

RESEARCH ARTICLE

Fences can support restoration in human-dominated ecosystems when rewilding with large predators

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The use of fences in conservation can be controversial, as artificial barriers constrain natural behavior and ecological dynamics. However, in the case of large predators inhabiting protected areas within a hostile human-dominated landscape, predators may remain at low densities if they face high mortality upon leaving the reserve. In turn, this may compromise the potential for density-dependent effects such as top-down regulation of prey species abundance. We simulate the hypothetical reintroduction of gray wolves (*Canis lupus*) to reserves in their former range (Scottish Highlands), with the objectives of identifying parameters that allow a viable wolf population and the potential for direct top-down forcing of red deer (*Cervus elaphus*) densities. We examine the extent to which the number of dispersing wolves leaving the protected area influences whether these objectives are achieved. Our simulations confirm that source-sink population dynamics can result in a self-perpetuating wolf population, but one that never achieves densities needed for strong top-down forcing. When wolf density is weakly controlled by intraspecific competition, strong top-down forcing occurs when 20% of dispersing wolves or less leave the population. When 20–35% of dispersing wolves leave, the strength of top-down forcing is highly variable. The wolf population remained viable when 35–60% of dispersing wolves left, but then did not exert strong top-down forcing. Wolves were vulnerable to extinction at greater than 60% disperser loss. Despite their negative connotations, fences (including semi-permeable ones) could increase the potential for interspecific density-dependent processes in some cases, thereby facilitating trophic rewilding.

Key words: deer, fences, predation, restoration, rewilding, wolf

Implications for Practice

- Species reintroduction is increasingly recognized as a tool for restoring ecological processes (interactions among organisms and between organisms and their environment).
- Reintroduction and conservation practitioners should consider the requirements of restoring not just viable, but also ecologically effective populations of predators.
- When reintroducing or managing large carnivores into protected areas in otherwise human-dominated landscapes, to avoid source-sink population dynamics preventing high predator densities and reducing the potential for top-down forcing of prey species, fencing reserves should be considered.
- While fences constrain some ecological dynamics themselves, in some circumstances, their ability to prevent human–wildlife conflict can allow more effective restoration of predation in some cases. However, fenced reserves would need to be large and will require some ongoing management.

trophic interactions to support self-sustaining and biodiverse ecosystems, known as “trophic rewilding” (Soulé & Noss 1998; Donlan 2005; Sandom et al. 2013; Svenning et al. 2016). The main objective of classical reintroduction is to establish a self-perpetuating (viable) population consistent with the original 1998 International Union for Conservation of Nature (IUCN) species reintroduction guidelines (IUCN/SSC 2013),

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Introduction

A distinction can be made between reintroduction for the purpose of species conservation, that is a “classical reintroduction,” and species reintroduction to restore top-down

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while successful trophic rewilding requires the restoration of ecological processes (interactions among organisms and between organisms and their environment) for ecosystem benefits (now recognized in the 2013 IUCN reintroduction guidelines; IUCN/SSC 2013). Trophic rewilding is controversial (e.g. Rubenstein & Rubenstein 2016), and moving forward will require empirical research and careful consideration of numerous important factors (Nogues-Bravo et al. 2016; Svenning et al. 2016).

Species reintroduction and rewilding in human-dominated “unnatural” landscapes (Angermeier 2000) poses particular challenges (Dorresteijn et al. 2015; Svenning et al. 2016). Anthropogenic constraints on species population dynamics, especially linear infrastructure, are an important consideration for any project seeking to restore ecological processes (Jones et al. 2014; Darimont et al. 2015). The situation becomes more complex where the landscape is a mosaic of different land uses with varying management objectives and human impacts (Dorresteijn et al. 2015). As animals move between these areas of different land use, there is a risk that management in one area will compromise objectives in neighboring areas (Bull et al. 2013). Large predators are especially challenging to conserve and reintroduce due to their size, low densities, large territories, long travel distances, and potential to cause human–wildlife conflict (Woodroffe 2001; Macdonald et al. 2014). For instance, in Hwange National Park, Zimbabwe, Loveridge et al. (2010) observed that trophy hunting, population control, and human–wildlife conflict outside protected areas can create boundary population sinks, which perturb lion (*Panthera leo*) social behavior and threaten population viability inside the reserve. If population sinks are established, by extension, densities in the corresponding source populations are likely to be suppressed through a drainage effect, even if the source population is protected (e.g. Delibes et al. 2001; Gundersen et al. 2001). A scenario may arise in which a perpetual sink is created outside a protected area, limiting the density (although not necessarily the population viability) of predators within the protected area. Conceptually, it might be expected that such sinks would limit the potential for certain interspecific density-dependent ecological processes exerted by the predator, such as direct top-down effects on prey species (e.g. suppressing abundance; Fig. 1A). In this case, to avoid human constraints on the ecological process of predation, it would be necessary to prevent dispersing predators being artificially drained from the population by manipulating the permeability of the boundary (Fig. 1B).

Boundary permeability could be altered by creating an artificial barrier, such as a physical fence at the perimeter of the protected area while ensuring population viability through a managed metapopulation approach where animals are translocated in and out of a metapopulation of protected areas. Other approaches to varying boundary permeability are possible; e.g. to encourage a wild dog pack to return to their typical home range Jackson et al. (2012) used translocated wild dog scent markers to simulate the presence of other wild dogs. Others have used the noise of swarming bees and chili to discourage elephants raiding crops (Osborn & Parker 2003; King et al.

2007). While large predator density is strongly linked to prey abundance, enclosed populations have the potential to reach particularly high population densities. For instance, Packer et al. (2013) report that lions in fenced reserves in Africa achieve densities significantly closer to their model-estimated carrying capacity than populations in unfenced reserves, and the wolves on the physically isolated Isle Royale similarly achieved high densities, 92 wolves per 1,000 km², before declining as the result of disease (Peterson & Page 1988). A boundary barrier could help the reintroduction of a viable predator population with the potential to reach densities that instigate strong top-down forcing, but at the expense of dispersal in and out of the protected area. Conservationists often consider mobile species and fences incompatible because of the negative implications for dispersal (Hayward & Kerley 2009); if all wolf populations in Europe were fenced, we would not be seeing the current expansion of wolves across the continent (Chapron et al. 2014). We also recognize the importance of distance dispersal; however, here we explore the implications of fencing or not on the process of predation.

