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3 **1 Fences can support restoration of human-dominated**
4 **2 ecosystems when rewilding with large predators**

5 Running title: *Fences can facilitate rewilding*
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34

35 **Abstract**

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

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57 Key words: *Deer, fences, predation, restoration, rewilding, wolf*

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59 Implications for Practice:

- 60 1. Species reintroduction is increasingly recognised as a tool for restoring ecological
61 processes (interactions amongst organisms and between organisms and their
62 environment).
- 63 2. Reintroduction and conservation practitioners should consider the requirements
64 of restoring not just viable, but also ecologically effective populations of
65 predators.

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3 66 3. When reintroducing or managing large carnivores into protected areas in
4 67 otherwise human-dominated landscapes, to avoid source-sink population
5 68 dynamics preventing high predator densities and reducing the potential for top-
6 69 down forcing of prey species, fencing reserves should be considered.
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9 70 4. While fences constrain some ecological dynamics themselves, in some
10 71 circumstances, their ability to prevent human-wildlife conflict can allow more
11 72 effective restoration of predation **in some cases**. However, fenced reserves would
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13 73 need to be large and will require some on-going management.
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80 Introduction

81 A distinction can be made between reintroduction for the purpose of species conservation, i.e.
82 a 'classical reintroduction', and species reintroduction **to restore top-down trophic interactions**
83 **to support self-sustaining and biodiverse ecosystems**, known as 'trophic rewilding' (Soulé &
84 Noss 1998; Donlan 2005; Sandom et al. 2013; Svenning et al. 2016). The main objective of
85 classical reintroduction is to establish a self-perpetuating (viable) population consistent with
86 the **original** 1998 International Union for Conservation of Nature (IUCN) species reintroduction
87 guidelines (IUCN/SSC 2013), whilst successful trophic rewilding requires the restoration of
88 ecological processes (interactions amongst organisms and between organisms and their
89 environment) for ecosystem benefits (now recognised in the 2013 IUCN reintroduction
90 guidelines IUCN/SSC 2013). Trophic rewilding is controversial (e.g. Rubenstein &
91 Rubenstein 2016), and moving forward will require empirical research and careful
92 consideration of numerous important factors (Nogues-Bravo et al. 2016; Svenning et al.
93 2016).

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95 Species reintroduction and rewilding in human-dominated 'unnatural' landscapes (Angermeier
96 2000) poses particular challenges (Dorresteijn et al. 2015; Svenning et al. 2016).
97 Anthropogenic constraints on species population dynamics, especially linear infrastructure,
98 are an important consideration for any project seeking to restore ecological processes (Jones
99 et al. 2014; Darimont et al. 2015). The situation becomes more complex where the landscape
100 is a mosaic of different land uses with varying management objectives and human impacts
101 (Dorresteijn et al. 2015). As animals move between these areas of different land use, there is
102 a risk that management in one area will compromise objectives in neighbouring areas (Bull et
103 al. 2013). Large predators are especially challenging to conserve and reintroduce due to their
104 size, low densities, large territories, long travel distances, and potential to cause human-
105 wildlife conflict (Woodroffe 2001; Macdonald et al. 2014). For instance, in Hwange National
106 Park, Zimbabwe, Loveridge et al. (2010) observed that trophy hunting, population control and
107 human-wildlife conflict outside protected areas can create boundary population sinks, which
108 perturb lion *Panthera leo* social behaviour and threaten population viability inside the reserve.
109 If population sinks are established, by extension, densities in the corresponding source
110 populations are likely to be suppressed through a drainage effect, even if the source
111 population is protected (e.g. Delibes et al. 2001; Gundersen et al. 2001). A scenario may
112 arise in which a perpetual sink is created outside a protected area, limiting the density
113 (although not necessarily the population viability) of predators within the protected area.
114 Conceptually, it might be expected that such sinks would limit the potential for certain inter-
115 specific density-dependent ecological processes exerted by the predator, such as direct top-
116 down effects on prey species (e.g. suppressing abundance; Fig. 1A). In this case, to avoid
117 human constraints on the ecological process of predation, it would be necessary to prevent
118 dispersing predators being artificially drained from the population by manipulating the
119 permeability of the boundary (Fig. 1B).

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3 120 Boundary permeability could be altered by creating an artificial barrier, such as a physical
4 121 fence at the perimeter of the protected area while ensuring population viability through a
5 122 managed metapopulation approach where animals are translocated in and out of a
6 123 metapopulation of protected areas. Other approaches to varying boundary permeability are
7 124 possible: for example, to encourage a wild dog pack to return to their typical home range
8 125 Jackson et al. (2012) used translocated wild dog scent markers to simulate the presence of
9 126 other wild dogs. Others have used of the noise of swarming bees and chilli to discourage
10 127 elephants raiding crops (Osborn & Parker 2003; King et al. 2007). While large predator
11 128 density is strongly linked to prey abundance, enclosed populations have the potential to reach
12 129 particularly high population densities. For instance, Packer et al. (2013) report that lions in
13 130 fenced reserves in Africa achieve densities significantly closer to their model-estimated
14 131 carrying capacity than populations in unfenced reserves, and the wolves on the physically
15 132 isolated Isle Royale similarly achieved high densities, 92 wolves per 1000 km² before
16 133 declining as the result of disease (Peterson & Page 1988). A boundary barrier could help the
17 134 reintroduction a viable predator population with the potential to reach densities that instigate
18 135 strong top-down forcing, but at the expense of dispersal in and out of the protected area.
19 136 Conservationists often consider mobile species and fences incompatible because of the
20 137 negative implications for dispersal (Hayward & Kerley 2009); if all wolf populations in Europe
21 138 were fenced we would not be seeing the current expansion of wolves across the continent
22 139 (Chapron et al. 2014). We also recognise the importance of distance dispersal, however, here
23 140 we explore the implications of fencing or not on the process of predation.

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33 142 *Wolves in the Scottish Highlands*

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35 143 A good hypothetical example of a case in which these challenges could arise from wolf
36 144 reintroduction is the Scottish Highlands. Gray wolves are considered 'least concern' by the
37 145 IUCN because of their widespread distribution and globally stable population trend (Mech et
38 146 al. 2010). **Nevertheless, they are extirpated or more or less functionally extinct in great parts**
39 147 **of the historical range (Mech et al. 2010).** A reintroduction of wolves to Scotland is likely to be
40 148 of relatively small benefit to the direct conservation of the species. However, the
41 149 reintroduction of this large predator could have important ecosystem level effects by
42 150 instigating a trophic cascade (Estes et al. 2011; Ripple et al. 2015), and thereby achieve
43 151 rewilding objectives. While the human population density is low in the Scottish Highlands
44 152 compared to most of Europe, humans still dominate the landscape. Historical logging has
45 153 reduced woodland cover, the native apex predator guild has been extirpated, management
46 154 has been used to maintain deer densities as a stalking resource, and sheep are prevalent
47 155 (Warren 2009). Consequently, the Highlands is thought to have a high red deer *Cervus*
48 156 *elaphus* abundance relative to ecological conditions, in turn preventing woodland
49 157 regeneration with consequences for biodiversity conservation (Hobbs 2009). Red deer density
50 158 is 40 per km² in some forested areas, and 20 per km² in open country (Apollonio et al. 2010).

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3 159 Red deer are within a size range for which predation has the potential to drive population
4 160 regulation (Hopcraft et al. 2010). Nilsen et al. (2007) proposed that the reintroduction of
5 161 wolves *Canis lupus* to Scotland could regulate the red deer population, improving conditions
6 162 for forest regeneration. This chimes with proposals for wolf conservation to be seen as a force
7 163 for ecosystem recovery, rather than primarily wolf population recovery (Licht et al. 2010).

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10 164 Trophic cascades are the trickle-down effects of ecological interactions from the top of food-
11 165 webs. For example, the reintroduction of wolves could alter the density and behaviour of their
12 166 prey species with implications for the intensity and distribution of herbivory and so the
13 167 structure and composition of the vegetation community and beyond. Direct, density-mediated
14 168 effects (predators killing prey) and indirect, behaviourally mediated effects (prey altering their
15 169 behaviour to avoid predation) have the potential to be important in driving cascades (e.g.
16 170 Ripple & Beschta 2012; Kuijper et al. 2016). Wolf reintroduction into Yellowstone National
17 171 Park (YNP) has been central to the controversial debate around whether and, if so, how
18 172 wolves drive trophic cascades (e.g. Kauffman et al. 2010; Beschta & Ripple 2013; Kauffman
19 173 et al. 2013). Since that reintroduction, the wolf population has expanded and achieved high
20 174 population densities in the Northern Range (~71 wolves per 1000 km²)¹, whilst their primary
21 175 prey, elk, has declined (from 15,000 to <6,000)¹ – although evidence suggests snowfall
22 176 patterns and human harvest are also important drivers of elk decline (Vucetich et al. 2005).
23 177 Equally, it is still discussed to which extent behaviourally-mediated wolf-elk interactions have
24 178 resulted in the recovery of trembling aspen (*Populus tremuloides*) in YNP (Kauffman et al.
25 179 2010; Beschta & Ripple 2013; Kauffman et al. 2013). Here, we focus on factors affecting
26 180 wolves' potential to exert strong density-mediated effects on their likely primary prey species
27 181 in the Scottish Highlands, red deer.

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37 183 Reintroduction of wolves to protected areas nested within a human-dominated landscape
38 184 could result in source-sink populations, within and outside protected areas respectively. If
39 185 wolves are reintroduced to a reserve that they perceive to have no boundaries, but beyond
40 186 which they are unprotected and persecuted to a greater degree, this may result in a
41 187 population sink outside the reserve. Dispersing wolves would likely leave the reserve, but few
42 188 packs would be established there. Consequently, few established wolf packs outside the
43 189 reserve would not constrain dispersers from leaving the reserve or provide a source of
44 190 dispersers coming into the protected area, resulting in restricted wolf density inside the
45 191 reserve. Again, whilst not preventing a viable wolf population establishing, this might not
46 192 enable restoration of key ecological processes associated with wolves – including density-
47 193 dependent top-down effects on red deer. Conversely, with a high-density situation in which
48 194 the reserve was fenced either naturally (e.g. an island) or artificially (a fence), so that no

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56 ¹ <https://www.nps.gov/yell/learn/nature/wolfreports.htm>

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3 195 wolves are lost via emigration, wolf density would only be limited by intra-specific competition
4 196 and prey abundance.

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8 198 Nilsen et al. (2007) found public attitudes towards wolf reintroduction in Scotland were
9 199 generally positive, but farmers and organisations representing rural issues were negative.
10 200 With livestock depredations probable, human-wildlife conflict should be expected as seen
11 201 elsewhere in Europe (Linnell et al. 2008; Liberg et al. 2012), although depending on mitigation
12 202 measures put in place (Linnell et al. 2012). Reintroductions require local support to be
13 203 successful (IUCN/SSC 2013). To minimise costs to farmers and other stakeholders, the use
14 204 of a fenced reserve has thus already been proposed in the Scottish Highlands to allow wolf
15 205 reintroduction (Manning et al. 2009; Sandom et al. 2012). Sandom et al. (2012) predict that an
16 206 area of at least 600 km² would be necessary for a 'viable' reintroduction (defined as an 80%
17 207 probability of the population surviving after 100 years), managed as a pseudo-metapopulation
18 208 (Johnson et al. 2010), and found that within their study region an area of 1200 km² was
19 209 theoretically available. Here, we explore whether the fencing of landscape-scale reserves
20 210 (rather than smaller scale fencing currently common in Scotland e.g. Plate 1B) would
21 211 enhance the potential for a reintroduced Scottish wolf population that is both demographically
22 212 viable (surviving population after 100 years) *and* ecologically functional (has the potential to
23 213 exert strong density-dependent top-down forcing of prey). We use this as a case study for
24 214 exploring the more general paradox that a conspicuously 'unnatural' intervention – the fencing
25 215 of landscape-scale reserves containing highly mobile species – may be an effective means to
26 216 restore both species and their associated ecological processes in human dominated
27 217 landscapes.

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38 219 We hypothesize that:

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40 220 [H1] Reintroduction of a viable wolf population may not necessarily result in the
41 221 reestablishment of the potential for density-mediated strong top-down forcing
42 222 upon red deer;

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44 223 [H2] If natural maximum pack densities are too low, this will limit maximum wolf
45 224 density and reduce the strength of density-mediated top-down forcing;

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47 225 [H3] Lower initial and maximum ungulate densities will increase the probability of
48 226 strong top-down forcing by reducing the maximum wolf density required to
49 227 exert a strong effect; and

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52 228 [H4] Increasing reserve boundary permeability to dispersing wolves will decrease
53 229 the maximum attainable long-term wolf density, increasing time needed to
54 230 achieve a long-term non-zero wolf density, and reducing the strength of top-
55 231 down forcing.

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233 **Methods**234 *Simulation model structure*

235 Individual based models (IBM) have proven useful for population viability assessments of
236 small wolf populations (Nilsen et al. 2007; Bull et al. 2009; Sandom et al. 2012). We
237 developed an IBM to explore what influence variously permeable perimeter barriers would
238 have in allowing a reintroduced wolf population to be both viable and have the potential to
239 exert density-dependent top-down forcing on red deer. The novelty of our approach was to
240 subject dispersing wolves to different constraints, exploring the importance of wolf and red
241 deer density thresholds in this regard.

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243 An existing and tested IBM for a hypothetical wolf population in a limited area reserve in
244 Scotland (Nilsen et al. 2007) was used to explore our hypotheses. The IBM had subsequently
245 been adapted for the case of the Alladale reserve in the Scottish Highlands, to explore the
246 relationship between predators and prey in a finite reserve of 1200 km² (Sandom et al. 2012).
247 Here, we develop new model functions relating to dispersing wolves and intraspecific
248 competition, so as to simulate the effect of changing the permeability of the reserve boundary.
249 The results were analysed to differentiate between simply restoring a viable wolf population
250 (classical reintroduction) and restoring one also capable of exerting strong density-dependent
251 top-down forcing (trophic rewilding).

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253 The model was coded in 'R' (R Core Development Team 2016). The structure and life history
254 traits of the modelled wolf population are outlined in the Appendices (Appendix S1, Fig. S1).
255 The population consists of individual wolves at different life stages, grouped into packs,
256 undergoing four life history stages every time step (one year). The stages were: survival;
257 reproduction; dispersal; and, the formation of new packs. Parameter values used are
258 described in the Appendices (Table S1). A sensitivity analysis was undertaken to determine
259 how sensitive our results were to prey carrying capacity and wolf kill and dispersal rates.

