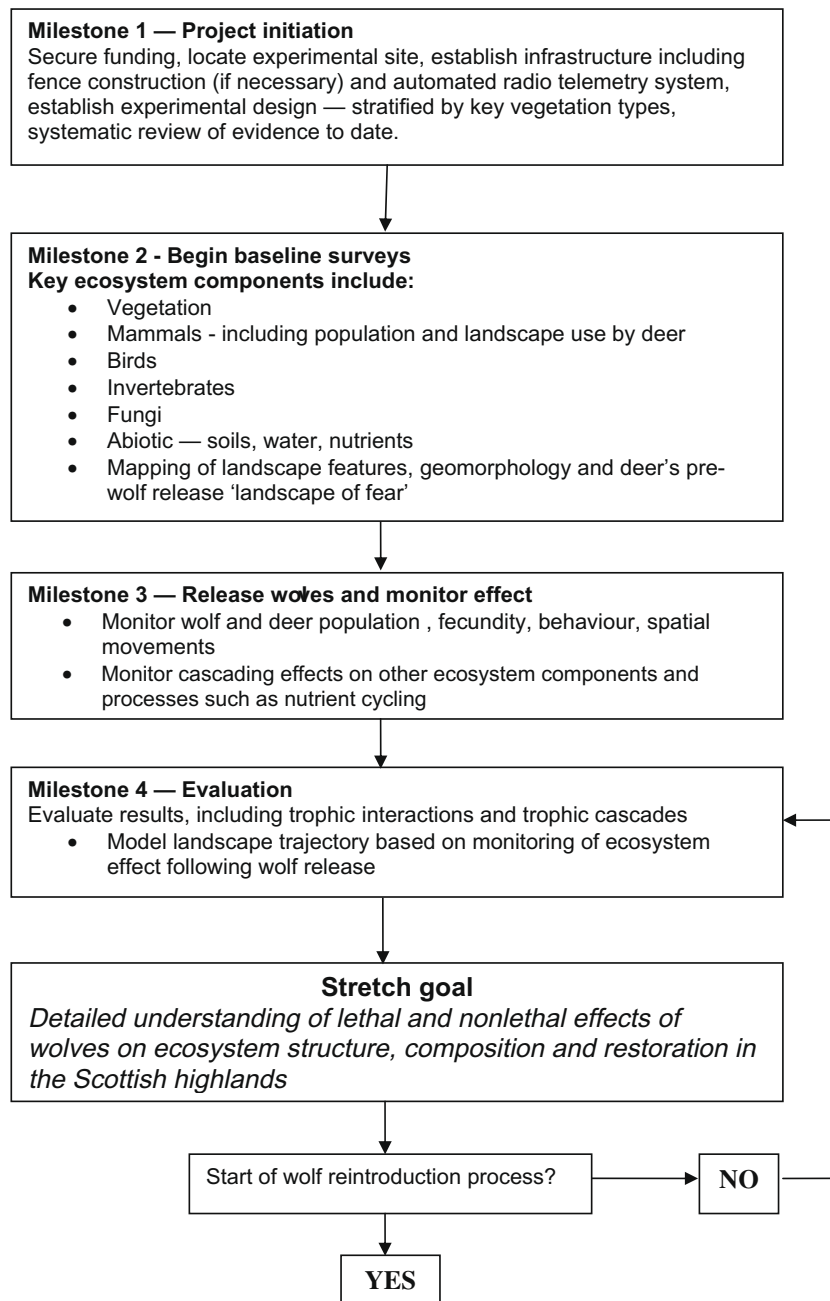


Fig. 3. A possible stretch-goal framework outlining a pathway for producing evidence of the ecosystem effects of wolf reintroduction in the Scottish context under controlled experimental conditions. At the evaluation milestone (4), Scotland may decide to proceed with a full reintroduction as part of a broader ecosystem restoration, or may not. The controlled experiment would inform, though not prejudice, that decision. If there was a decision not to proceed, the experiment could continue in perpetuity as an 'outdoor laboratory' for understanding ecosystem restoration in the long term.

complex nature of such a project, it is useful to place it within a 'stretch-goals' framework. Stretch-goals are "ambitious long-term goals used to inspire creativity and innovation to achieve outcomes that currently seem impossible" (p. 487, Manning et al., 2006). The target stretch-goal is consciously not "to reintroduce wolves", as this is not the responsibility of research scientists; but rather to provide the scientific evidence to inform that decision. The pathway includes key milestones towards the stretch-goal. Ongoing systematic reviews of relevant research would also help provide a scientific foundation for the final decision. Importantly, as a long-term ecological experiment investigating ecosystem restoration (which happens to include wolves), the project should not prejudice that decision and could continue in perpetuity, even if full reintroduction did not proceed.