Wolves in the Scottish Highlands

A good hypothetical example of a case in which these challenges could arise from wolf reintroduction is the Scottish Highlands. Gray wolves are considered “least concern” by the IUCN because of their widespread distribution and globally stable population trend (Mech et al. 2010). Nevertheless, they are extirpated or more or less functionally extinct in great parts of their historical range (Mech et al. 2010). A reintroduction of wolves to Scotland is likely to be of relatively small benefit to the direct conservation of the species. However, the reintroduction of this large predator could have important ecosystem-level effects by instigating a trophic cascade (Estes et al. 2011; Ripple et al. 2015), and thereby achieve rewilding objectives. Although the human population density is low in the Scottish Highlands compared to most of Europe, humans still dominate the landscape. Historical logging has reduced woodland cover, the native apex predator guild has been extirpated, management has been used to maintain deer densities as a stalking resource, and sheep are prevalent (Warren 2009). Consequently, the Highlands is thought to have a high red deer (*Cervus elaphus*) abundance relative to ecological conditions, in turn preventing woodland regeneration with consequences for biodiversity conservation (Hobbs 2009). Red deer density is 40/km² in some forested areas, and 20/km² in open country (Apollonio et al. 2010). Red deer are within a size range for which predation has the potential to drive population regulation (Hopcraft et al. 2010). Nilsen et al. (2007) proposed that the reintroduction of wolves (*Canis lupus*) to Scotland could regulate the red deer population, improving conditions for forest regeneration. This chimes with proposals for wolf conservation to be seen as a force for ecosystem recovery, rather than primarily wolf population recovery (Licht et al. 2010).

Trophic cascades are the trickle-down effects of ecological interactions from the top of food webs. For example, the

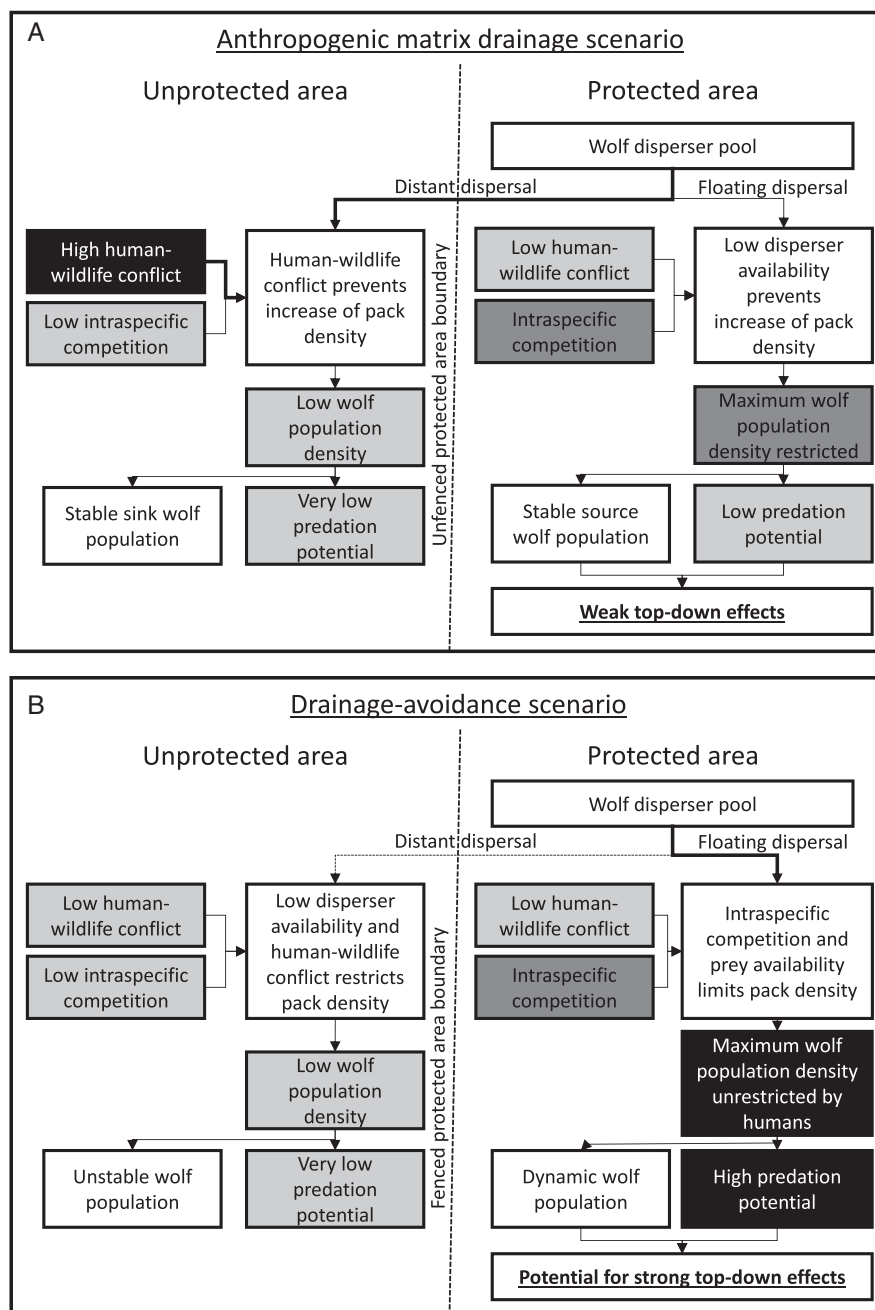


Figure 1. Conceptual models of two scenarios conducive to promoting wolf conservation alone (A, unfenced) or also achieve restoration of top-down trophic forcing potential (B, fenced). Relative darkness of boxes (excluding white) and lines indicates stronger effects. In model A, dispersing wolves perceive intraspecific competition as the greatest threat and seek territory space outside the protected area. In model B, wolves are prevented from leaving the protected area which increases floating dispersal inside the reserve.

reintroduction of wolves could alter the density and behavior of their prey species with implications for the intensity and distribution of herbivory and so the structure and composition of the vegetation community and beyond. Direct, density-mediated effects (predators killing prey) and indirect, behaviorally mediated effects (prey altering their behavior to avoid predation) have the potential to be important in driving cascades (e.g. Ripple & Beschta 2012; Kuiper et al. 2016).