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

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269 We simulated the impact of altering the conditions affecting dispersing wolves, given
270 uncertain ecological limits on maximum attainable pack density. The propensity of dispersers
271 to leave the reserve was treated as representative of the permeability of the reserve
272 boundary. In this context, dispersing wolves were any wolves that left a pack and had the
273 potential to form a new pack. Sub-adult wolves had some probability of leaving their natal
274 pack in any year (Appendix S1). If both alpha adults in any one pack died, the remaining
275 individuals in that pack became dispersers. For each scenario modelled, a maximum pack
276 density was selected. The probability of wolves establishing a new pack decreased linearly as
277 pack density increased (Appendix S1), representing increased intraspecific competition (Mech
278 & Boitani 2003). Thus, even with sufficient prey, the wolf population was unable to expand
279 without limit, recognizing that density dependence plays a role in survival rates. There was
280 nothing in the model to limit the number of wolves allowed in any one pack, except the annual
281 probability that individual wolves dispersed or died.

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

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

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5 307 Wolf and red deer population trajectories were simulated over a 100-year period, which was
6 308 considered sufficient to allow both the viability of the wolf population (with respects to the four
7 309 basic life history functions) and the effects of top-down forcing to become apparent. As the
8 310 model was stochastic, each simulation was repeated 100 times to capture average behaviour.
9 311 Key output variables (red deer density, wolf density, wolf pack density, number of red deer
10 312 predated upon, and number of wolves dispersing) were recorded for each time step. For
11 313 every 100-year simulation, it was then possible to establish the minimum and maximum red
12 314 deer densities, minimum and maximum wolf population and pack densities, and the year in
13 315 which these minima and maxima occurred. Both behaviour and predator-prey population
14 316 dynamics were assessed by plotting these data and examining non-linear responses and
15 317 thresholds.

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22 319 The hypotheses [H1-4] primarily involved exploring the effect of a perimeter fence (or some
23 320 other kind of permeable barrier) in restoring the process of predation. The IBM used to test
24 321 the hypotheses has been shown to capture wolf population dynamics, but is non-spatial.
25 322 Hence, the implementation of a fence was tested via proxy, by varying dispersal dynamics.
26 323 During simulations in which the fence was considered an absolute barrier to movement,
27 324 dispersing wolves could form packs given any vacant territories in the reserve, die, or (to an
28 325 extent determined by the competition function) increase the wolf pack density, but could not
29 326 leave the reserve. In simulations in which the reserve boundary was permeable, then the
30 327 permeability was the likelihood that dispersing wolves would leave the reserve.

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37 329 The model was validated against wolf population reintroduction dynamics in YNP, US., which
38 330 offers a unique opportunity for evaluation as it is a well monitored reintroduction with annually
39 331 published reports on wolf and prey population abundance. We used the same demographic
40 332 structure for wolf population re-introduced to YNP as a starting population in the model, and
41 333 then simulated the expected population trajectory. This trajectory was compared against the
42 334 observed historical YNP population trajectory since re-introduction. As conditions vary
43 335 between the hypothetical Scottish example and YNP this comparison was a test for the
44 336 general plausibility of the model only.

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49 338 **Results**

50 339 *Model validation*

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54 340 Simulated results compared favourably with empirical YNP wolf and red deer population
55 341 dynamics (Fig. S2). A similar rate of initial growth and maximum wolf density was recorded for

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3 342 the observed population in YNP's Northern Range and our simulated population using the
4 343 same starting red deer density (12 per km²), 0% – 10% boundary permeability and a
5 344 maximum pack density of 18.3 packs per 1000 km² (Fig. S2).

7 345 As would be expected, higher maximum wolf density generally corresponded with higher wolf
8 346 pack density, but only up to a certain threshold. The threshold was dependent upon the initial
9 347 deer density, i.e. prey availability (Fig. 2a). This facet of our model output indicates that with
11 348 greater prey availability comes a greater propensity for wolves to stay in their natal packs
12 349 within our simulated population.

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16 17 351 *Importance of wolf density for the strength of top-down forcing*

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19 352 Crucially, whilst the model does predict that viable wolf populations are able to establish in the
20 353 hypothetical Scottish reserve (Sandom et al. 2012), we found that wolves did not exhibit
21 354 strong top-down forcing upon the red deer population at lower maximum wolf pack densities
22 355 (Fig. 2b). This supports our contention that a wolf population large enough to be self-
23 356 sustaining does not necessarily have the potential to exert strong density-dependent top-
24 357 down forcing (H1).

27 358 In scenarios in which a higher maximum pack density was permitted, the minimum red deer
28 359 density was lower (Fig. 2b), supporting H2. The relationship between minimum deer density
29 360 and maximum pack density was non-linear, with strong top-down forcing exerted only past
30 361 certain thresholds of wolf pack density (Fig. 2b). Such a result might be expected since the
31 362 deer population was strongly dependent upon reproduction and mortality, so the threshold
32 363 would be the point at which the wolves were numerous enough in relation to deer that the kill
33 364 rate began to overhaul reproduction rates. The lower the value for initial deer density used in
34 365 the simulation, the lower that wolf pack density had to be in order to achieve strong density-
35 366 dependent effects (Fig. 2b), which provides support for H3.

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41 42 368 *Permeability of boundary, and wolf density*

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44 369 Boundary permeability had a strong influence on whether either or both reintroduction
45 370 objectives were achieved [H4]. Increasing boundary permeability: a) decreased maximum
46 371 wolf densities, b) increased time taken to achieve maximum non-zero wolf density, c) reduced
47 372 the wolves capacity to exert strong top-down forcing, and d) increased the probability of wolf
48 373 survival until the loss of dispersers was too great to support the population (Fig. 3a-3d).
49 374 Maximum wolf density decreased rapidly when the population lost more than 50% of
50 375 dispersers (Fig. 3a).

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3 377 Conversely, the time taken for the wolf population to achieve maximum density demonstrated
4 378 a unimodal response to boundary permeability when maximum pack density was ≥ 15 packs
5 379 per 1000 km² (Fig. 3b). The unimodal response in this variable arose because, at lower
6 380 boundary permeability, the wolf population rose quickly and then collapsed due to lack of
7 381 prey. At higher boundary permeability, the wolves never attained a high population at all, so
8 382 again the maximum population was effectively achieved early on in the simulation. At high
9 383 and low boundary permeability, time to maximum wolf density was at a minimum, and at a
10 384 maximum at intermediate permeability. This unimodal response (Fig. 3b) appeared to reflect
11 385 the interaction between decreasing rate of population growth and a decreasing maximum
12 386 population, with increasing boundary permeability. With a low limit (≤ 11.6 per 1000 km²) on
13 387 wolf pack densities, the response was not unimodal – as the wolf population never reached
14 388 sufficient density to cause a collapse in deer numbers – and time taken to reach maximum
15 389 wolf density in that run of the model decreased with increased boundary permeability. These
16 390 model outputs support H4 in that attainable wolf density decreased with increased boundary
17 391 permeability, and that the rate of population growth, if the population could grow, decreased
18 392 with increased boundary permeability.

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20 394 Minimum red deer density and maximum wolf density, under the 18.3 maximum pack density
21 395 scenario, were negatively correlated. This again suggested that beyond a threshold wolf
22 396 density, there was significantly increased potential for top-down forcing on red deer
23 397 populations (Fig. 4a). A wolf density > 80 individuals per 1000 km² was required (but not
24 398 guaranteed) to exert strong top-down forcing. The variability in response to high wolf densities
25 399 may be explained by the decreasing rate at which the wolf population grows under increased
26 400 boundary permeability. In those simulations in which wolves did strongly reduce deer density,
27 401 the time taken for wolf population to reach a maximum was an important factor and was
28 402 generally short (Fig. 4b).

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30 404 Wolves only exerted strong top-down forcing of red deer when pack densities could achieve
31 405 15 packs per 1000 km² or greater (Fig. 3c). When pack density was restricted to no more than
32 406 8.3 packs per 1000 km² the wolf population had almost no impact on deer density. An
33 407 intermediate scenario was recorded when pack density could achieve 11.3 packs per 1000
34 408 km² or higher. However, top-down forcing was regulated by boundary permeability in a
35 409 sigmoid relationship. When 60% or more of dispersing wolves were lost, no impact on deer
36 410 density was recorded. The degree to which boundary permeability limited top-down forcing
37 411 was related to maximum pack density, with progressively less impact on the deer population
38 412 with reduced maximum pack density.

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3 414 Minimum wolf density had a unimodal relationship with boundary permeability (Fig. 3d). At low
4 415 boundary permeability, minimum wolf density strongly reflected the strength of top-down
5 416 forcing of prey density, with very low minimum deer densities corresponding to wolf extinction.
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7 417 Minimum wolf density decreased from a maximum at around 30 to 50% boundary
8 418 permeability depending on maximum pack density setting. The wolf population could not
9 419 survive losing 70% or more of the dispersing population yearly.

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12 13 421 *Sensitivity analysis*

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15 422 An extensive sensitivity analysis using this model structure and set of parameters has already
16 423 been completed (Sandom et al. 2012). However, we carried out a simple sensitivity analysis
17 424 here, given that modifications had been made to the original code. The main findings were
18 425 that varying the asymptotic kill rate (a), deer starting population and carrying capacity had a
19 426 strong impact on the strength of top-down forcing (Figs. S3, S4), but varying dispersal rates
20 427 had no noticeable impact on the strength of top-down forcing of deer density (Fig. S5).

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25 26 429 **Discussion**

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28 430 The outcomes of our simulations support the suggestion that restoring a viable wolf
29 431 population does not necessarily restore the potential for density-dependent top-down forcing
30 432 upon prey. This has implications for the management of apex predators in protected areas in
31 433 human-dominated ecosystems. The outcomes of our simulations, in terms of the strength of
32 434 top-down forcing, were sensitive to at least four important factors: prey carrying capacity,
33 435 maximum wolf pack density, kill rate, and boundary permeability. The latter relates to our
34 436 main objective, i.e. exploring whether the permeability of a reserve boundary (i.e. barrier)
35 437 could affect the ability of predators to exert strong density-dependent top-down forcing.

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40 41 439 *Possible scenarios following reintroduction*

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43 440 The results can be grouped into four probable ecological outcomes following wolf
44 441 reintroduction, dependent upon the boundary permeability and assuming maximum wolf pack
45 442 density is only limited by prey availability:

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48 443 i. Very low permeability (0.00 - 0.20), e.g. an impassable boundary fence. This would
49 444 promote rapid wolf population growth and high maximum wolf densities, although
50 445 strong top-down forcing in the red deer population caused prey population collapse
51 446 and consequent wolf extinction. This scenario might be expected in an unmanaged
52 447 fenced reserve in the Scottish Highlands.
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54 448 ii. Low permeability (0.20 – 0.35), e.g. a less effective physical boundary,
55 449 metapopulation management, or less favourable, but not intolerable conditions
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3 450 surrounding the reintroduction site. Rapid wolf population growth and high wolf
4 451 population maxima would exert density-dependent top-down forcing on deer, but the
5 452 strength of the effect decreases with increasing boundary permeability, in turn
6 453 reducing probability of wolf extinction, perhaps the ideal scenario from a trophic
7 454 rewilding standpoint.

8 455 iii. High permeability (0.35 - 0.60), e.g. up to sixty percent of all dispersing wolves leave
9 456 the reserve or are killed as a result of intraspecific competition. High losses of
10 457 dispersers from the population would mean relatively slow wolf population growth rate
11 458 and a low maximum density, preventing the possibility of strong density-dependent
12 459 top-down forcing upon the red deer population. However, wolf density would still be
13 460 sufficient for a sustained wolf population.

14 461 iv. Very high permeability (0.60 – 1.00), e.g. leaving the reserve was appealing to
15 462 dispersers. Insufficient individuals would remain in the reserve to sustain a wolf
16 463 population.

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24 465 The complexity of wolf-prey systems, with each system often having a unique combination of
25 466 relevant social, ecological and physical factors, probably explains why there is no scientific
26 467 consensus on the role of wolf predation in prey population dynamics (Mech & Peterson 2003;
27 468 Peterson et al. 2014). However, there are 'real world' examples, which offer indications of
28 469 when wolves may influence their prey. The Isle Royale National Park (IRNP) wolf population
29 470 is entirely contained without any other major ungulate predator present. The population
30 471 crashed from high densities (92 wolves per 1000 km²) as a result of disease during 1980-82,
31 472 which coincided with a marked rise in moose calves/cow ratio (from 22/100 cows to 60/100
32 473 cows; Peterson & Page 1988) and, over the following fifteen years with a continuingly very
33 474 low wolf density, with the moose density markedly rising to 4/km² – ten times usual North
34 475 American mainland densities (Messier 1994). The response of the IRNP moose to an
35 476 expanding wolf population is less clear. A rising wolf population in the early and mid-seventies
36 477 was followed, with a lag of a year or two, by a decline in the moose population (Peterson &
37 478 Page 1988), but the same rise in the wolf population was associated with a preceding rise in
38 479 moose numbers. Thus, it seems that whilst moose in IRNP exhibit strong direct density
39 480 dependence during years of wolf decline, they exhibit only weak direct density dependence
40 481 but strong delayed density dependence during years of wolf increase (Mech & Peterson
41 482 2003). It is clear that predation by wolves on Isle Royale moose is strongly additive – annual
42 483 variation in predation rate is a major factor influencing moose population growth rate ($R^2 =$
43 484 0.55, Vucetich 2017).