5. Conclusion

In writing this paper, it has not been our intention to advocate either for or against full wolf reintroduction in Scotland. This is a much broader question for Scottish society to consider. However, we do advocate that the debate be broader than the lethal effects of wolves on deer populations, and includes all of the nonlethal ecological aspects of potential reintroduction. We also believe that a controlled experiment could help bridge the knowledge gap about the potential effect of wolves in Scottish ecosystems. A broader discussion in Scotland could give rise to ecological debate on risk effects in other parts of the world where wolf reintroductions are being considered both now and in the future.

Acknowledgements

Thanks to Tim Coulson, Scott Creel, David Hetherington, Robert Manning, Michellé Mabile, Colin McClean and Diana Raper for comments on earlier drafts of this manuscript. Thanks to Joel Berger and Brett Howland for providing literature. A.D.M. thanks David Lindenmayer for his ongoing academic support. We are grateful to Alison Hester for permission to use the photo in Fig. 1.

References

- Albon, S.D., Brewer, M.J., O'Brien, S., Nolan, A.J., Cope, D., 2007. Quantifying the grazing impacts associated with different herbivores on rangelands. *Journal of Applied Ecology* 44, 1176–1187.
- Amphlett, A., 2002. Contexts, developing ideas and merging issues in the conservation management of RSPB Abernethy Forest Reserve. *Botanical Journal of Scotland* 55, 135–148.
- BBC News, 1999. Call for return of Scottish wolves. <http://news.bbc.co.uk/2/hi/sci/tech/specials/sheffield_99/450318.stm>.
- BBC News, 2002. Call for wolves to be reintroduced. <http://news.bbc.co.uk/2/hi/uk_news/scotland/2065794.stm>.
- BBC News, 2008. Call for serious debate on wolf. <http://news.bbc.co.uk/2/hi/uk_news/scotland/highlands_and_islands/7268765.stm>.
- Berger, J., 2005. Hunting by carnivores and humans: does functional redundancy occur and does it matter? In: Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.), *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, DC, pp. 315–341.
- Berger, K.M., Conner, M.M., 2008. Recolonizing wolves and mesopredator suppression of coyotes: Impacts on pronghorn population dynamics. *Ecological Applications* 18, 599–612.
- Berger, J., Stacey, P.B., Bellis, L., Johnston, M.P., 2001. A mammalian predator–prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications* 11, 947–960.
- Bergman, E.J., Garrott, R.A., Creel, S., Borkowski, J.J., Jaffe, R., Watson, F.G.R., 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecological Applications* 16, 273–284.
- Beschta, R.L., Ripple, W.J., 2007. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Canadian Journal of Forest Research* 37, 1873–1885.
- Beschta, R.L., Ripple, W.J., 2008. Wolves, trophic cascades, and rivers in western Olympic National Park. *Ecohydrology* 1, 118–130.
- Brown, J.S., Laundré, J.W., Gurung, M., 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80, 385–399.
- Clutton-Brock, T.H., Coulson, T., Milner, J.M., 2004. Red deer stocks in the highlands of Scotland. *Nature* 429, 261–262.
- Creel, S., Christianson, D., 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23, 194–201.
- Creel, S., Winnie, J.A., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86, 3387–3397.
- Creel, S., Christianson, D., Liley, S., Winnie, J.A., 2007. Predation risk affects reproductive physiology and demography of elk. *Science* 315, 960.
- Deer Commission for Scotland, 2008. Scotland's Wild Deer: A National Approach.
- Dobson, A.P., Bradshaw, A.D., Baker, A.J.M., 1997. Hopes for the future: restoration ecology and conservation biology. *Science* 277, 515–522.
- Esseen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forests. *Ecological Bulletins* 46, 16–47.
- Forestry Commission Scotland, 2006. The Scottish Forestry Strategy, Forestry Commission Scotland, Edinburgh, UK. <[http://www.forestry.gov.uk/pdf/SFS2006fcfc101.pdf/\\$FILE/SFS2006fcfc101.pdf](http://www.forestry.gov.uk/pdf/SFS2006fcfc101.pdf/$FILE/SFS2006fcfc101.pdf)>.
- Fortin, D., Beyer, L.B., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86.
- Gordon, I.J., 1989. Vegetation community selection by ungulates on the Isle of Rhum. III. Determinants of vegetation community selection. *Journal of Applied Ecology* 26, 65–79.
- Gordon, I.J., Hester, A.J., Festa-Bianchet, M., 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* 41, 1021–1031.
- Gorman, M.L., 2007. Restoring ecological balance to the British mammal fauna. *Mammal Review* 37, 316–325.
- Halofsky, J.S., Ripple, W.J., 2008. Fine-scale predation risk on elk after wolf reintroduction in Yellowstone National Park, USA. *Oecologia* 155, 869–877.
- Halofsky, J.S., Ripple, W.J., Beschta, R.L., 2008. Recoupling fire and aspen recruitment after wolf reintroduction in Yellowstone National Park, USA. *Forest Ecology and Management* 256, 1004–1008.
- Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86, 2135–2144.
- Hester, A.J., Edenius, L., Buttenschon, R.M., Kuiters, A.T., 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry* 73, 381–391.
- Hetherington, D., 2006. The lynx in Britain's past, present and future. *ECOS* 27, 66–74.
- Hobbs, R.J., Harris, J.A., 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restoration Ecology* 9, 239–246.
- Illius, A.W., Gordon, I.J., 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56, 989–999.
- Jayakody, S., Sibbald, A.M., Gordon, I.J., Lambin, X., 2008. Red deer *Cervus elaphus* vigilance behaviour differs with habitat and type of human disturbance. *Wildlife Biology* 14, 81–91.
- John Muir Trust, 2004. Wildland Policy. <<http://www.jmt.org/policy-wild-land.asp>>. (accessed 14.04.09).
- Laundré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the landscape of fear in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79, 1401–1409.
- Lima, S.L., 1998. Nonlethal effects in the ecology of predator–prey interactions. *Bioscience* 48, 25–34.
- Manning, A.D., Lindenmayer, D.B., Fischer, J., 2006. Stretch-goals and backcasting: approaches for overcoming barriers to large-scale ecological restoration. *Restoration Ecology* 14, 487–492.
- Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M., Merrill, E.H., 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69, 1691–1707.
- McMorran, R., Price, M.F., McVittie, A., 2006. A review of the benefits and opportunities attributed to Scotland's landscapes of wild character. Scottish Natural Heritage Commissioned Report No. 194 (ROAME No. F04NC18), Scottish Natural Heritage, Inverness.
- McVean, D.N., 1963. Ecology of Scots Pine in the Scottish Highlands. *The Journal of Ecology* 51, 671–686.
- Mech, D.L., 1977. Wolf-pack buffer zones as prey reservoirs. *Science* 198, 320–321.
- Millennium Ecosystem Assessment, 2005. *Ecosystems and Human Well-Being: Biodiversity Synthesis*. Island Press, Washington, DC.
- Miller, J.R., 2005. Biodiversity conservation and the extinction of experience. *Trends in Ecology and Evolution* 20, 430–434.
- Morgan, J., 2007. Crying wolf, now with added bite. *The Herald*. <http://www.theherald.co.uk/search/display.var.1160642.0.crying_wolf_now_with_added_bite.php>.
- National Trust for Scotland, 2002. Wildland Policy. <http://www.nts.org.uk/conserve/downloads/wild_land_policy_2002.pdf>. (accessed 14.04.09).
- Nilsen, E.B., Milner-Gulland, E.J., Schofield, L., Myrsterud, A., Stenseth, N.C., Coulson, T., 2007. Wolf reintroduction to Scotland: public attitudes and consequences for red deer management. *Proceedings of the Royal Society: Series B, Biological Sciences* 274, 995–1002.
- O'Connell, S., 2008. Back from the dead: could wolves and wild boar roam Britain again? *The Independent*. <<http://www.independent.co.uk/environment/nature/back-from-the-dead-could-wolves-and-wild-boar-roam-britain-again-806900.html>>.
- Paine, R.T., 1969. A note on trophic complexity and community stability. *American Naturalist* 103, 91–93.
- Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* 10, 430–444.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. *BioScience* 46, 609–620.
- Radford, T., 1999. Foxes are fine, but bring back the wolf. *The Guardian*. <<http://www.guardian.co.uk/1999/sep/18/hunting.ruralaffairs>>.
- Ripple, W.J., Beschta, R.L., 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184, 299–313.
- Ripple, W.J., Beschta, R.L., 2006a. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation* 133, 397–408.
- Ripple, W.J., Beschta, R.L., 2006b. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* 230, 96–106.
- Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138, 514–519.
- Schmitz, O.J., Beckerman, A.P., O'Brien, K.M., 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78, 1388–1399.
- Schmitz, O.J., Hambäck, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *The American Naturalist* 155, 141–153.
- Schmitz, O.J., Grabowski, J.H., Peckarsky, B.L., Preisser, E.L., Trussell, G.C., Vonesh, J.R., 2008. From individuals to ecosystem function: Toward an integration of evolutionary and ecosystem ecology. *Ecology* 89, 2436–2445.
- Scott, D., Welch, D., Thurlow, M., Elston, D.A., 2000. Regeneration of *Pinus sylvestris* in a natural pinewood in NE Scotland following reduction in grazing by *Cervus elaphus*. *Forest Ecology and Management* 130, 199–211.
- Scottish Executive, 2004. Scotland's Biodiversity: It's In Your Hands. Scottish Executive, Edinburgh, UK. <<http://www.scotland.gov.uk/Resource/Doc/25954/0014583.pdf>>.
- Scottish Parliament, 2004. Nature Conservation (Scotland) Act.
- Scottish Wildlife Trust, 2009. Ecosystem-Scale Conservation. <<http://www.swt.org.uk/about-us/policy/ecosystem-scale-conservation>>. (accessed 23.03.09).
- Searle, K.R., Stokes, C.J., Gordon, I.J., 2008. When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. *Behavioural Ecology* 19, 475–482.