Wolf reintroduction into Yellowstone National Park (YNP) has been central to the controversial debate around whether and, if so, how wolves drive trophic cascades (e.g. Kauffman et al. 2010; Beschta & Ripple 2013; Kauffman et al. 2013). Since that reintroduction, the wolf population has expanded and achieved high population densities in the Northern Range (approximately 71 wolves per 1,000 km²), while their primary prey, elk, has declined (from 15,000 to <6,000) (<https://www.nps.gov/yell/>)

learn/nature/wolfreports.htm)—although evidence suggests snowfall patterns and human harvest are also important drivers of elk decline (Vucetich et al. 2005). Equally, it is still discussed to which extent behaviorally mediated wolf–elk interactions have resulted in the recovery of trembling aspen (*Populus tremuloides*) in YNP (Kauffman et al. 2010; Beschta & Ripple 2013; Kauffman et al. 2013). Here, we focus on factors affecting wolves' potential to exert strong density-mediated effects on their likely primary prey species in the Scottish Highlands, red deer.

Reintroduction of wolves to protected areas nested within a human-dominated landscape could result in source-sink populations, within and outside protected areas, respectively. If wolves are reintroduced to a reserve that they perceive to have no boundaries, but beyond which they are unprotected and persecuted to a greater degree, this may result in a population sink outside the reserve. Dispersing wolves would likely leave the reserve, but few packs would be established there. Consequently, few established wolf packs outside the reserve would not constrain dispersers from leaving the reserve or provide a source of dispersers coming into the protected area, resulting in restricted wolf density inside the reserve. Again, while not preventing a viable wolf population establishing, this might not enable restoration of key ecological processes associated with wolves—including density-dependent top-down effects on red deer. Conversely, with a high-density situation in which the reserve was fenced either naturally (e.g. an island) or artificially (a fence), so that no wolves are lost via emigration, wolf density would only be limited by intraspecific competition and prey abundance.

Nilsen et al. (2007) found public attitudes toward wolf reintroduction in Scotland were generally positive, but farmers and organizations representing rural issues were negative. With livestock depredations probable, human–wildlife conflict should be expected as seen elsewhere in Europe (Linnell et al. 2008; Liberg et al. 2012), although depending on mitigation measures put in place (Linnell et al. 2012). Reintroductions require local support to be successful (IUCN/SSC 2013). To minimize costs to farmers and other stakeholders, the use of a fenced reserve has thus already been proposed in the Scottish Highlands to allow wolf reintroduction (Manning et al. 2009; Sandom et al. 2012). Sandom et al. (2012) predict that an area of at least 600 km² would be necessary for a “viable” reintroduction (defined as an 80% probability of the population surviving after 100 years), managed as a pseudo-metapopulation (Johnson et al. 2010), and found that within their study region an area of 1,200 km² was theoretically available. Here, we explore whether the fencing of landscape-scale reserves (rather than smaller scale fencing currently common in Scotland, e.g. Fig. 2) would enhance the potential for a reintroduced Scottish wolf population that is both demographically viable (surviving population after 100 years) and ecologically functional (has the potential to exert strong density-dependent top-down forcing of prey). We use this as a case study for exploring the more general paradox that a conspicuously “unnatural” intervention—the fencing of landscape-scale reserves containing highly mobile species—may be an effective means to restore both species

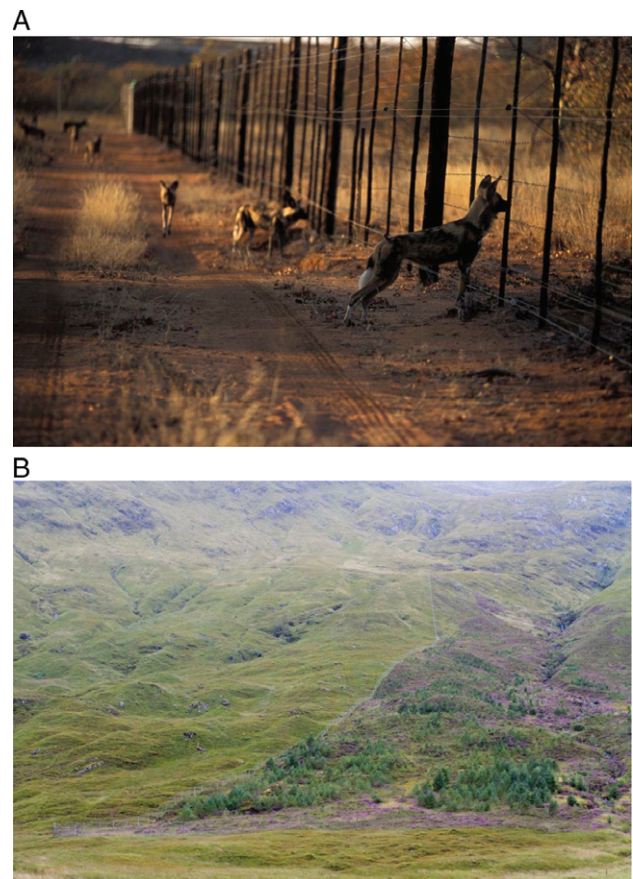


Figure 2. (A) African fenced enclosure with wild dogs (photo by A. L. Harrington). (B) Fenced woodland regeneration enclosure in the Scottish Highlands as an example of how fences are already used in Scotland (photo by C. Sandom).

and their associated ecological processes in human-dominated landscapes.