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51 485 Determining the rate of dispersal in real world examples is difficult. In Minnesota, Fuller
52 486 (1989) reviewed dispersal rates that ranged between 21% and 35%, but in a population
53 487 where 80% of wolf mortality was anthropogenic. Pletscher et al. (1997) record a dispersal rate
54 488 of 44%, including many wolves leaving the relative safety of Glacier National Park for areas

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3 489 where hunting was legal. Our modelling suggests that higher dispersal rates (i.e. when the
4 490 boundary is more permeable) are not conducive to strong top-down forcing upon deer when
5 491 deer density is ≥ 20 per km^2 . Correspondingly, Pletscher et al. (1997) recorded wolf densities
6 492 of 35 per 1000 km^2 12 years after re-colonisation. However, dispersal rates in Minnesota
7 493 might have allowed strong top-down forcing at lower prey densities, if wolf persecution had
8 494 been limited. Behaviourally-mediated trophic cascades have been recorded in the region
9 495 (Callan et al. 2013). In Canada, Stronen et al. (2012) found that there was limited gene flow
10 496 between the wolves of Riding Mountain National Park (RMNP) and other wolf populations in
11 497 protected areas in the region, and reported no successful wolf dispersal from RMNP over
12 498 several multi-year tracking studies since 1974. There are no physical barriers separating the
13 499 populations, but agriculture now dominates the region, such that RMNP is considered a
14 500 'wilderness island in an agricultural region'. Parks Canada recorded a maximum wolf
15 501 population of 113 individuals in 2011/12, a density of ~ 40 wolves per 1000 km^2 . In Finland,
16 502 Kojola et al. (2006) reported that all wolves dispersing from an expanding wolf population into
17 503 a reindeer management area were shot before being able to reproduce, but 10 out of 16 bred
18 504 successfully when dispersing outside this area. In Białowieża National Park, surrounding
19 505 human land use and activity has created a spatiotemporal barrier to wolf movement patterns
20 506 (Theuerkauf et al. 2003), indicating human land use can act as a dispersal barrier in some
21 507 circumstances.
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31 *Important considerations*

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33 510 Intraspecific wolf behaviour would be similarly strong determinants of wolf population growth
34 511 alongside dispersal dynamics. These are not issues that the model was designed to explore –
35 512 the focus was rather on the capacity of changing dispersal rates and reserve boundary
36 513 conditions to bring about different predator-prey interaction scenarios. It is likely that the
37 514 results would be modified if these additional factors were considered. Similarly, disease is a
38 515 factor that might have a particularly strong influence upon rewilding efforts (Nogues-Bravo et
39 516 al. 2016), that we have not included in our model. The reality is that some form of
40 517 management for disease may well be required – although given that the situation we model is
41 518 of large wild predators in a large fenced reserve, management of some form would likely be
42 519 required in any case.
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47 520 As mentioned previously, Isle Royale offers an example of a natural island harbouring wolves
48 521 and the process of predation at a scale that is theoretically achievable in Scotland. However,
49 522 it is worth noting that these wolves are now suffering from inbreeding depression and are on
50 523 the brink of extinction (Räikkönen et al. 2009). A fenced reserve would ideally be considerably
51 524 larger than Isle Royale and managed as part of a metapopulation to limit the threat of
52 525 inbreeding, as has been employed with other isolated large carnivore populations (e.g.
53 526 Johnson et al. 2010).
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3 527 Red deer are a herding species that alter distribution with habitat heterogeneity, seasonality
4 528 and predation. In the winter, aggregations of up to 1000 animals may occupy restricted
5 529 ranges (Walker & Nowak 1991). Behaviourally-mediated effects of wolves may create a
6 530 'landscape of fear', i.e. a landscape in which ungulates disperse to areas of reduced
7 531 predation risk, such as boundary zones between territories (Hoskinson & Mech 1976;
8 532 Hernandez & Laundre 2005; Valeix et al. 2009). A heterogeneous distribution of ungulates
9 533 will have a spatially uneven impact upon the landscape, potentially allowing woodland
10 534 regeneration in some areas while keeping others open. Such heterogeneity can be beneficial
11 535 to biodiversity overall and may be close to a 'natural' situation in Northwest Europe (Svenning
12 536 2002; Sandom et al. 2014). In this way, the indirect effects of wolves upon prey could also be
13 537 seen as positive for conservation and land management, regardless of whether density-
14 538 dependent top-down forcing occurs. The further question of how the presence of an artificial
15 539 barrier (i.e. a fence) might interplay with fear dynamics in such a system is an interesting one,
16 540 and a potential direction for future research, but is beyond the scope of this paper.

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23 24 542 *Implications for wolf reintroduction to the Scottish Highlands*

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26 543 The outcomes of the simulation model we present do not necessarily predict exactly what
27 544 would happen to a wolf population in the Highlands – rather, they indicate likely qualitative
28 545 trends, and highlight those facets of the system that would need to be closely monitored and
29 546 potentially managed. These include the density of prey before wolves were reintroduced, the
30 547 relative densities of wolves and prey, the amount of territory occupied by each pack, and the
31 548 permeability of the reserve boundary i.e. the rate at which dispersers are lost from the
32 549 population. Based upon these results, enclosing such a wolf population within an
33 550 impermeable or semi-permeable barrier (or managed as part of a wider metapopulation)
34 551 might be necessary to allow wolves the potential of sufficiently high densities to reduce red
35 552 deer numbers. However, a completely impassable fence could also result in deer density
36 553 being sufficiently reduced to cause a collapse in the wolf population, i.e. scenario (i) above.
37 554 Arguably, the ideal scenario from a conservation standpoint in human dominated landscapes,
38 555 i.e. scenario (ii) above, would require either a reserve boundary that enabled some dispersing
39 556 wolves to escape, or the intentional removal of a number of wolves from the reserve every
40 557 generation. While our modelling offers insights into what might happen the next step would be
41 558 to test these ideas by creating an enclosed reserve, reintroducing wolves, and closely
42 559 monitoring the system (Manning et al. 2009). The main conclusion we draw here is that not
43 560 only is a viable wolf population possible in a fenced reserve, but that such a population could
44 561 result in the restoration of density-dependent trophic interactions, with likely positive
45 562 biodiversity effects. More generally, barriers in some form might have a more important role to
46 563 play in establishing modern wild land than might be assumed.

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3 565 *Implications for trophic rewilding*

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5 566 Trophic rewilding is a process of establishing ecosystems (through species reintroductions
6 567 that restore top-down trophic effects) that 1) reduces or removes the need for on-going
7 568 human management, and 2) make an important contribution to biodiversity and ecosystem
8 569 service restoration and conservation (Svenning et al. 2016; Sandom & Wynne-Jones in
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10 570 press). Our results highlight that in spatially restricted rewilding projects in human-dominated
11 571 landscapes, boundary effects have important implications for the functioning of ecological
12 572 processes and so ecosystem outcomes. As a result, some management of rewilding projects
13 573 might be needed to replicate ecological processes that cannot be restored. In our example,
14 574 where there is no perimeter barrier, human influences on predation should be considered and
15 575 potentially managed, and where there is a perimeter barrier, similar consideration is needed
16 576 for dispersal dynamics. This type of compromise is likely to be required in **many** rewilding
17 577 projects in human-dominated landscapes, and the level of compromise is likely to increase as
18 578 the spatial scales of rewilding projects decrease.

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26
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44 593 **References**

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- 1
2
3 594 Angermeier PL (2000) The Natural Imperative for Biological Conservation. *Conservation*
4 595 *Biology* 14:373-381
- 5 596 Apollonio M, Andersen R, Putman R. (2010) European Ungulates and Their Management in
6 597 the 21st Century. Cambridge University Press,
- 7 598 Beschta RL, Ripple WJ (2013) Are wolves saving Yellowstone's aspen? A landscape-level test
8 599 of a behaviorally mediated trophic cascade: comment. *Ecology* 94:1420-1425
- 9 600 Bull J, Nilsen EB, Mysterud A, Milner-Gulland EJ (2009) Survival on the border: a population
10 601 model to evaluate management options for Norway's wolves *Canis lupus*. *Wildlife*
11 602 *Biology* 15:412-424
- 12 603 Bull JW, Suttle KB, Singh NJ, Milner-Gulland EJ (2013) Conservation when nothing stands still:
13 604 moving targets and biodiversity offsets. *Frontiers in Ecology and the Environment*
14 605 11:203-210
- 15 606 Callan R, Nibbelink NP, Rooney TP, Wiedenhoef JE, Wydeven AP (2013) Recolonizing wolves
16 607 trigger a trophic cascade in Wisconsin (USA). *Journal of Ecology* 101:837-845
- 17 608 Chapron G, Kaczensky P, Linnell JDC, Von Arx M, Huber D, Andren H, Lopez-Bao JV, Adamec
18 609 M, Alvares F, Anders O, Balciuskas L, Balys V, Bedo P, Bego F, Blanco JC,
19 610 Breitenmoser U, Broseth H, Bufka L, Bunikyte R, Ciucci P, Dutsov A, Engleder T,
20 611 Fuxjager C, Groff C, Holmala K, Hoxha B, Iliopoulos Y, Ionescu O, Jeremic J, Jerina K,
21 612 Kluth G, Knauer F, Kojola I, Kos I, Krofel M, Kubala J, Kunovac S, Kusak J, Kutal M,
22 613 Liberg O, Majic A, Mannil P, Manz R, Marboutin E, Marucco F, Melovski D, Mersini K,
23 614 Mertzanis Y, Myslajek RW, Nowak S, Odden J, Ozolins J, Palomero G, Paunovic M,
24 615 Persson J, Potocnik H, Quenette PY, Rauer G, Reinhardt I, Rigg R, Ryser A, Salvatori V,
25 616 Skrbinek T, Stojanov A, Swenson JE, Szemethy L, Trajce A, Tsingarska-Sedefcheva E,
26 617 Vana M, Veeroja R, Wabakken P, Wolf M, Wolf S, Zimmermann F, Zlatanova
27 618 D, Boitani L (2014) Recovery of large carnivores in Europe's modern human-
28 619 dominated landscapes. *Science* 346:1517-1519
- 29 620 Darimont CT, Fox CH, Bryan HM, Reimchen TE (2015) The unique ecology of human
30 621 predators. *Science* 349:858-860
- 31 622 Delibes M, Gaona P, Ferreras P (2001) Effects of an attractive sink leading into maladaptive
32 623 habitat selection. *American Naturalist* 158:277-285
- 33 624 Donlan J (2005) Re-wilding North America. *Nature* 436:913-914
- 34 625 Dorresteijn I, Schultner J, Nimmo DG, Fischer J, Hanspach J, Kuemmerle T, Kehoe L, Ritchie EG
35 626 (2015) Incorporating anthropogenic effects into trophic ecology: predator-prey
36 627 interactions in a human-dominated landscape. *Proceedings of the Royal Society B-*
37 628 *Biological Sciences* 282:105-112
- 38 629 Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE,
39 630 Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pritchard EK, Ripple
40 631 WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soule ME, Virtanen
41 632 R, Wardle DA (2011) Trophic Downgrading of Planet Earth. *Science* 333:301-306
- 42 633 Fuller TK (1989) Population-Dynamics of Wolves in North-Central Minnesota. *Wildlife*
43 634 *Monographs*:1-41
- 44 635 Gundersen G, Johannesen E, Andreassen HP, Ims RA (2001) Source-sink dynamics: how sinks
45 636 affect demography of sources. *Ecology Letters* 4:14-21
- 46 637 Hayward MW, Hayward GJ, Druce DJ, Kerley GIH (2009) Do fences constrain predator
47 638 movements on an evolutionary scale? Home range, food intake and movement
48 639 patterns of large predators reintroduced to Addo Elephant National Park, South
49 640 Africa. *Biodiversity and Conservation* 18:887-904
- 50 641 Hayward MW, Kerley GIH (2009) Fencing for conservation: Restriction of evolutionary
51 642 potential or a riposte to threatening processes? *Biological Conservation* 142:1-13
- 52
53
54
55
56
57
58
59
60

- 1
2
3 643 Hernandez L,Laundre JW (2005) Foraging in the 'landscape of fear' and its implications for
4 644 habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife*
5 645 *Biology* 11:215-220
6 646 Hobbs R (2009) Woodland restoration in Scotland: Ecology, history, culture, economics,
7 647 politics and change. *Journal of Environmental Management* 90:2857-2865
8 648 Hopcraft JGC, Olff H,Sinclair A (2010) Herbivores, resources and risks: alternating regulation
9 649 along primary environmental gradients in savannas. *Trends in Ecology & Evolution*
10 650 25:119-128
11 651 Hoskinson RL,Mech LD (1976) White-Tailed Deer Migration and Its Role in Wolf Predation.
12 652 *Journal Of Wildlife Management* 40:429-441
13 653 Iucn/Scs. (2013) Guidelines for Reintroductions and Other Conservation
14 654 Translocations Gland, Switzerland. IUCN Species Survival Commission
15 655 Jackson CR, Mcnutt JW,Apps PJ (2012) Managing the ranging behaviour of African wild dogs
16 656 (*Lycaon pictus*) using translocated scent marks. *Wildlife Research* 39:31-34
17 657 Johnson WE, Onorato DP, Roelke ME, Land ED, Cunningham M, Belden RC, McBride R,
18 658 Jansen D, Lotz M, Shindle D, Howard J, Wildt DE, Penfold LM, Hostetler JA, Oli
19 659 MK,O'brien SJ (2010) Genetic Restoration of the Florida Panther. *Science* 329:1641-
20 660 1645
21 661 Jones IL, Bull JW, Milner-Gulland EJ, Esipov AV,Suttle KB (2014) Quantifying habitat impacts
22 662 of natural gas infrastructure to facilitate biodiversity offsetting. *Ecology and*
23 663 *Evolution* 4:79-90
24 664 Kauffman MJ, Brodie JF,Jules ES (2010) Are wolves saving Yellowstone's aspen? A landscape-
25 665 level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742-2755
26 666 Kauffman MJ, Brodie JF,Jules ES (2013) Are wolves saving Yellowstone's aspen? A landscape-
27 667 level test of a behaviorally mediated trophic cascade: reply. *Ecology* 94:1425-1431
28 668 King LE, Douglas-Hamilton I,Vollrath F (2007) African elephants run from the sound of
29 669 disturbed bees. *Current Biology* 17:R832-R833
30 670 Kojola I, Aspi J, Hakala A, Heikkinen S, Ilmoni C,Ronkainen S (2006) Dispersal in an expanding
31 671 wolf population in Finland. *Journal of Mammalogy* 87:281-286
32 672 Kuijper DPJ, Sahlen E, Elmhagen B, Chamaille-Jammes S, Sand H, Lone K,Cromsigt JPGM
33 673 (2016) Paws without claws? Ecological effects of large carnivores in anthropogenic
34 674 landscapes. *Proceedings of the Royal Society B-Biological Sciences* 283
35 675 Liberg O, Chapron G, Wabakken P, Pedersen HC, Hobbs NT,Sand H (2012) Shoot, shovel and
36 676 shut up: cryptic poaching slows restoration of a large carnivore in Europe.
37 677 *Proceedings of the Royal Society B-Biological Sciences* 279:910-915
38 678 Licht DS, Millspaugh JJ, Kunkel KE, Kochanny CO,Peterson RO (2010) Using Small Populations
39 679 of Wolves for Ecosystem Restoration and Stewardship. *Bioscience* 60:147-153
40 680 Linnell JDC, J. O,Mertens A (2012) Mitigation methods for conflicts associated with carnivore
41 681 depredation on livestock. Pages 314-333 In: Boitani L and Powell RA, (eds) *Carnivore*
42 682 *ecology and conservation: A handbook of techniques*. Oxford University Press
43 683 Linnell JDC, Salvatori V,Boitani L. (2008) Guidelines for population level management plans
44 684 for large carnivores in Europe. A Large Carnivore Initiative for Europe report
45 685 prepared for the European Commission. European Commission
46 686 Loveridge AJ, Wang SW, Frank L,Seidensticker J (2010) People and wild felids: conservation
47 687 of cats and management of conflicts. Pages 161-196 In: Macdonald DW and
48 688 Loveridge AJ, (eds) *Biology and conservation of wild felids*. Oxford University Press.,
49 689 New York
50 690 Macdonald DW, Boitani L, Dinerstein E, Fritz H,Wrangham R (2014) Conserving large
51 691 mammals: are they a special case? In: Macdonald DW and Willis KJ, (eds) *Key Topics*
52 692 *in Conservation Biology* 2. John Wiley & Sons