- Staines, B.W., Balharry, R., Welch, D., 1995. The impact of red deer and their management on the natural heritage in the uplands. In: Thompson, D.B.A., Hester, A.J., Usher, M.B. (Eds.), *Heaths and Moorland: Cultural Landscapes*. HMSO, Edinburgh, pp. 294–295.
- Summers, R.W., Wilkinson, N.I., Wilson, E.R., 2008. Age structure and history of *Pinus sylvestris* in Abernethy Forest, Scotland. *Scandinavian Journal of Forest Research* 23, 28–37.
- Taylor, P., 2005. *Beyond Conservation: A Wildland Strategy*. Earthscan Publications Ltd., London.
- Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Okarma, H., Ruczyński, I., Śnieżko, S., Gula, R., 2003. Daily patterns and duration of wolf activity in the Białowieża forest, Poland. *Journal of Mammalogy* 84, 243–253.
- UK Parliament, 1996. *Deer (Scotland) Act*.
- Watson, A., 1983. Eighteenth century deer numbers and pine regeneration near Braemar. *Scotland Biological Conservation* 25, 289–305.
- Watson Featherstone, A., 1997. The wild heart of the Highlands. *ECOS* 18, 48–61.
- Watson Featherstone, A., 2004a. Restoring wilderness, transforming the individual: the need for wilderness restoration in Scotland. In: Martin, V.G., Andrew, M. (Eds.), *Wilderness and Human communities: The Spirit of the 21st Century*. Proceedings from the seventh World Wilderness Congress, Port Elizabeth, South Africa. Fulcrum Publishing, Golden, Colorado.
- Watson Featherstone, A., 2004b. Rewilding in the north-central Highlands – an update. *ECOS* 25, 4–10.
- Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M., 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72, 909–916.
- Wilson, C.J., 2004. Could we live with reintroduced large carnivores in the UK. *Mammal Review* 34, 211–232.
- Wisdom, M.J. (Ed.), 2005. *The Starkey Project: A Synthesis of Long-Term Studies of Elk and Mule Deer*. Alliance Communications Group, Lawrence, Kansas, USA.
- Yalden, D.W., 1993. The problems of reintroducing carnivores. *Symposia of the Zoological Society of London* 65, 289–306.
- Yalden, D., 1999. *The history of British mammals*. T. & A. D. Poyser, Ltd., London, UK.