We hypothesize that (1) reintroduction of a viable wolf population may not necessarily result in the reestablishment of the potential for density-mediated strong top-down forcing upon red deer; (2) if natural maximum pack densities are too low, this will limit maximum wolf density and reduce the strength of density-mediated top-down forcing; (3) lower initial and maximum ungulate densities will increase the probability of strong top-down forcing by reducing the maximum wolf density required to exert a strong effect, and (4) increasing reserve boundary permeability to dispersing wolves will decrease the maximum attainable long-term wolf density, increasing time needed to achieve a long-term nonzero wolf density, and reducing the strength of top-down forcing.

Methods

Simulation Model Structure

Individual-based models (IBMs) have proven useful for population viability assessments of small wolf populations (Nilsen

et al. 2007; Bull et al. 2009; Sandom et al. 2012). We developed an IBM to explore what influence variously permeable perimeter barriers would have in allowing a reintroduced wolf population to be both viable and have the potential to exert density-dependent top-down forcing on red deer. The novelty of our approach was to subject dispersing wolves to different constraints, exploring the importance of wolf and red deer density thresholds in this regard.

An existing and tested IBM for a hypothetical wolf population in a limited area reserve in Scotland (Nilsen et al. 2007) was used to explore our hypotheses. The IBM had subsequently been adapted for the case of the Alladale Wilderness Reserve in the Scottish Highlands, to explore the relationship between predators and prey in a finite reserve of 1,200 km² (Sandom et al. 2012). Here, we develop new model functions relating to dispersing wolves and intraspecific competition, so as to simulate the effect of changing the permeability of the reserve boundary. The results were analyzed to differentiate between simply restoring a viable wolf population (classical reintroduction) and restoring one also capable of exerting strong density-dependent top-down forcing (trophic rewilding).

The model was coded in “R” (R Core Development Team 2016). The structure and life history traits of the modeled wolf population are outlined in Appendix S1 (Fig. S1, Supporting Information). The population consists of individual wolves at different life stages, grouped into packs, undergoing four life history stages every time step (1 year). The stages were survival, reproduction, dispersal, and the formation of new packs. Parameter values used are described in Table S1. A sensitivity analysis was undertaken to determine how sensitive our results were to prey carrying capacity and wolf kill and dispersal rates.

The predator–prey system assumes a single prey species (red deer), which was not demographically or spatially substructured, but modeled as an abundance of red deer subject to stochastic proportional reproduction and mortality (including wolf predation). Red deer starting density and carrying capacity were varied from 10 to 40/km², to represent the disparate ungulate densities recorded in nature or as a result of culling. The model included a mechanism for bottom-up control of the wolf population by red deer, in that wolf survival rates were modified annually to account for the red deer–wolf ratio (Appendix S1).

We simulated the impact of altering the conditions affecting dispersing wolves, given uncertain ecological limits on maximum attainable pack density. The propensity of dispersers to leave the reserve was treated as representative of the permeability of the reserve boundary. In this context, dispersing wolves were any wolves that left a pack and had the potential to form a new pack. Subadult wolves had some probability of leaving their natal pack in any year (Appendix S1). If both alpha adults in any one pack died, the remaining individuals in that pack became dispersers. For each scenario modeled, a maximum pack density was selected. The probability of wolves establishing a new pack decreased linearly as pack density increased (Appendix S1), representing increased intraspecific competition (Mech & Boitani 2003). Thus, even with sufficient prey, the wolf population was unable to expand without limit, recognizing that density dependence plays a role in survival rates. There was

nothing in the model to limit the number of wolves allowed in any one pack, except the annual probability that individual wolves dispersed or died.

The behavior and mortality rates of dispersing animals affected pack establishment rates and consequently the overall breeding potential of the wolf population. In reality, dispersers are subject to higher mortality rates than nondispersers, due to intraspecific competition and increased human conflict (Pletscher et al. 1997). This justified the use of separate dispersal and mortality dynamics for dispersers and for those remaining within packs. Dispersing animals that failed to establish a pack explored the fringes of established wolf pack territories. In this case, they were either killed by incumbent wolves, or tolerated. The degree to which either possibility was realized would in reality depend on social interactions between wolves, and possibly prey biomass as has been observed for apex predators elsewhere (Hayward et al. 2009). Alternatively, dispersers could be attracted across the protected area boundary, if conditions outside seemed preferable to those within. Such conditions might arise in reality if wolf density were high within a reserve but low outside (Macdonald & Carr 1989). These wolves were removed from the modeled population entirely (presumed either successful in establishing external territories or killed). We assume that due to human–wildlife conflict and consequent high mortality rates outside the reserve immigration would be negligible.

The effect of a disperser dying or leaving the reserve was effectively the same for the wolf population within the reserve. These were consequently treated as a compound variable: the proportion of dispersing wolves removed from the population in any year (ranging between a mean of 0 and 95% at 5% intervals, subject to stochastic variation). Although in reality dispersal rates are likely to vary, it is conceivable that dispersal rates may be constant over an extended period if the population were surrounded by a perpetual population sink, as investigated here.

Wolf and red deer population trajectories were simulated over a 100-year period, which was considered sufficient to allow both the viability of the wolf population (with respect to the four basic life history functions) and the effects of top-down forcing to become apparent. As the model was stochastic, each simulation was repeated 100 times to capture average behavior. Key output variables (red deer density, wolf density, wolf pack density, number of red deer predated upon, and number of wolves dispersing) were recorded for each time step. For every 100-year simulation, it was then possible to establish the minimum and maximum red deer densities, minimum and maximum wolf population and pack densities, and the year in which these minima and maxima occurred. Both behavior and predator–prey population dynamics were assessed by plotting these data and examining nonlinear responses and thresholds.

The hypotheses (H1–H4) primarily involved exploring the effect of a perimeter fence (or some other kind of permeable barrier) in restoring the process of predation. The IBM used to test the hypotheses has been shown to capture wolf population dynamics, but is nonspatial. Hence, the implementation of a fence was tested via proxy, by varying dispersal dynamics.