- 1
2
3 693 Macdonald DW, Carr GM (1989) Food security and the rewards of tolerance. Pages 75-99 In:
4 694 Standen V and Foley R, (eds) Comparative socioecology: the behavioural ecology of
5 695 humans and other mammals. Blackwell Scientific Publications, Oxford
6 696 Manning AD, Gordon IJ, Ripple WJ (2009) Restoring landscapes of fear with wolves in the
7 697 Scottish Highlands. *Biological Conservation* 142:2314-2321
8 698 Mech D, Boitani L. (2003) *Wolves: Behaviour, Ecology & Conservation*. The University of
9 699 Chicago Press, Chicago
10 700 Mech LD, Boitani L, (IUCN Ssc Wolf Specialist Group), (2010) *Canis lupus*. The IUCN Red List of
11 701 Threatened Species 2010 URL [http://dx.doi.org/10.2305/IUCN.UK.2010-](http://dx.doi.org/10.2305/IUCN.UK.2010-4.RLTS.T3746A10049204.en)
12 702 [4.RLTS.T3746A10049204.en](http://dx.doi.org/10.2305/IUCN.UK.2010-4.RLTS.T3746A10049204.en) (accessed 22 February 2018
13 703 Mech LD, Peterson RO (2003) Wolf-prey relations. Pages 131-157 In: Mech LD and Boitani L,
14 704 (eds) *Wolves: behavior, ecology, and conservation*. University of Chicago Press
15 705 Messier F (1994) Ungulate Population-Models with Predation - a Case-Study with the North-
16 706 American Moose. *Ecology* 75:478-488
17 707 Nilsen EB, Milner-Gulland EJ, Schofield L, Myrseth A, Stenseth NC, Coulson T (2007) Wolf
18 708 reintroduction to Scotland: public attitudes and consequences for red deer
19 709 management. *Proceedings of the Royal Society B: Biological Sciences* 274:995-1003
20 710 Nogues-Bravo D, Simberloff D, Rahbek C, Sanders NJ (2016) Rewilding is the new Pandora's
21 711 box in conservation. *Current Biology* 26:R87-R91
22 712 Osborn FV, Parker GE (2003) Towards an integrated approach for reducing the conflict
23 713 between elephants and people: a review of current research. *Oryx* 37:80-84
24 714 Packer C, Loveridge A, Canney S, Caro T, Garnett ST, Pfeifer M, Zander KK, Swanson A,
25 715 Macnulty D, Balme G, Bauer H, Begg CM, Begg KS, Bhalla S, Bissett C, Bodasing T,
26 716 Brink H, Burger A, Burton AC, Clegg B, Dell S, Delsink A, Dickerson T, Dloniak SM,
27 717 Druce D, Frank L, Funston P, Gichohi N, Groom R, Hanekom C, Heath B, Hunter L,
28 718 Deiongh HH, Joubert CJ, Kasiki SM, Kissui B, Knocker W, Leathem B, Lindsey PA,
29 719 Maclennan SD, Mcnutt JW, Miller SM, Naylor S, Nel P, Ng'weno C, Nicholls K, Ogotu
30 720 JO, Okot-Omoya E, Patterson BD, Plumpton A, Salerno J, Skinner K, Slotow R,
31 721 Sogbohossou EA, Stratford KJ, Winterbach C, Winterbach H, Polasky S (2013)
32 722 Conserving large carnivores: dollars and fence. *Ecology Letters* 16:635-641
33 723 Peterson RO, Page RE (1988) The rise and fall of Isle Royale Wolves, 1975-1986. *Journal of*
34 724 *Mammalogy* 69:89-99
35 725 Peterson RO, Vucetich JA, Bump JM, Smith DW (2014) Trophic Cascades in a Multicausal
36 726 World: Isle Royale and Yellowstone. *Annual Review of Ecology, Evolution, and*
37 727 *Systematics*, Vol 45 45:325-+
38 728 Pletscher DH, Ream RR, Boyd DK, Fairchild MW, Kunkel KE (1997) Population dynamics of a
39 729 recolonizing wolf population. *Journal Of Wildlife Management* 61:459-465
40 730 R Core Development Team (2016) R: A language and environment for statistical computing v.
41 731 3.3.2. R Foundation for Statistical Computing, Vienna, Austria
42 732 Räikkönen J, Vucetich JA, Peterson RO, Nelson MP (2009) Congenital bone deformities and
43 733 the inbred wolves (*Canis lupus*) of Isle Royale. *Biological Conservation* 142:1025-
44 734 1031
45 735 Ripple WJ, Beschta RL (2012) Trophic cascades in Yellowstone: The first 15 years after wolf
46 736 reintroduction. *Biological Conservation* 145:205-213
47 737 Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M, Hayward MW, Kerley GIH,
48 738 Levi T, Lindsey PA, Macdonald DW, Malhi Y, Painter LE, Sandom CJ, Terborgh J,
49 739 E., Van Valkenburgh B (2015) Collapse of the world's largest herbivores. *Science*
50 740 *Advances* 1:e1400103
51 741 Rubenstein DR, Rubenstein DI (2016) From Pleistocene to trophic rewilding: A wolf in sheep's
52 742 clothing. *Proceedings of the National Academy of Sciences of the United States of*
53 743 *America* 113:E1-E1

- 1
2
3 744 Sandom C, Bull J, Canney S, Macdonald DW (2012) Exploring the value of wolves (*Canis lupus*)
4 745 in landscape-scale fenced reserves for ecological restoration in the Scottish
5 746 Highlands. Pages 245-276 In: *Fencing for Conservation*. Springer
6 747 Sandom C, Donlan CJ, Svenning JC, Hansen D (2013) Rewilding. *Key Topics in Conservation*
7 748 *Biology* 2:430-451
8 749 Sandom CJ, Ejrnaes R, Hansen MDD, Svenning JC (2014) High herbivore density associated
9 750 with vegetation diversity in interglacial ecosystems. *Proceedings of the National*
10 751 *Academy of Sciences of the United States of America* 111:4162-4167
11 752 Sandom CJ, Wynne-Jones S (in press) Rewilding a country: Britain as a case study In: Pettorelli
12 753 N, Durant S and Du Toit J, (eds) *Rewilding*. Cambridge University Press
13 754 Soulé M, Noss R (1998) Rewilding and Biodiversity: Complementary Goals for Continental
14 755 Conservation. *Wild Earth*:1-11
15 756 Stronen AV, Forbes GJ, Paquet PC, Goulet G, Sallows T, Musiani M (2012) Dispersal in a plain
16 757 landscape: short-distance genetic differentiation in southwestern Manitoba wolves,
17 758 Canada. *Conservation Genetics* 13:359-371
18 759 Svenning JC (2002) A review of natural vegetation openness in north-western Europe.
19 760 *Biological Conservation* 104:133-148
20 761 Svenning JC, Pedersen PBM, Donlan CJ, Ejrnaes R, Faurby S, Galetti M, Hansen DM, Sandel B,
21 762 Sandom CJ, Terborgh JW, Vera FWM (2016) Science for a wilder Anthropocene:
22 763 Synthesis and future directions for trophic rewilding research. *Proceedings of the*
23 764 *National Academy of Sciences of the United States of America* 113:898-906
24 765 Theuerkauf J, Jedrzejewski W, Schmidt K, Gula R (2003) Spatiotemporal segregation of
25 766 wolves from humans in the Bialowieza Forest (Poland). *Journal Of Wildlife*
26 767 *Management* 67:706-716
27 768 Valeix M, Loveridge AJ, Chamaille-Jammes S, Davidson Z, Murindagomo F, Fritz H, Macdonald
28 769 DW (2009) Behavioral adjustments of African herbivores to predation risk by lions:
29 770 Spatiotemporal variations influence habitat use. *Ecology* 90:23-30
30 771 Vucetich JA, (2017) The Population Biology of Isle Royale Wolves and Moose: An Overview
31 772 URL <http://www.isleroyalewolf.org/data/data/home.html> (accessed 29/11/2017
32 773 Vucetich JA, Smith DW, Stahler DR (2005) Influence of harvest, climate and wolf predation on
33 774 Yellowstone elk, 1961-2004. *Oikos* 111:259-270
34 775 Walker E, Nowak R. (1991) *Walker's mammals of the world*. John Hopkins University Press,
35 776 Warren C. (2009) *Managing Scotland's Environment*. Edinburgh University Press, Edinburgh
36 777 Woodroffe R (2001) Strategies for carnivore conservation: lessons from contemporary
37 778 extinctions. *Carnivore Conservation* 5:61-92

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780 **Figure and plate captions**

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

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3 789 **Figure 2:** Simulation results, using four different values of initial red deer density, for
4 790 maximum wolf density in relation to maximum wolf pack density (a) and mean minimum red
5 791 deer density in relation to maximum pack density (b), where a drop in the former is
6 792 considered a sign of strong top-down forcing.

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11 794 **Figure 3:** Mean ($n = 100$, S.E.) maximum wolf density (a), time to maximum wolf density (b),
12 795 minimum red deer density (c), and minimum wolf density (d) against boundary permeability
13 796 where 0 = no dispersing wolves leave the population and 1 = 100% dispersing wolves leave
14 797 the population. Line colours represent scenarios of varying maximum pack density. Red deer
15 798 starting and carrying capacity was set at 20 per km². Roman numerals correspond to distinct
16 799 scenarios where i) represents strong prey suppression but high wolf extinction risk; ii)
17 800 relatively strong top-down forcing and medium wolf extinction probability; iii) weak top-down
18 801 forcing but high wolf survival probability; iv) weak top-down forcing and high wolf extinction
19 802 probability.

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25 804 **Figure 4:** Minimum red deer density against maximum wolf population achieved (a) and time
26 805 taken for the wolf population to reach its maximum (b) under varying disperser removal rates.
27 806 Lighter points = high disperser removal, darker points = low disperser removal. Cluster A of
28 807 points in the top left represents the wolf population dying out quickly in the simulation and
29 808 never suppressing red deer. Cluster B represents those cases where the wolf population has
30 809 expanded rapidly within 20 years, which has made suppression of red deer much more likely.

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36 811 **Plate 1:** A) African fenced enclosure with wild dogs (photo by A. L. Harrington). B) Fenced
37 812 woodland regeneration enclosure in the Scottish Highlands as an example of how fences are
38 813 already used in Scotland (photo by C. Sandom).