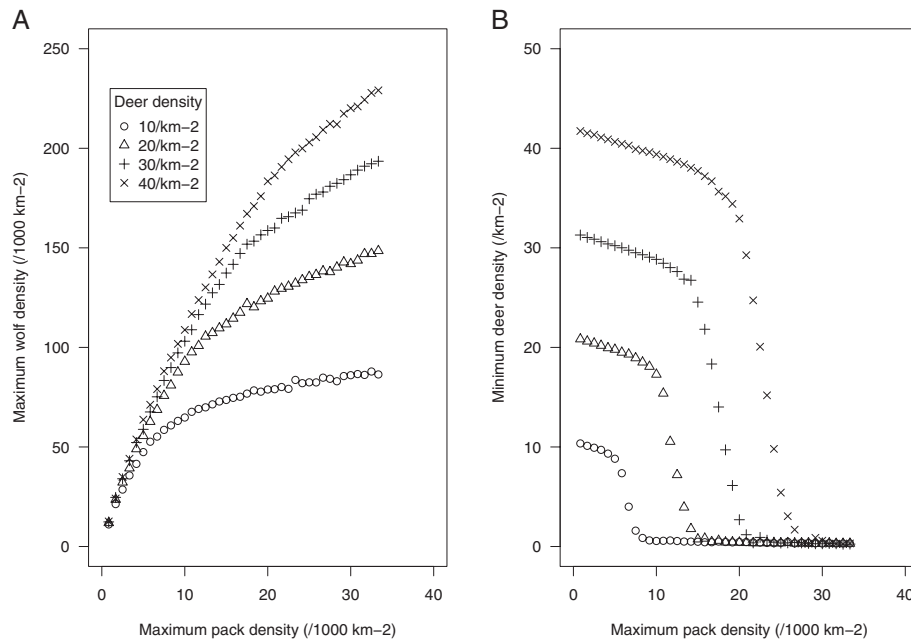


Figure 3. Simulation results, using four different values of initial red deer density, for maximum wolf density in relation to maximum wolf pack density (A) and mean minimum red deer density in relation to maximum pack density (B), where a drop in the former is considered a sign of strong top-down forcing.

During simulations in which the fence was considered an absolute barrier to movement, dispersing wolves could form packs given any vacant territories in the reserve, die, or (to an extent determined by the competition function) increase the wolf pack density, but could not leave the reserve. In simulations in which the reserve boundary was permeable, then the permeability was the likelihood that dispersing wolves would leave the reserve.

The model was validated against wolf population reintroduction dynamics in YNP, U.S.A., which offers a unique opportunity for evaluation as it is a well-monitored reintroduction with annually published reports on wolf and prey population abundance. We used the same demographic structure for wolf population reintroduced to YNP as a starting population in the model, and then simulated the expected population trajectory. This trajectory was compared against the observed historical YNP population trajectory since reintroduction. As conditions vary between the hypothetical Scottish example and YNP, this comparison was a test for the general plausibility of the model only.

Results

Model Validation

Simulated results compared favorably with empirical YNP wolf and red deer population dynamics (Fig. S2). A similar rate of initial growth and maximum wolf density was recorded for the observed population in YNP's Northern Range and our simulated population using the same starting red deer density (12/km²), 0–10% boundary permeability and a maximum pack density of 18.3 packs per 1,000 km² (Fig. S2).

As would be expected, higher maximum wolf density generally corresponded with higher wolf pack density, but only up to

a certain threshold. The threshold was dependent on the initial deer density, that is prey availability (Fig. 3A). This facet of our model output indicates that with greater prey availability comes a greater propensity for wolves to stay in their natal packs within our simulated population.

Importance of Wolf Density for the Strength of Top-Down Forcing

Crucially, while the model does predict that viable wolf populations are able to establish in the hypothetical Scottish reserve (Sandom et al. 2012), we found that wolves did not exhibit strong top-down forcing on the red deer population at lower maximum wolf pack densities (Fig. 3B). This supports our contention that a wolf population large enough to be self-sustaining does not necessarily have the potential to exert strong density-dependent top-down forcing (H1).

In scenarios in which a higher maximum pack density was permitted, the minimum red deer density was lower (Fig. 3B), supporting H2. The relationship between minimum deer density and maximum pack density was nonlinear, with strong top-down forcing exerted only past certain thresholds of wolf pack density (Fig. 3B). Such a result might be expected as the deer population was strongly dependent on reproduction and mortality, so the threshold would be the point at which the wolves were numerous enough in relation to deer that the kill rate began to overhaul reproduction rates. The lower the value for initial deer density used in the simulation, the lower that wolf pack density had to be in order to achieve strong density-dependent effects (Fig. 3B), which provides support for H3.

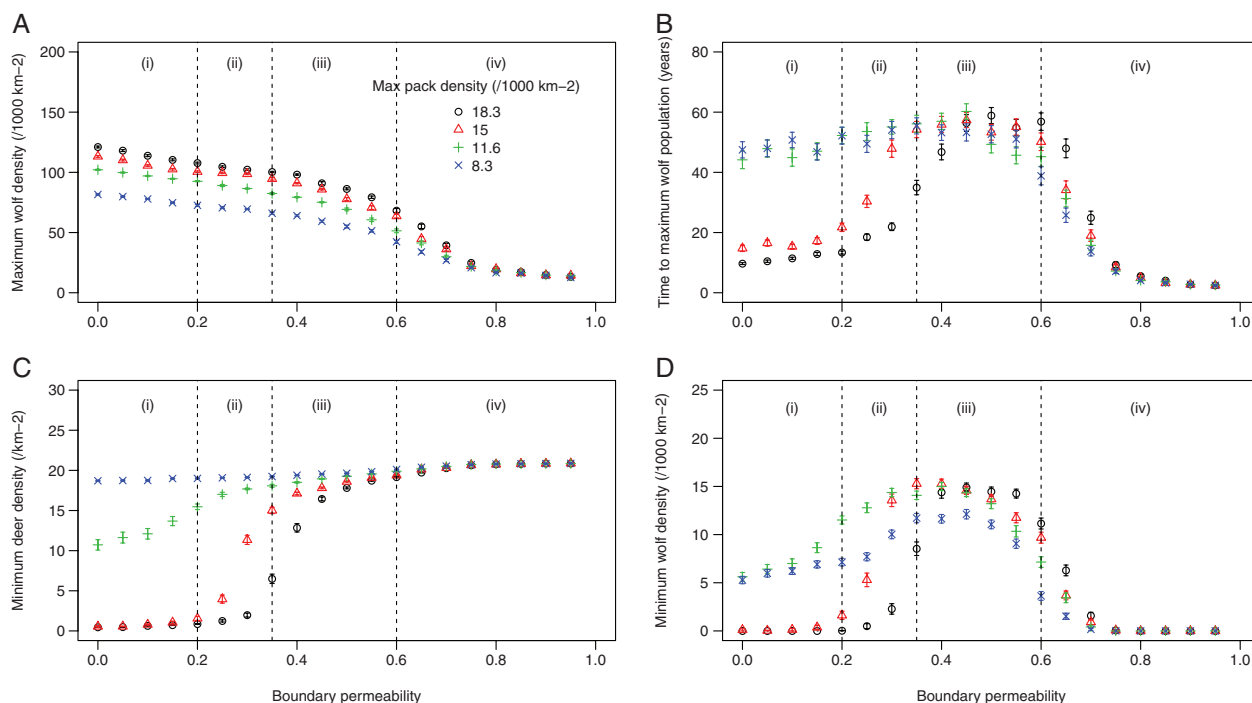


Figure 4. Mean ($n = 100$, SE) maximum wolf density (A), time to maximum wolf density (B), minimum red deer density (C), and minimum wolf density (D) against boundary permeability where 0 = no dispersing wolves leave the population and 1 = 100% dispersing wolves leave the population. Line colors represent scenarios of varying maximum pack density. Red deer starting and carrying capacity was set at 20/km². Roman numerals correspond to distinct scenarios where (i) represents strong prey suppression but high wolf extinction risk; (ii) relatively strong top-down forcing and medium wolf extinction probability; (iii) weak top-down forcing but high wolf survival probability; (iv) weak top-down forcing and high wolf extinction probability.

Permeability of Boundary and Wolf Density

Boundary permeability had a strong influence on whether either or both reintroduction objectives were achieved (H4). Increasing boundary permeability (1) decreased maximum wolf densities, (2) increased time taken to achieve maximum nonzero wolf density, (3) reduced the wolves' capacity to exert strong top-down forcing, and (4) increased the probability of wolf survival until the loss of dispersers was too great to support the population (Fig. 4A–D). Maximum wolf density decreased rapidly when the population lost more than 50% of dispersers (Fig. 4A).

Conversely, the time taken for the wolf population to achieve maximum density demonstrated a unimodal response to boundary permeability when maximum pack density was ≥ 15 packs per 1,000 km² (Fig. 4B). The unimodal response in this variable arose because, at lower boundary permeability, the wolf population rose quickly and then collapsed due to lack of prey. At higher boundary permeability, the wolves never attained a high population at all, so again the maximum population was effectively achieved early on in the simulation. At high and low boundary permeability, time to maximum wolf density was at a minimum, and at a maximum at intermediate permeability. This unimodal response (Fig. 4B) appeared to reflect the interaction between decreasing rate of population growth and a decreasing maximum population, with increasing boundary permeability. With a low limit (≤ 11.6 per 1,000 km²) on wolf pack densities, the response was not unimodal—as the wolf population never reached sufficient density to cause a collapse in deer

numbers—and time taken to reach maximum wolf density in that run of the model decreased with increased boundary permeability. These model outputs support H4 in that attainable wolf density decreased with increased boundary permeability, and that the rate of population growth, if the population could grow, decreased with increased boundary permeability.

Minimum red deer density and maximum wolf density, under the 18.3 maximum pack density scenario, were negatively correlated. This again suggested that beyond a threshold wolf density, there was significantly increased potential for top-down forcing on red deer populations (Fig. 5A). A wolf density > 80 individuals per 1,000 km² was required (but not guaranteed) to exert strong top-down forcing. The variability in response to high wolf densities may be explained by the decreasing rate at which the wolf population grows under increased boundary permeability. In those simulations in which wolves did strongly reduce deer density, the time taken for wolf population to reach a maximum was an important factor and was generally short (Fig. 5B).

Wolves exerted strong top-down forcing of red deer only when pack densities could achieve 15 packs per 1,000 km² or greater (Fig. 4C). When pack density was restricted to no more than 8.3 packs per 1,000 km² the wolf population had almost no impact on deer density. An intermediate scenario was recorded when pack density could achieve 11.3 packs per 1,000 km² or higher. However, top-down forcing was regulated by boundary permeability in a sigmoid relationship. When 60% or more of dispersing wolves were lost, no impact on deer density was

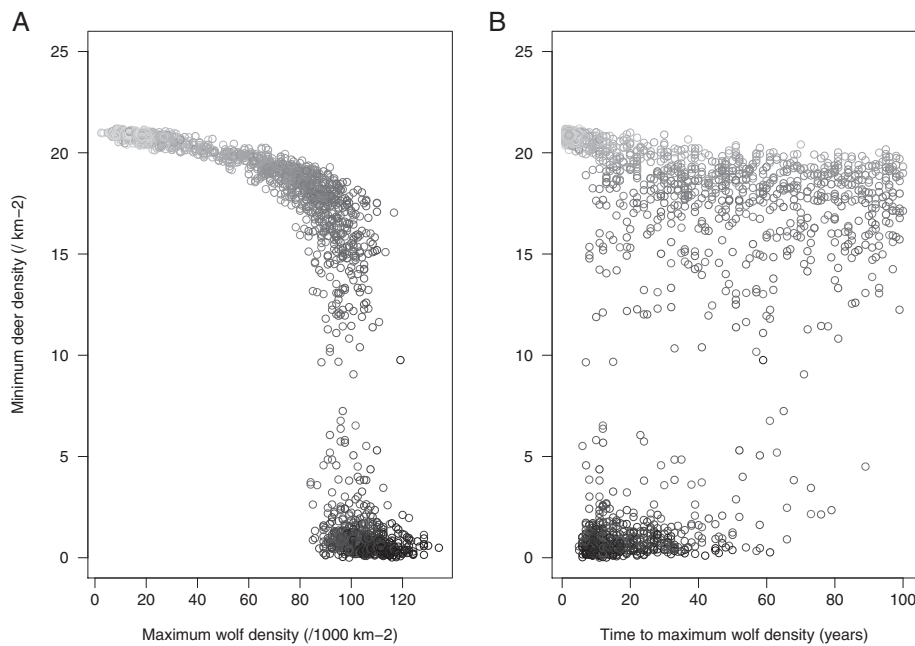


Figure 5. Minimum red deer density against maximum wolf population achieved (A) and time taken for the wolf population to reach its maximum (B) under varying disperser removal rates. Lighter points = high disperser removal; darker points = low disperser removal. Cluster A of points in the top left represents the wolf population dying out quickly in the simulation and never suppressing red deer. Cluster B represents those cases where the wolf population has expanded rapidly within 20 years, which has made suppression of red deer much more likely.