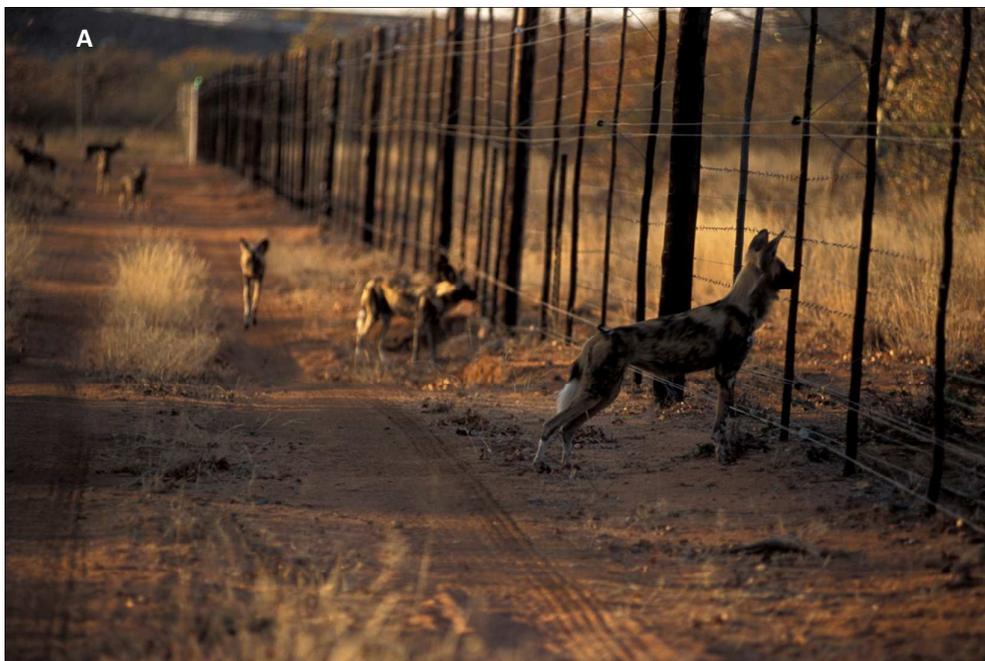
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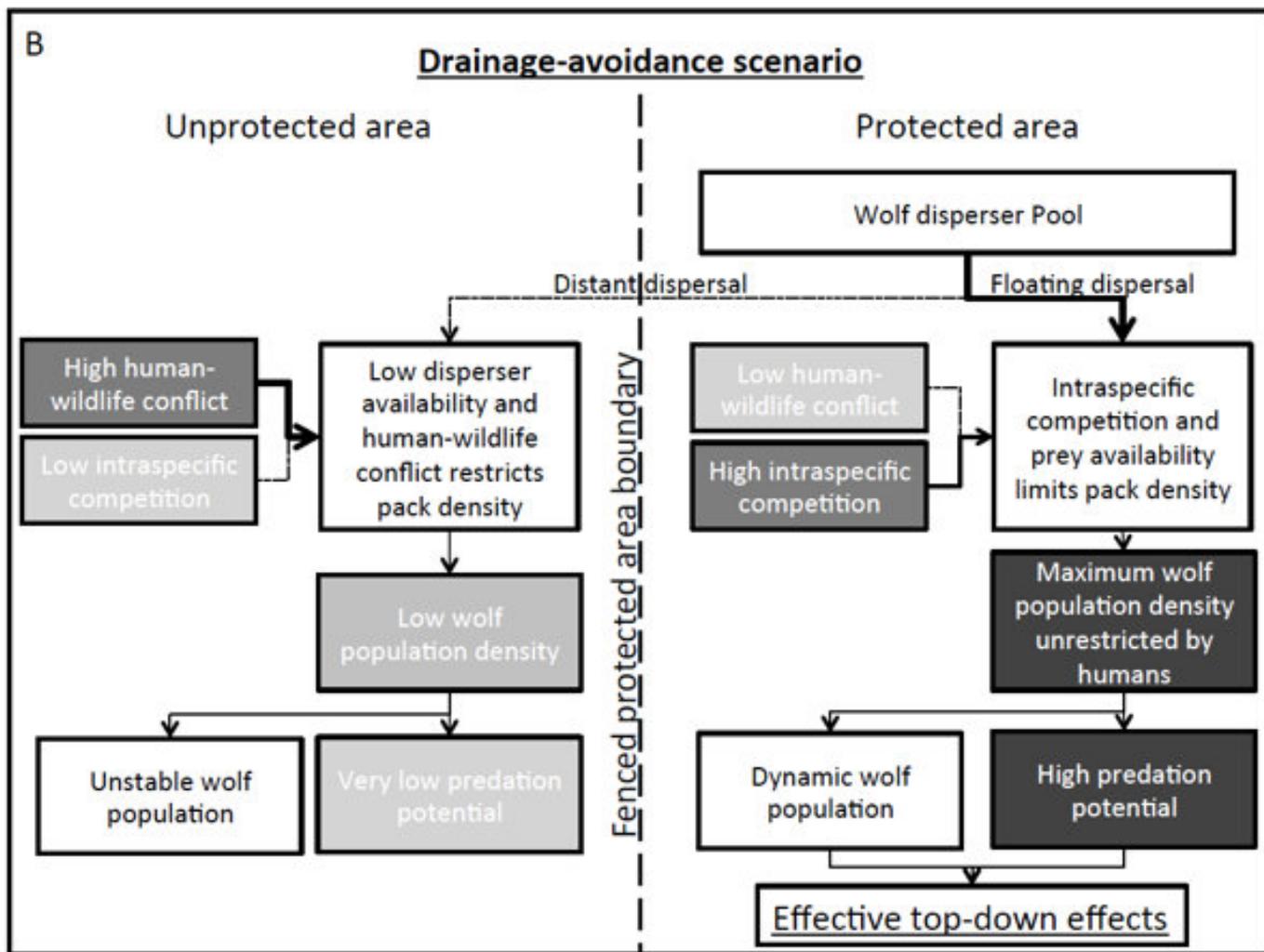
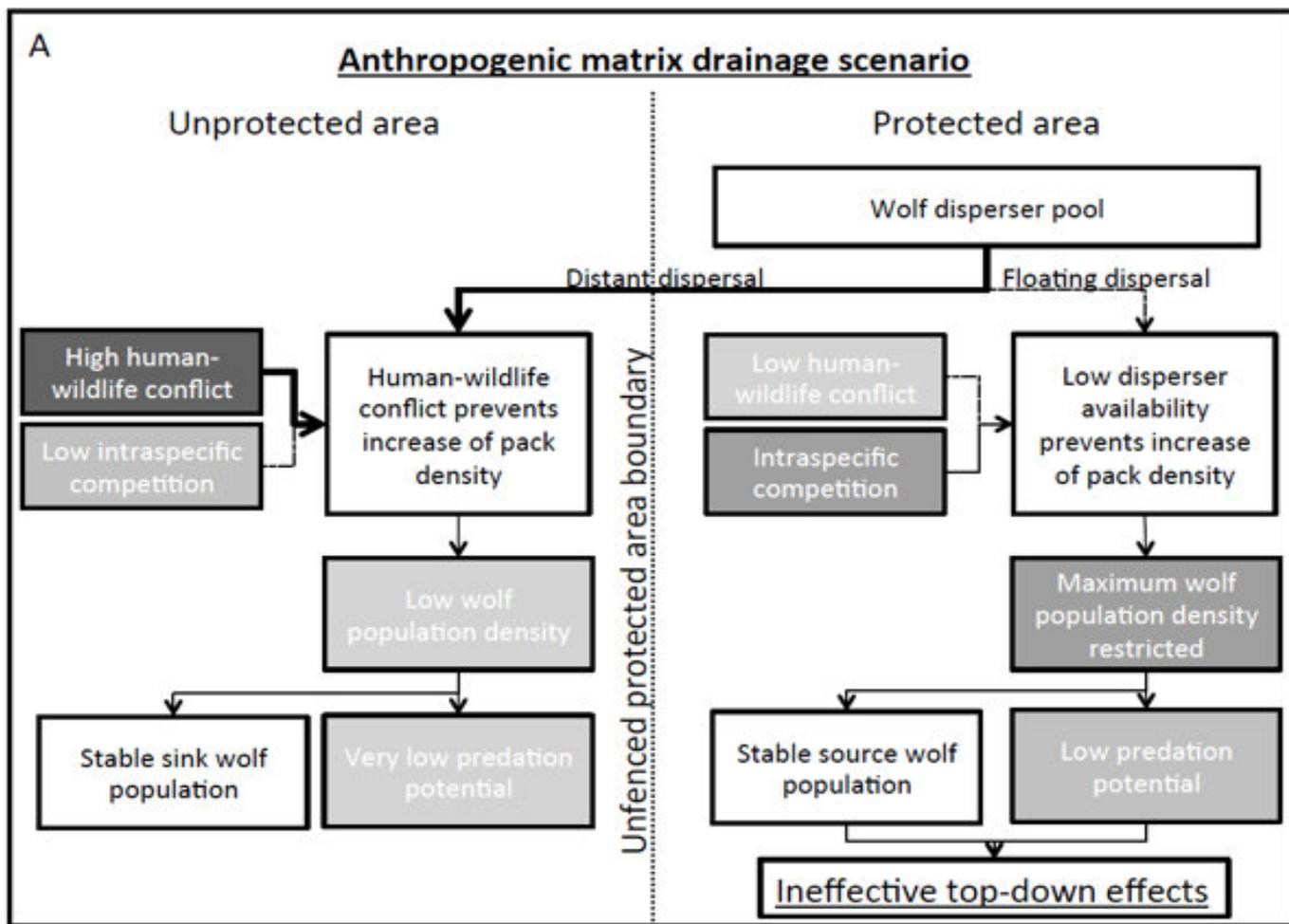
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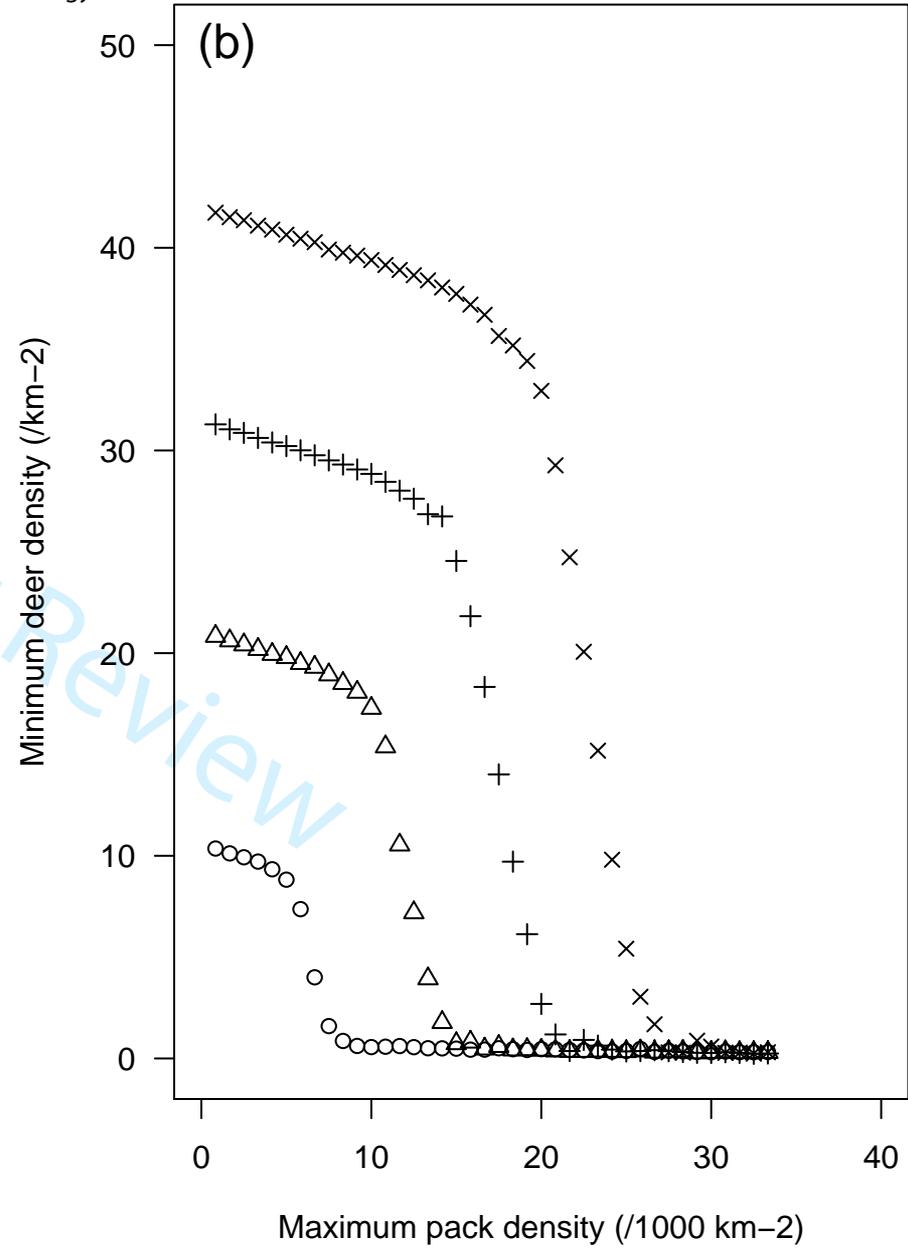
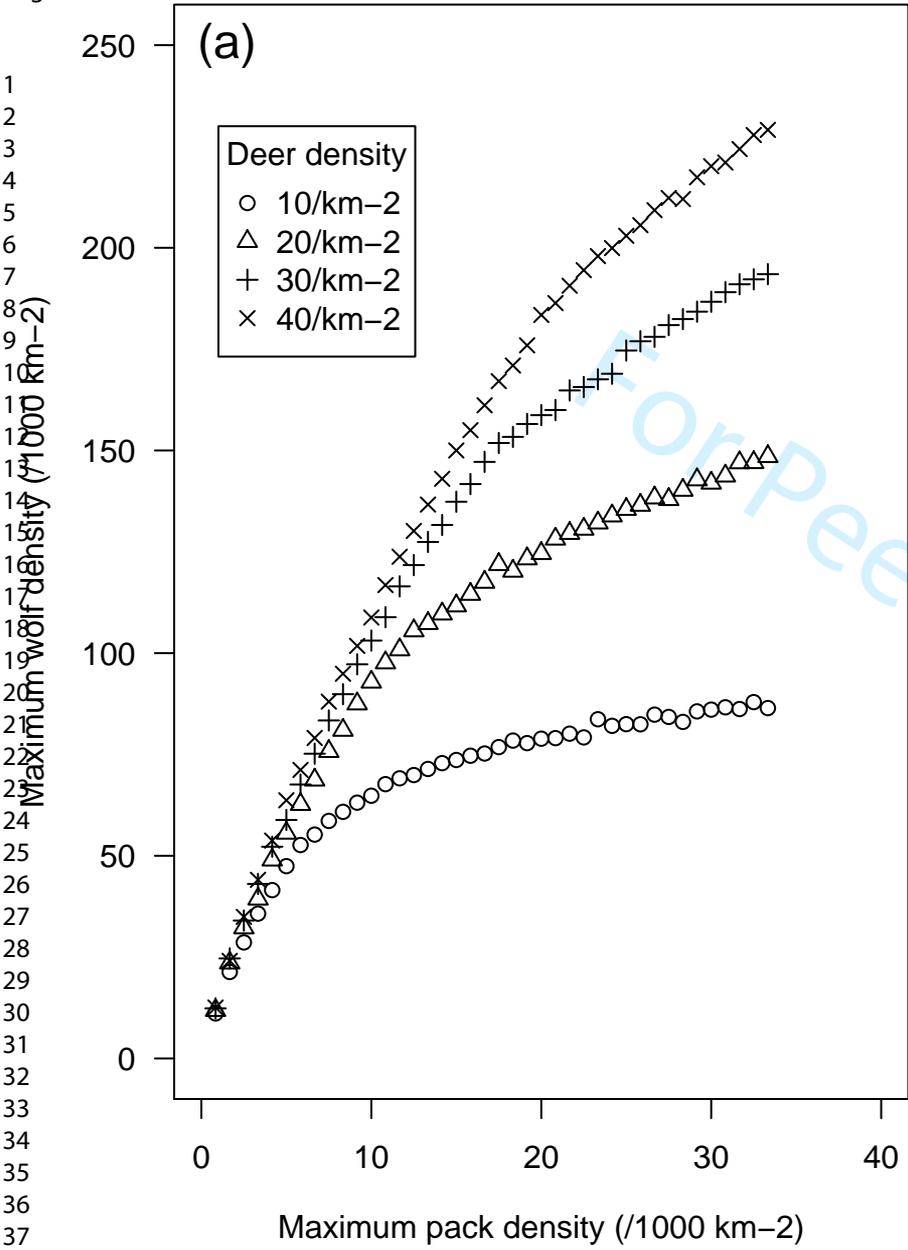
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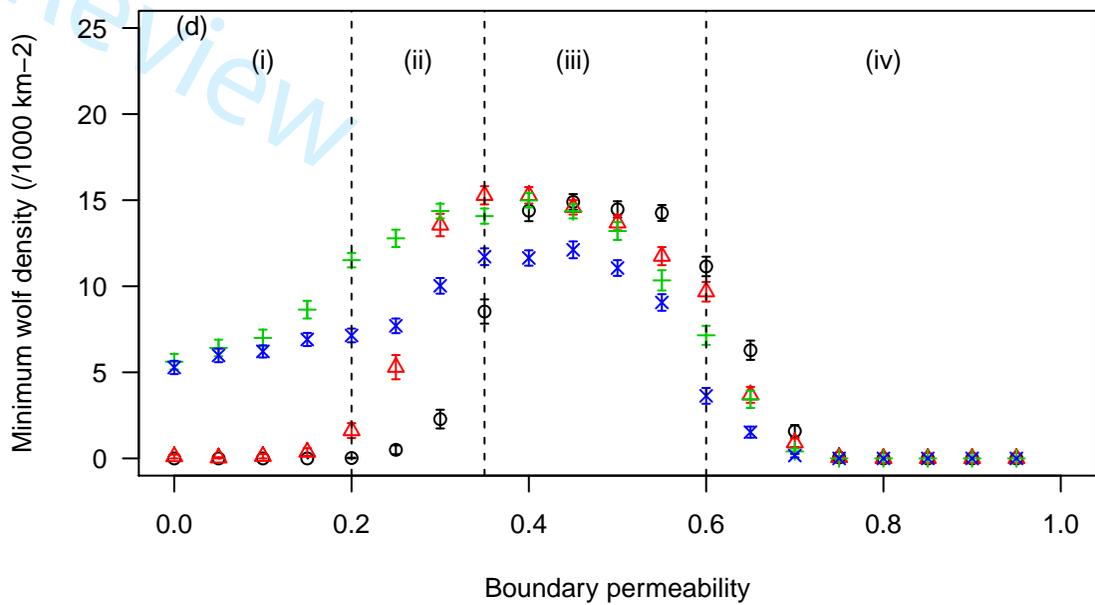
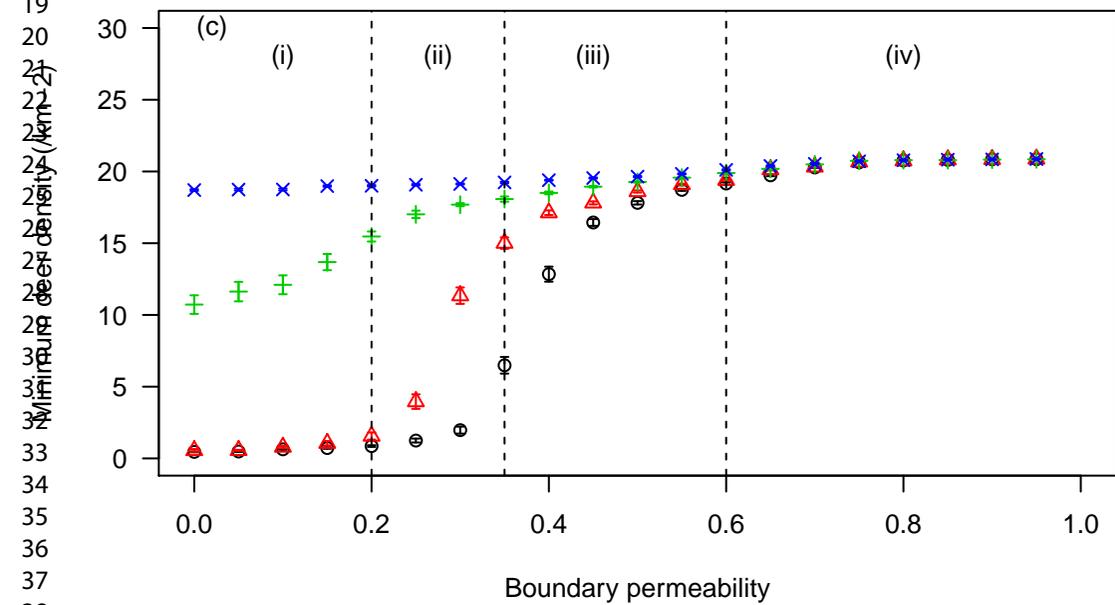
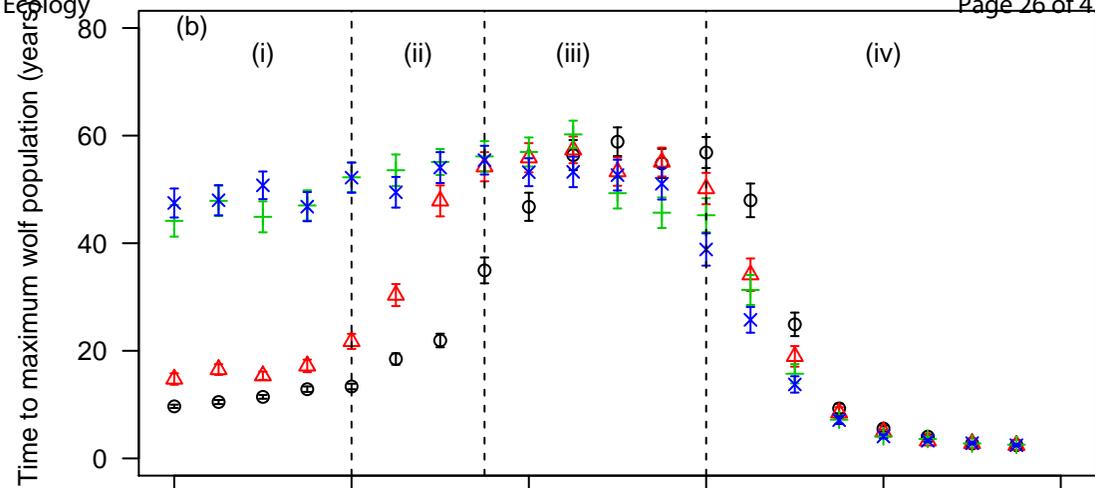
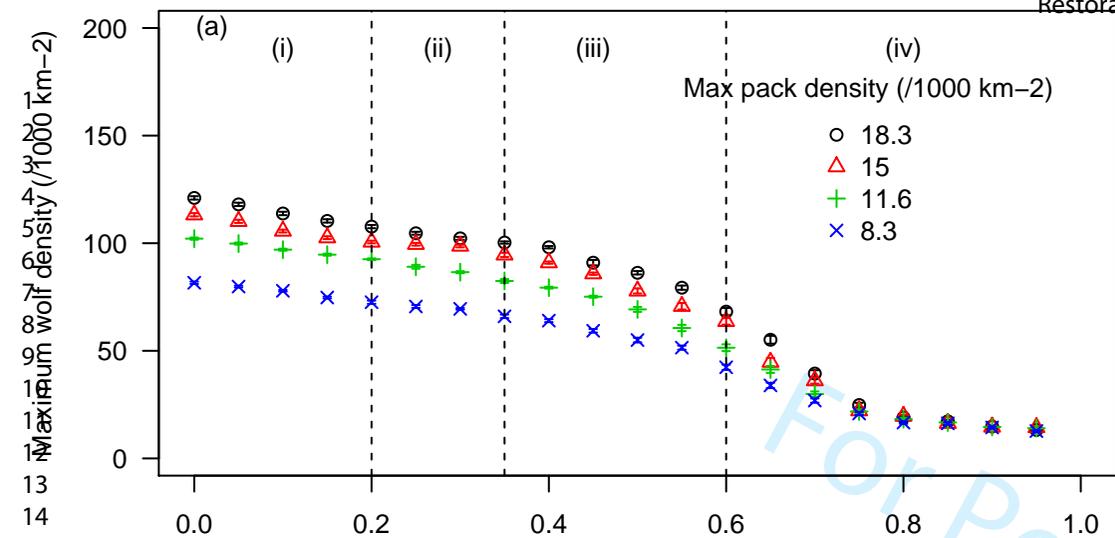
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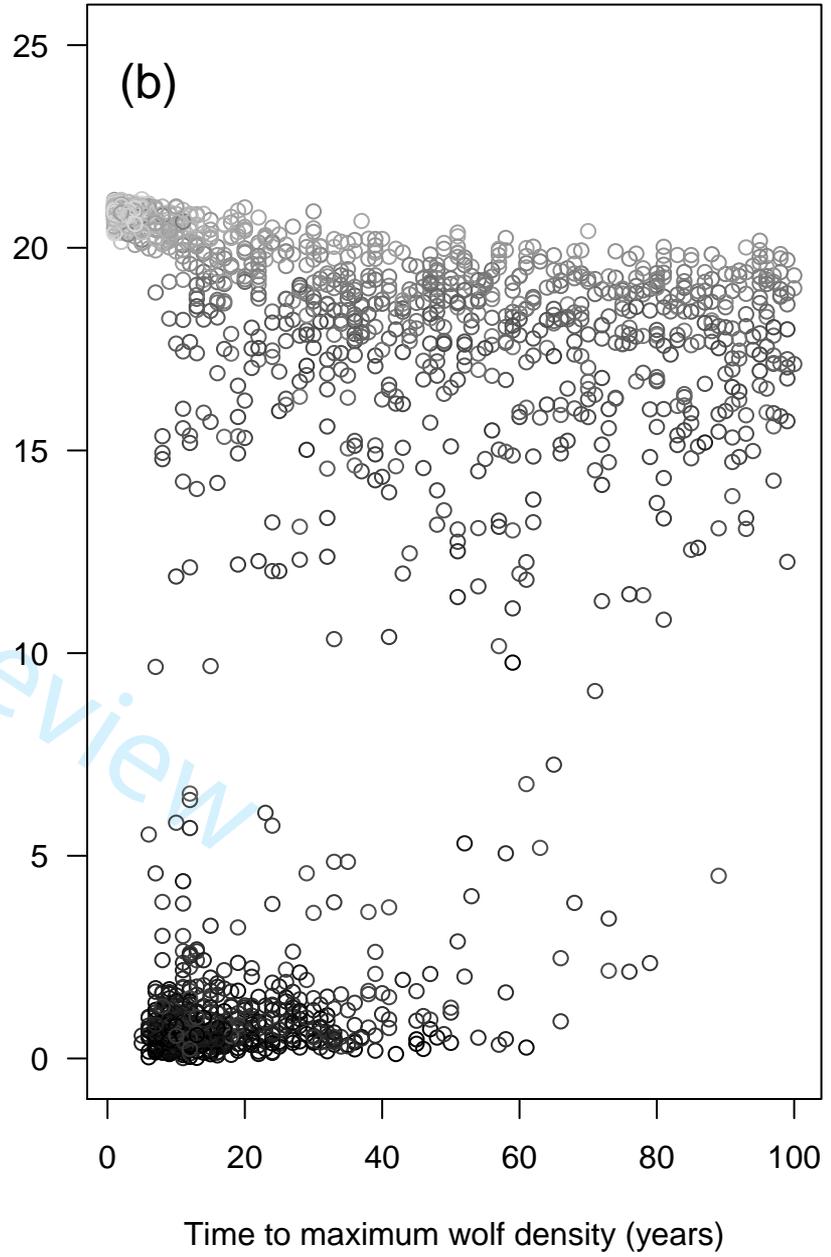
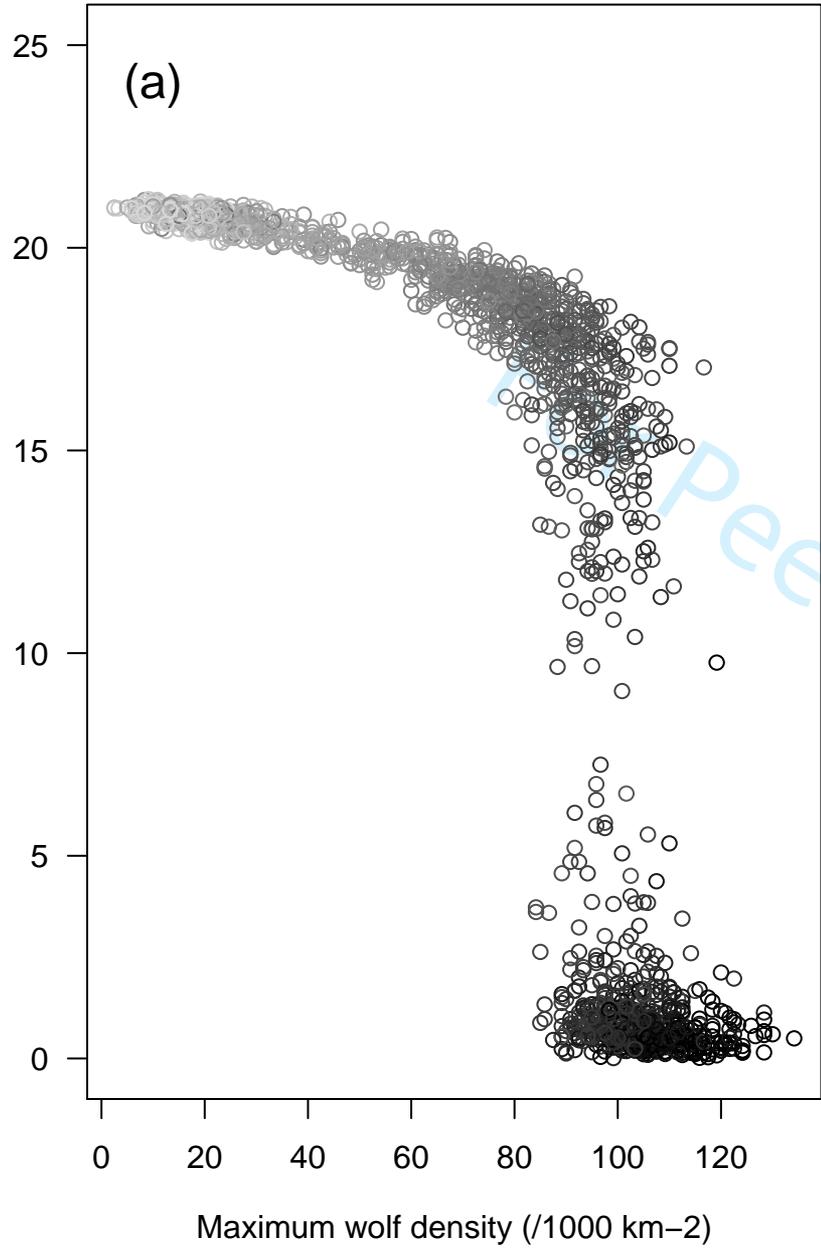