recorded. The degree to which boundary permeability limited top-down forcing was related to maximum pack density, with progressively less impact on the deer population with reduced maximum pack density.

Minimum wolf density had a unimodal relationship with boundary permeability (Fig. 4D). At low boundary permeability, minimum wolf density strongly reflected the strength of top-down forcing of prey density, with very low minimum deer densities corresponding to wolf extinction. Minimum wolf density decreased from a maximum at around 30–50% boundary permeability depending on maximum pack density setting. The wolf population could not survive losing 70% or more of the dispersing population yearly.

Sensitivity Analysis

An extensive sensitivity analysis using this model structure and set of parameters has already been completed (Sandom et al. 2012). However, we carried out a simple sensitivity analysis here, given that modifications had been made to the original code. The main findings were that varying the asymptotic kill rate, deer starting population and carrying capacity had a strong impact on the strength of top-down forcing (Figs. S3 & S4), but varying dispersal rates had no noticeable impact on the strength of top-down forcing of deer density (Fig. S5).

Discussion

The outcomes of our simulations support the suggestion that restoring a viable wolf population does not necessarily restore

the potential for density-dependent top-down forcing on prey. This has implications for the management of apex predators in protected areas in human-dominated ecosystems. The outcomes of our simulations, in terms of the strength of top-down forcing, were sensitive to at least four important factors: prey carrying capacity, maximum wolf pack density, kill rate, and boundary permeability. The latter relates to our main objective, that is exploring whether the permeability of a reserve boundary (i.e. barrier) could affect the ability of predators to exert strong density-dependent top-down forcing.

Possible Scenarios Following Reintroduction

The results can be grouped into four probable ecological outcomes following wolf reintroduction, dependent on the boundary permeability and assuming maximum wolf pack density is only limited by prey availability:

- 1 Very low permeability (0.00–0.20), e.g. an impassable boundary fence. This would promote rapid wolf population growth and high maximum wolf densities, although strong top-down forcing in the red deer population caused prey population collapse and consequent wolf extinction. This scenario might be expected in an unmanaged fenced reserve in the Scottish Highlands.
- 2 Low permeability (0.20–0.35), e.g. a less effective physical boundary, metapopulation management, or less favorable, but not intolerable conditions surrounding the reintroduction site. Rapid wolf population growth and high wolf population maxima would exert density-dependent top-down forcing on

deer, but the strength of the effect decreases with increasing boundary permeability, in turn reducing probability of wolf extinction, perhaps the ideal scenario from a trophic rewilding standpoint.

- 3 High permeability (0.35–0.60), e.g. up to 60% of all dispersing wolves leave the reserve or are killed as a result of intraspecific competition. High losses of dispersers from the population would mean relatively slow wolf population growth rate and a low maximum density, preventing the possibility of strong density-dependent top-down forcing on the red deer population. However, wolf density would still be sufficient for a sustained wolf population.
- 4 Very high permeability (0.60–1.00), e.g. leaving the reserve was appealing to dispersers. Insufficient individuals would remain in the reserve to sustain a wolf population.

The complexity of wolf–prey systems, with each system often having a unique combination of relevant social, ecological, and physical factors, probably explains why there is no scientific consensus on the role of wolf predation in prey population dynamics (Mech & Peterson 2003; Peterson et al. 2014). However, there are “real world” examples, which offer indications of when wolves may influence their prey. The Isle Royale National Park (IRNP) wolf population is entirely contained without any other major ungulate predator present. The population crashed from high densities (92 wolves per 1,000 km²) as a result of disease during 1980–1982, which coincided with a marked rise in moose calves/cow ratio (from 22/100 cows to 60/100 cows; Peterson & Page 1988), and over the following 15 years with a continually very low wolf density, with the moose density markedly rising to 4/km²—10 times usual North American mainland densities (Messier 1994). The response of the IRNP moose to an expanding wolf population is less clear. A rising wolf population in the early- and mid-1970s was followed, with a lag of a year or two, by a decline in the moose population (Peterson & Page 1988), but the same rise in the wolf population was associated with a preceding rise in moose numbers. Thus, it seems that although moose in IRNP exhibit strong direct density dependence during years of wolf decline, they exhibit only weak direct density dependence but strong delayed density dependence during years of wolf increase (Mech & Peterson 2003). It is clear that predation by wolves on Isle Royale moose is strongly additive—annual variation in predation rate is a major factor influencing moose population growth rate ($R^2 = 0.55$; Vucetich 2017).