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Fences can support restoration of human-dominated ecosystems when rewilding with large predators

Joseph W. Bull, Rasmus Ejrnæs, David W. Macdonald, Jens-Christian Svenning, Christopher J. Sandom

Appendix S1: Model details

This investigation relied upon a simple individual based model (IBM) that captures key features of wolf biology and social interaction.

Previous versions of this IBM have been shown to make realistic predictions regarding the population dynamics of introduced wolf populations, when compared to empirical data sets (Bull et al. 2009, Sandom et al. 2011). The scenario explored here involved a small reintroduced (hence, known) wolf population. In this scenario, the choices made by dispersing individuals are proposed to influence the outcomes for the wolf population as a whole, as well as their prey. As such, the use of an IBM is appropriate.

Each wolf within the population was individually defined by five characteristics: 'Age' (in years), 'Sex' (Male/Female), 'ID' (identification number), 'Pack number' (a unique number for each pack) and 'Social group'. Wolves were classified as belonging to one of four social groups: (1) cubs; (2) sub-dominant wolves; (3) dispersers; and, (4) dominant (alpha) wolves. Wolves in their first year of life were considered 'cubs'; from the second year onwards, they became 'sub-dominant' and remain so until they chose to leave their natal pack (i.e. disperse), or died. Dispersing wolves remained 'dispersers' until they established a new territory and became 'alpha' wolves, replaced a deceased alpha in an existing territory, or died. Alpha wolves remain alphas until they die.

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5 The behaviour of dispersing wolves was central to this entire
6 investigation. Dependant upon both the nature of the barrier around the
7 hypothetical reserve (e.g. closed, open, porous) and the availability of
8 territories within it, dispersing wolves could choose to leave the reserve
9 and thus cease to influence the population. In this simulation, the land
10 outside the reserve acted as a population sink, hence wolves were
11 assumed not to disperse back into the population from outside.
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18 As per Nilsen et al. (2007), the wolf's primary biological processes were
19 grouped into four functions that were repeated annually: 'survival',
20 'recruitment', 'dispersal', and 'new pack formation'. The 'survival'
21 function applied to all individuals: wolves from each social group had a
22 likelihood of surviving any given year based upon both natural mortality
23 rates and the availability of prey in that year. With regards to the latter,
24 survival rates for all wolves were multiplied by a factor "*preyfac*" where:
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$$32 \quad \textit{preyfac} \quad = \quad r / (g + r)$$

$$33 \quad r \quad = \quad \textit{number of C. elaphus / number of wolves}$$

$$34 \quad g \quad = \quad 70$$

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41 'Recruitment' applied to all alpha pairs, which produced a litter of cubs
42 of varying size. All sub-dominant wolves had a chance of 'dispersal',
43 and if both alpha animals in a pack had died in any one year, it was
44 assumed that the remainder of the pack dispersed. Finally, all
45 dispersing wolves could either join a lone alpha of the opposite sex in
46 an existing pack, or potentially form a new pack if there was space and
47 it is permitted under that model scenario. All survival, recruitment,
48 dispersal and new pack formation rates were simply applied to the
49 relevant individuals as multipliers (Table S1). An element of
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3 stochasticity was introduced by varying these rates annually, using a
4 uniform distribution based upon the standard deviation (also given in
5 Table S1) and a pseudorandom number generator.
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10 The wolf's prey (the *C. elaphus* population) was not sub-structured: as it
11 was assumed that the wolves could not sufficiently reduce prey density
12 such that the *C. elaphus* population would be significantly influenced by
13 internal demographic stochasticity. Instead, the *C. elaphus* population
14 was simply characterised by the total number of *C. elaphus* alive in any
15 one year. Each year, this population number was multiplied by factors
16 corresponding to reproduction (1.20 ± 0.05) (CluttonBrock et al. 1997),
17 mortality from depredation ("wolfkill"), and mortality from other natural
18 causes (0.924 ± 0.020), where:
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$$26 \quad \text{wolfkill} \quad = \text{number of wolves} * \text{killrate}$$

$$27 \quad \text{killrate} \quad = (a * C. \text{elaphus density}) / (h + C. \text{elaphus density})$$

$$28 \quad * \exp(\epsilon)$$

$$29 \quad \epsilon \quad = 0.0 \pm 0.1$$

$$30 \quad a \quad = 30$$

$$31 \quad h \quad = 0.5$$

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43 Figure S1 represents the key functions applied to both wolf and *C.*
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elaphus populations in one time step.

The model is analytical and consequently designed to investigate
hypothetically the processes that might underlie a wolf reintroduction into a
fenced reserve. It is not intended fully to capture, and make firm predictions
about, an actual scenario. As such, we have applied the principle of
parsimony in the model wherever possible. Nevertheless this model, as

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3 described in the preceding paragraphs, demonstrates encouraging behaviour
4 when used to simulate wolf reintroduction at YNP, and compared to empirical
5 data from this reintroduction (Fig. S2).
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10 **Results**

11 The model was consistent with wolf population dynamics recorded in YNP
12 (Fig S2), closely matching our low dispersal rate scenarios. However, only red
13 deer were included in our model while in YNP Bison bison Smith 1827, Alces
14 alces L. 1758 and other ungulates are also present and may help account for
15 high maximum wolf densities. The faster decline in the red deer population
16 may have been because of anthropogenic hunting pressure (Vucetich et al.
17 2005) that was not included within our model which may in turn explain the
18 faster rate of wolf decline than was modelled. Our modelled results suggest
19 that wolves achieved a density that could reduce red deer density if they
20 matched the kill rate modelled here, and that wolf-caused mortality was
21 additive (White & Garrott 2005). Using the unlimited pack density scenario the
22 average wolf kill rate was 2.3 red deer/wolf/month, which was slightly greater
23 than the 2.2 kills/wolf/month (a variety of prey was taken in this study,
24 however, 90% was red deer) recorded in late winter in YNP in Smith et al.
25 (2004). However, extrapolating winter kill rates to an annual kill rate may be
26 conservative as Sand et al. (2008) records increased summer kill rates,
27 although this was recorded in a wolf-elk (*Alces alces*) system. An outbreak of
28 disease within the YNP wolf population (Jimenez et al. 2009) and/or a density-
29 dependent change in dispersal dynamics may also help explain the rapid rate
30 of wolf decline, and highlights again that consideration of important factors
31 such as disease would in all likelihood result in quantitative modifications to
32 the simulated results presented here.
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References

- Bull, J., E. B. Nilsen, A. Mysterud, and E. J. Milner-Gulland. 2009. Survival on the border: a population model to evaluate management options for Norway's wolves *Canis lupus*. *Wildlife Biology* **15**:412-424.
- CluttonBrock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: An empirical analysis. *American Naturalist* **149**:195-219.
- Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves (*Canis-lupus*) in north eastern Minnesota, 1969-1989. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **69**:2946-2955.
- Liberg, O., Sand, H., Pedersen, H.C., Wabakken, P. 2008. Dodlighet och illegal jakt I den skandinaviska vargstammen. *Viltskadecenter Rapport*.
- Mech, L. D. 1970. *The Wolf*. Natural History Press, New York.
- National Park Service. 2012. Winter Count Shows Decline in Northern Elk Herd Population. <http://www.nps.gov/yell/parknews/11005.htm>.
- Nilsen, E. B., E. J. Milner-Gulland, L. Schofield, A. Mysterud, N. C. Stenseth, and T. Coulson. 2007. Wolf reintroduction to Scotland: public attitudes and consequences for red deer management. *Proceedings of the Royal Society B: Biological Sciences* **274**:995-1003.
- Nilsson, T. 2004. Integrating effects of hunting policy, catastrophic events, and inbreeding depression, in PVA simulation: the Scandinavian wolf population as an example. *Biological Conservation* **115**:227-239.
- Pedersen, H. C., P. Wabakken, J. M. Arnemo, S. M. Brainerd, H. Broseth, H. Gundersen, O. Hjeljord, O. Liberg, H. Sand, E. J. Solberg, T. Storaas, T. H. Stromseth, H. Wam, and B. Zimmermann. 2005. Det Skandinaviske ulveprosjektet - Skandulv: Oversikt over gjennomførte aktiviteter i 2000 – 2004. *NINA* **117**.
- Sandom, C., J. Bull, S. M. Canney, and D. W. Macdonald. 2011. Exploring the Value of Wolves (*Canis lupus*) in Landscape-Scale Fenced Reserves for Ecological Restoration in the Scottish Highlands. *in* M. Hayward and M. Somers, editors. *Fencing for Conservation*. Springer.
- U.S. Fish & Wildlife Service. 2011. Gray wolves in the Northern Rocky Mountains. U.S. Fish and Wildlife Service, Montana Fish, Wildlife & Parks, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Washington Department of Wildlife, Oregon Department of Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services., USFWS, Ecological Services, 585 Shepard Way, Helena, Montana.
- White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. *Biological Conservation* **125**:141-152.

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

| Parameter | Baseline value | Standard Deviation | Source |
|---|----------------|--------------------|--|
| Cub dispersal rate | 0.35 | 0.15 | (Gese and Mech 1991) |
| Sub-adult dispersal rate | 0.50 | 0.25 | (Gese and Mech 1991) |
| Adult dispersal rate | 0.90 | 0.20 | (Gese and Mech 1991) |
| Probability of establishing a territory | 0.8 | 0.1 | (Pedersen et al. 2005) |
| “Small” litter size (# cubs) | 2 | 1 | (Mech 1970) |
| “Large” litter size (# cubs) | 5 | 1 | (Nilsson 2004) |
| Probability of a large rather than a small litter | 0.73 | 0.15 | Calculated from (Pedersen et al. 2005) |
| Cub survival rate | 0.903 | 0.15 | (Liberg 2008) |
| Survival rate for wolves aged 2 – 8 years | 0.903 | 0.17 | (Liberg 2008) |
| Survival rate for wolves aged 9 years | 0.40 | 0.08 | (Mech 1970) |
| Survival rate for wolves aged 10 years | 0.25 | 0.05 | (Mech 1970) |

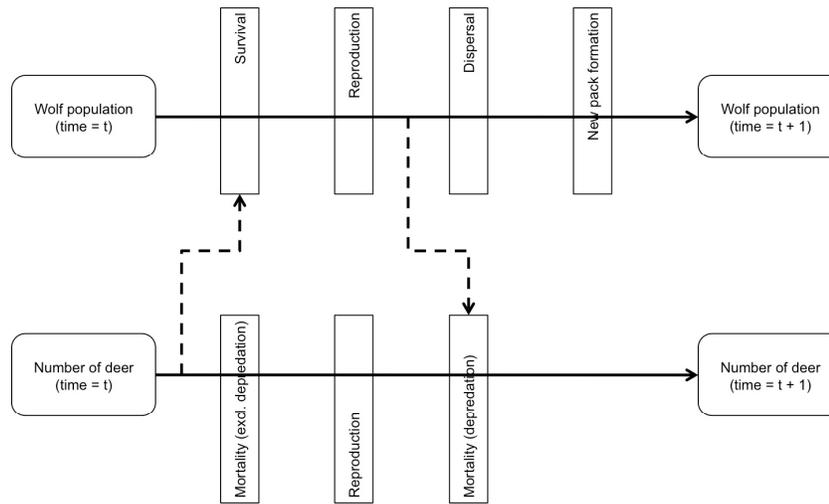
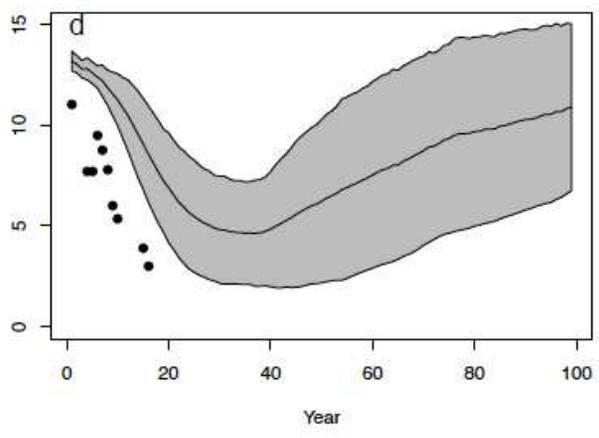
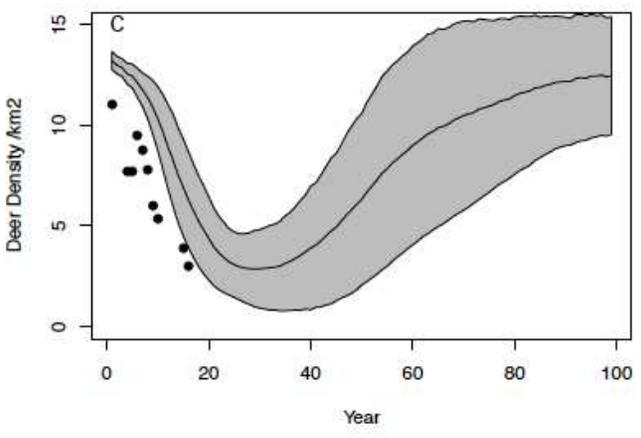
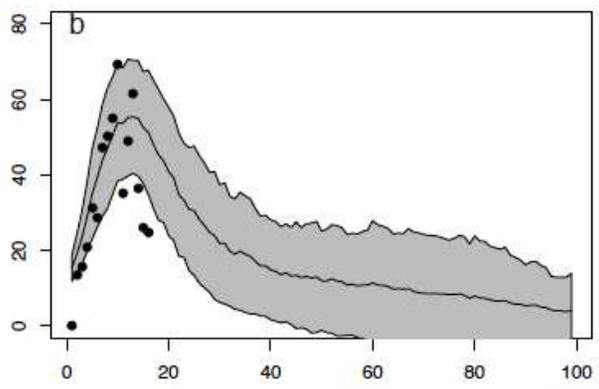
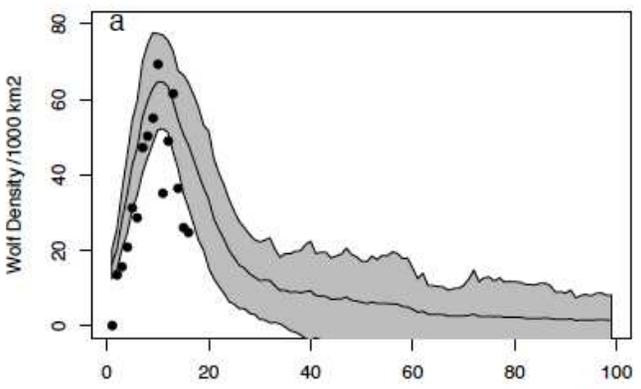


Figure S1: Schematic representation of key processes in wolf model, including prey factor. Dashed lines = interaction between populations