Determining the rate of dispersal in real-world examples is difficult. In Minnesota, Fuller (1989) reviewed dispersal rates that ranged between 21 and 35%, but in a population where 80% of wolf mortality was anthropogenic. Pletscher et al. (1997) record a dispersal rate of 44%, including many wolves leaving the relative safety of Glacier National Park for areas where hunting was legal. Our modeling suggests that higher dispersal rates (i.e. when the boundary is more permeable) are not conducive to strong top-down forcing on deer when deer density is $\geq 20/\text{km}^2$. Correspondingly, Pletscher et al. (1997) recorded wolf densities of 35 per 1,000 km² 12 years after recolonization. However, dispersal rates in Minnesota might have allowed

strong top-down forcing at lower prey densities, if wolf persecution had been limited. Behaviorally mediated trophic cascades have been recorded in the region (Callan et al. 2013). In Canada, Stronen et al. (2012) found that there was limited gene flow between the wolves of Riding Mountain National Park (RMNP) and other wolf populations in protected areas in the region, and reported no successful wolf dispersal from RMNP over several multiyear tracking studies since 1974. There are no physical barriers separating the populations, but agriculture now dominates the region, such that RMNP is considered a “wilderness island in an agricultural region.” Parks Canada recorded a maximum wolf population of 113 individuals in 2011/2012, a density of approximately 40 wolves per 1,000 km². In Finland, Kojola et al. (2006) reported that all wolves dispersing from an expanding wolf population into a reindeer management area were shot before being able to reproduce, but 10 out of 16 bred successfully when dispersing outside this area. In Białowieża National Park, surrounding human land use and activity has created a spatiotemporal barrier to wolf movement patterns (Theuerkauf et al. 2003), indicating human land use can act as a dispersal barrier in some circumstances.

Important Considerations

Intraspecific wolf behavior would be similarly strong determinants of wolf population growth alongside dispersal dynamics. These are not issues that the model was designed to explore—the focus was rather on the capacity of changing dispersal rates and reserve boundary conditions to bring about different predator–prey interaction scenarios. It is likely that the results would be modified if these additional factors were considered. Similarly, disease is a factor that might have a particularly strong influence on rewilding efforts (Nogues-Bravo et al. 2016), which we have not included in our model. The reality is that some form of management for disease may well be required—although given that the situation we model is of large wild predators in a large fenced reserve, management of some form would likely be required in any case.

As mentioned previously, Isle Royale offers an example of a natural island harboring wolves and the process of predation at a scale that is theoretically achievable in Scotland. However, it is worth noting that these wolves are now suffering from inbreeding depression and are on the brink of extinction (Räikkönen et al. 2009). A fenced reserve would ideally be considerably larger than Isle Royale and managed as part of a metapopulation to limit the threat of inbreeding, as has been employed with other isolated large carnivore populations (e.g. Johnson et al. 2010; Davies-Mostert et al. 2014).

Red deer are a herding species that alter distribution with habitat heterogeneity, seasonality, and predation. In the winter, aggregations of up to 1,000 animals may occupy restricted ranges (Walker & Nowak 1991). Behaviorally mediated effects of wolves may create a “landscape of fear,” that is a landscape in which ungulates disperse to areas of reduced predation risk, such as boundary zones between territories (Hoskinson & Mech 1976; Hernandez & Laundre 2005; Valeix et al. 2009). A heterogeneous distribution of ungulates will have a spatially

uneven impact on the landscape, potentially allowing woodland regeneration in some areas while keeping others open. Such heterogeneity can be beneficial to biodiversity overall and may be close to a “natural” situation in Northwest Europe (Svenning 2002; Sandom et al. 2014). In this way, the indirect effects of wolves on prey could also be seen as positive for conservation and land management, regardless of whether density-dependent top-down forcing occurs. The further question of how the presence of an artificial barrier (i.e. a fence) might interplay with fear dynamics in such a system is an interesting one, and a potential direction for future research, but is beyond the scope of this paper.

Implications for Wolf Reintroduction to the Scottish Highlands

The outcomes of the simulation model we present do not necessarily predict exactly what would happen to a wolf population in the Highlands—rather, they indicate likely qualitative trends, and highlight those facets of the system that would need to be closely monitored and potentially managed. These include the density of prey before wolves were reintroduced, the relative densities of wolves and prey, the amount of territory occupied by each pack, and the permeability of the reserve boundary, that is the rate at which dispersers are lost from the population. Based on these results, enclosing such a wolf population within an impermeable or semi-permeable barrier (or managed as part of a wider metapopulation) might be necessary to allow wolves the potential of sufficiently high densities to reduce red deer numbers. However, a completely impassable fence could also result in deer density being sufficiently reduced to cause a collapse in the wolf population, that is scenario (i) above. Arguably, the ideal scenario from a conservation standpoint in human-dominated landscapes, that is scenario (ii) above, would require either a reserve boundary that enabled some dispersing wolves to escape, or the intentional removal of a number of wolves from the reserve every generation. While our modeling offers insights into what might happen the next step would be to test these ideas by creating an enclosed reserve, reintroducing wolves, and closely monitoring the system (Manning et al. 2009). The main conclusion we draw here is that not only is a viable wolf population possible in a fenced reserve, but that such a population could result in the restoration of density-dependent trophic interactions, with likely positive biodiversity effects. More generally, barriers in some form might have a more important role to play in establishing modern wild land than might be assumed.

Implications for Trophic Rewilding

Trophic rewilding is a process of establishing ecosystems (through species reintroductions that restore top-down trophic effects) that (1) reduces or removes the need for ongoing human management and (2) make an important contribution to biodiversity and ecosystem service restoration and conservation (Svenning et al. 2016; Sandom & Wynne-Jones 2018). Our results highlight that in spatially restricted rewilding projects

in human-dominated landscapes, boundary effects have important implications for the functioning of ecological processes and so ecosystem outcomes. As a result, some management of rewilding projects might be needed to replicate ecological processes that cannot be restored. In our example, where there is no perimeter barrier, human influences on predation should be considered and potentially managed, and where there is a perimeter barrier, similar consideration is needed for dispersal dynamics. This type of compromise is likely to be required in many rewilding projects in human-dominated landscapes, and the level of compromise is likely to increase as the spatial scales of rewilding projects decrease.

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Model details.

Figure S1. Schematic representation of key processes in wolf model, including prey factor.

Figure S2. Mean ($n = 100$) wolf and deer population dynamics over the 100-year modeling period in a 1,400-km² area.

Figure S3. Minimum red deer density under modeling scenarios (kill rate) with varying boundary permeability.

Figure S4. Minimum red deer density under modeling scenarios (carrying capacity) with varying boundary permeability.

Figure S5. Minimum red deer density under modeling scenarios (cub, sub-adult and adult dispersal) with varying boundary permeability.

Table S1. Parameters and sources used in the wolf model adapted from (Bull et al. 2009).

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