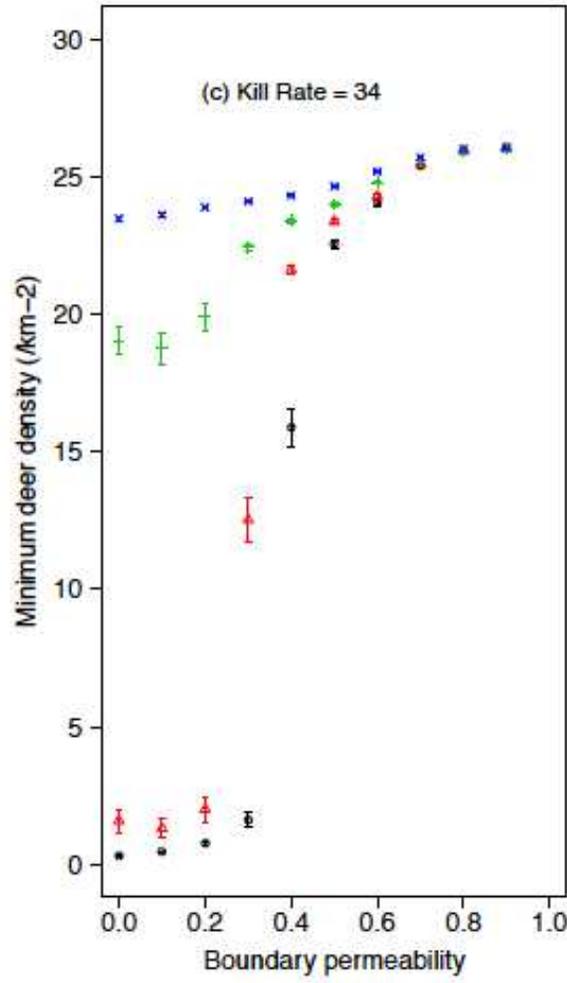
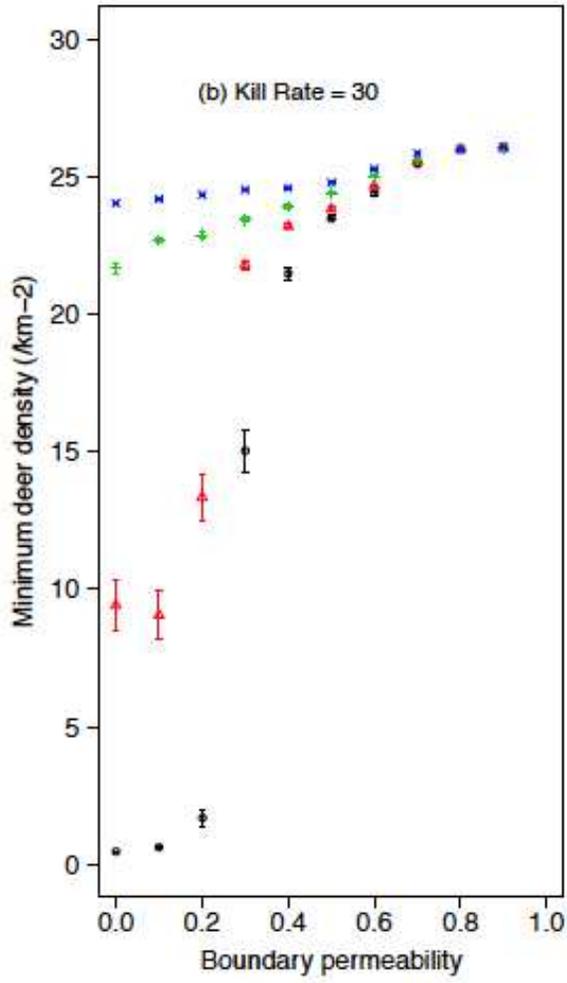
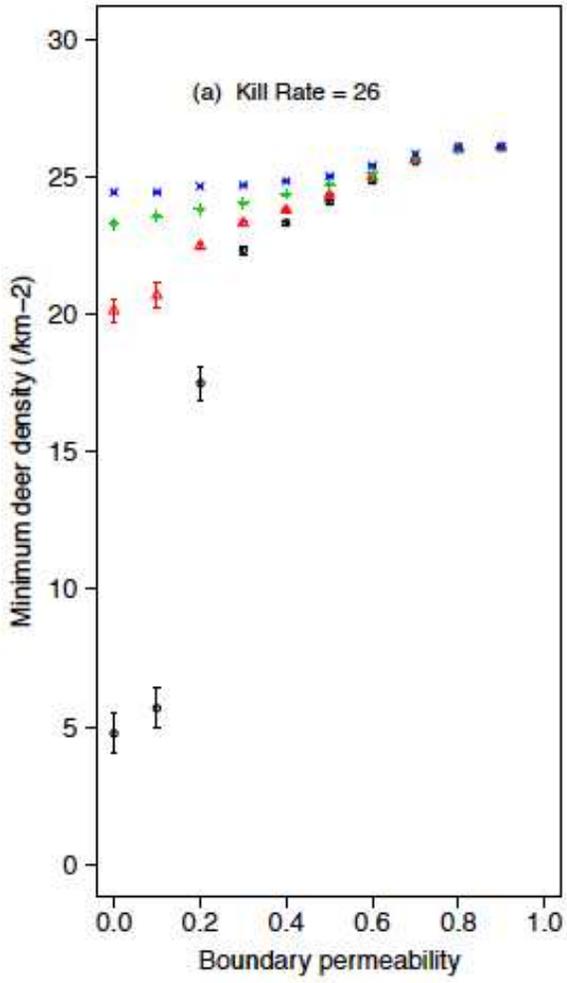
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6 **Figure S2:** Mean ($n=100$) wolf and deer population dynamics over the 100 year modelling period in a 1400 km² area. Black circles
7 are empirical data recorded from YNP's Northern Range from 1995 when wolves were first introduced. (a) wolves with a boundary
8 permeability of 0% (b) wolves with a boundary permeability of 10% (c) deer with a boundary permeability of 0% (d) deer with a
9 boundary permeability of 10%. Wolf and deer data between 1995 and 2004 were gathered from White and Garrott (2005), C.
10 elaphus data for 2009 and 2010 from National Park Service (2012) and wolf data post-2004 U.S. Fish & Wildlife Service (2011).
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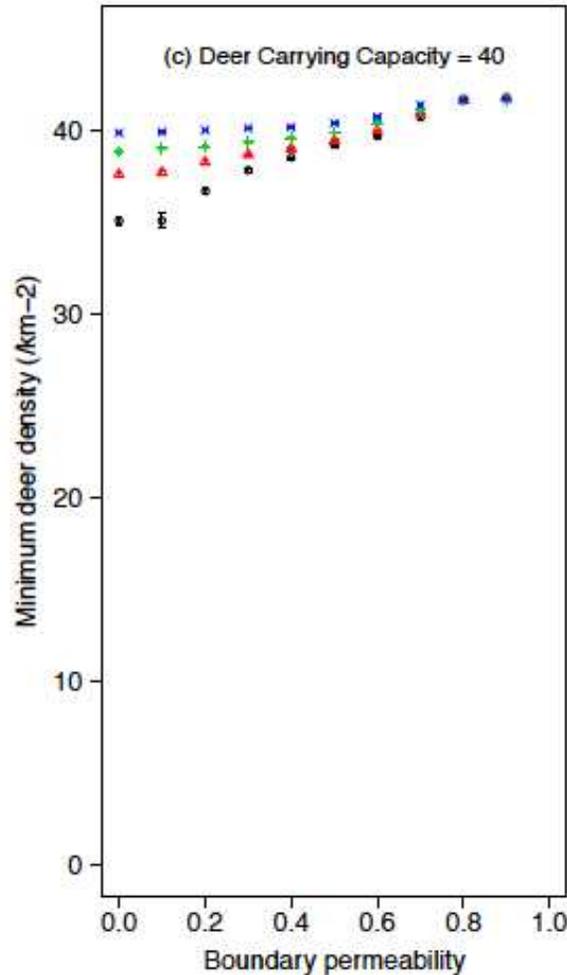
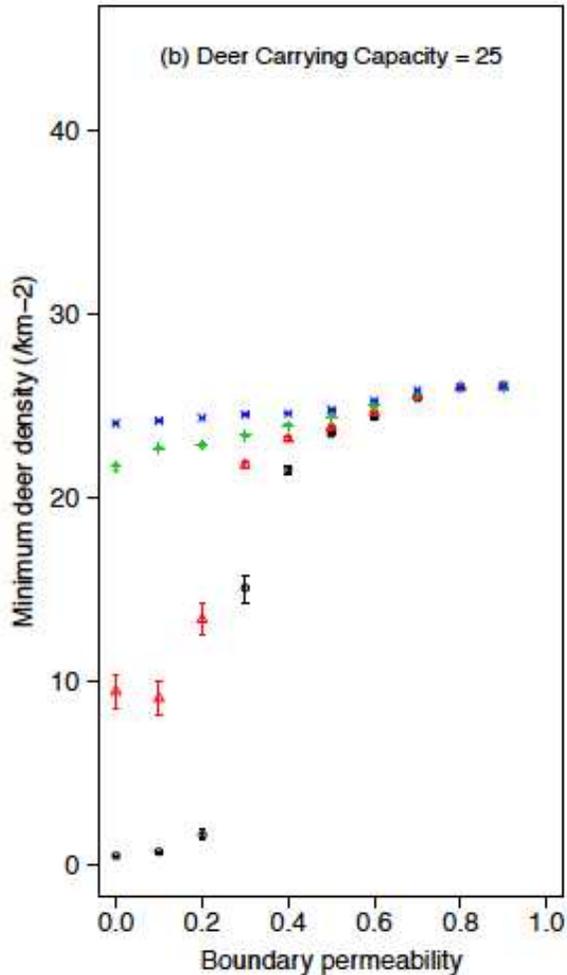
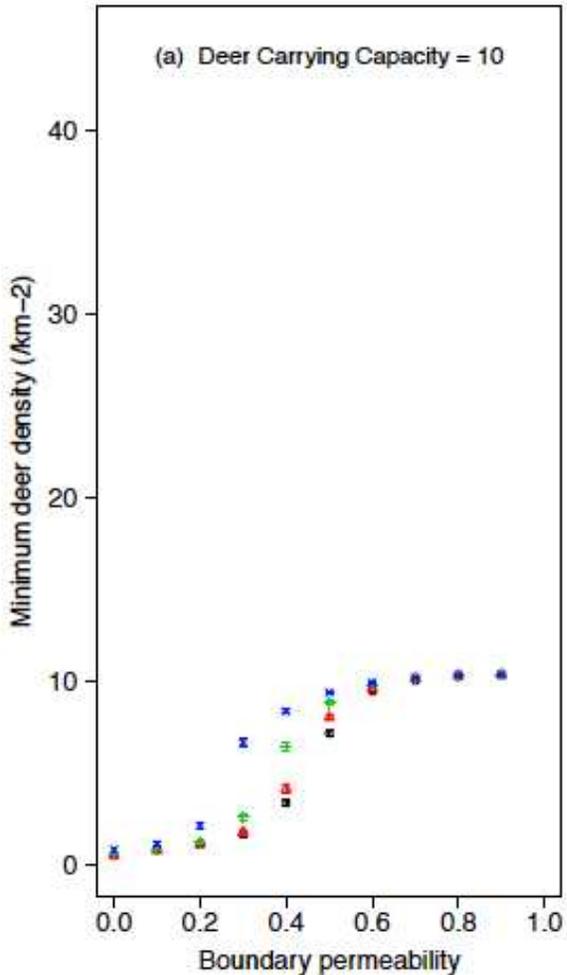
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7 **Figure S3:** Minimum red deer density under modelling scenarios with varying boundary permeability, where 0 = no dispersing
8 wolves leave the population and 1 = 100% dispersing wolves leave the population. Line colours represent scenarios of varying
9 maximum pack density: Black circles = 18.3, Red triangles = 15, Green cross = 11.6, and blue x = 8.3 packs/1000km². The wolf kill
10 rate varied across the panels a, b, and c as indicated in the panels. Red deer starting and carrying capacity was set at 20 per km².
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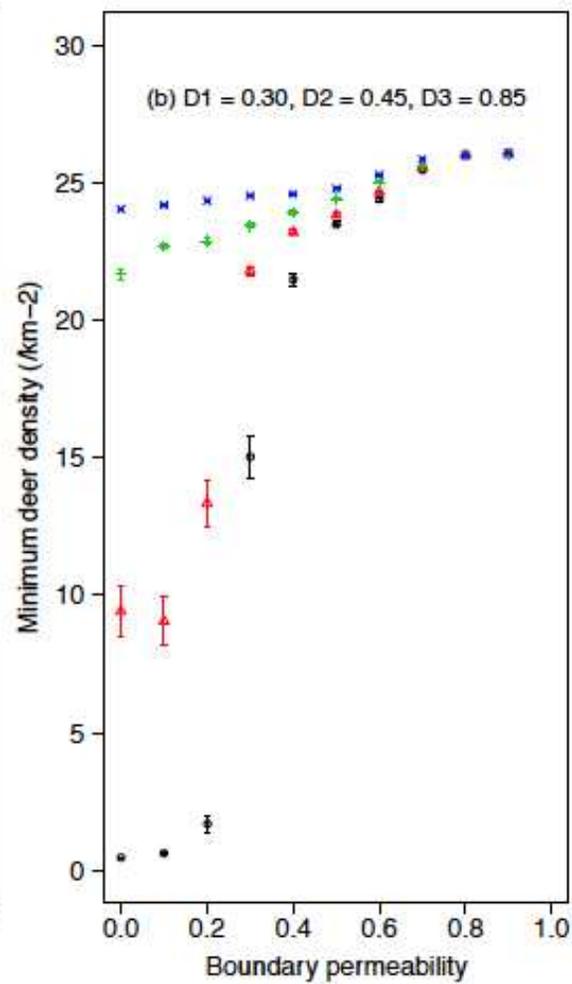
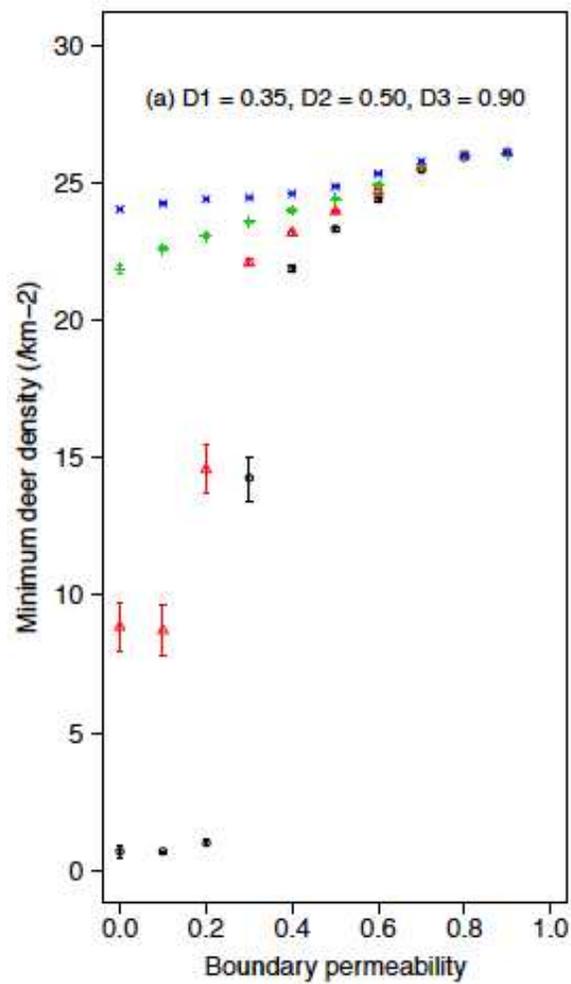
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7 **Figure S4:** Minimum red deer density under modelling scenarios with varying boundary permeability, where 0 = no dispersing
8 wolves leave the population and 1 = 100% dispersing wolves leave the population. Line colours represent scenarios of varying
9 maximum pack density: Black circles = 18.3, Red triangles = 15, Green cross = 11.6, and blue x = 8.3 packs/1000km². The deer
10 carrying capacity varied across the panels a, b, and c as indicated in the panels. Red deer starting and carrying capacity was set at
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For Peer Review

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20 per km².

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7 **Figure S5:** Minimum red deer density under modelling scenarios with varying boundary permeability, where 0 = no dispersing
8 wolves leave the population and 1 = 100% dispersing wolves leave the population. Line colours represent scenarios of varying
9 maximum pack density: Black circles = 18.3, Red triangles = 15, Green cross = 11.6, and blue x = 8.3 packs/1000km². The
10 probability of wolves dispersing varied across the panels a, b, and c, where D1 = cub dispersal rate, D2 = Sub-adult dispersal rate,
11 and D3 = Adult dispersal rate. Red deer starting and carrying capacity was set at 20 per km².
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