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Wolf reintroduction to Scotland: public attitudes and consequences for red deer management

Erlend B. Nilsen[1,2,*], E. J. Milner-Gulland[3], Lee Schofield[4], Atle Mysterud[1], Nils Chr. Stenseth[1] and Tim Coulson[3]

[1] *Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway*
[2] *Department of Forestry and Wildlife Management, Hedmark University College, 2480 Koppang, Norway*
[3] *Division of Biology and Centre for Population Biology, Imperial College London, Silwood Park, Ascot, Berks SL5 7PY, UK*
[4] *Centre for Environmental Policy, Imperial College London, Exhibition Road, London SW7 2PY, UK*

Reintroductions are important tools for the conservation of individual species, but recently more attention has been paid to the restoration of ecosystem function, and to the importance of carrying out a full risk assessment prior to any reintroduction programme. In much of the Highlands of Scotland, wolves (*Canis lupus*) were eradicated by 1769, but there are currently proposals for them to be reintroduced. Their main wild prey if reintroduced would be red deer (*Cervus elaphus*). Red deer are themselves a contentious component of the Scottish landscape. They support a trophy hunting industry but are thought to be close to carrying capacity, and are believed to have a considerable economic and ecological impact. High deer densities hamper attempts to reforest, reduce bird densities and compete with livestock for grazing. Here, we examine the probable consequences for the red deer population of reintroducing wolves into the Scottish Highlands using a structured Markov predator–prey model. Our simulations suggest that reintroducing wolves is likely to generate conservation benefits by lowering deer densities. It would also free deer estates from the financial burden of costly hind culls, which are required in order to achieve the Deer Commission for Scotland's target deer densities. However, a reintroduced wolf population would also carry costs, particularly through increased livestock mortality. We investigated perceptions of the costs and benefits of wolf reintroductions among rural and urban communities in Scotland and found that the public are generally positive to the idea. Farmers hold more negative attitudes, but far less negative than the organizations that represent them.

Keywords: Markov model; predator–prey dynamics; trophy harvest; wildlife economics

1. INTRODUCTION

Large predators have been extirpated from much of their historical range (e.g. Mech 1995). This has resulted in elevated densities of large herbivores in areas where human hunting has not replaced natural predation in limiting population growth (see e.g. Gordon *et al.* 2004). Such high herbivore densities are sometimes considered detrimental to the environment as they may hamper attempts to reforest (Putman & Moore 1998), reduce bird densities (Fuller & Gough 1999) and compete with livestock for grazing (Clutton-Brock & Albon 1989). One suggested route to reducing deer densities is to reintroduce large carnivores (Wilson 2004). Indeed, reintroduction programmes have received an increasing amount of attention over the last decade (Carroll *et al.* 2003). The aim of such programmes has usually been simply to preserve the species being reintroduced. However, it is also important to consider whether the species' ecosystem function can also be restored (Soulé *et al.* 2003). As reintroductions have wide-ranging implications (Soulé *et al.* 2003), it is important that a proper assessment of the ecological implications is carried out in advance. Furthermore, the success of the programme will be strongly influenced by the opinions of local people (Fritts *et al.* 1997)

In much of the Highlands of Scotland, red deer (*Cervus elaphus*) densities are currently thought to be close to the food-limited carrying capacity (Clutton-Brock *et al.* 2004). Red deer populations at current densities are widely considered to impact negatively on the environment due to overgrazing (Hester 1996). However, the deer population in Scotland is difficult to control by hunting, as there is little economic demand for hunting. Instead, managers cull deer in order to control their densities, with the Deer Commission for Scotland having a stated management objective of six deer per square kilometre. This culling of hinds is accompanied by trophy hunting for stags, but the operation barely breaks even overall (Milner-Gulland *et al.* 2004). Owing to this failure to control deer numbers (Clutton-Brock *et al.* 2004), the interaction between deer and land management has become a controversial issue within the UK. One solution to reducing deer numbers that has been discussed is the reintroduction of red deer predators—particularly grey wolves (*Canis lupus*)—into the Highlands. Wolf

* Author for correspondence (erlend.nilsen@sue.hihm.no).

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reintroduction into the Highlands is currently a contentious issue within the UK, with opponents and supporters holding strong views.

In this paper, we attempt to provide an unbiased quantitative insight into two aspects of the possible consequences of a wolf reintroduction. First, we developed a simulation model to assess the expected effects of wolf reintroduction on the population dynamics of Highland red deer. Transient dynamics, equilibrium densities and the implications for deer hunting were examined. Livestock depredation was not included in the model, but the issue is considered in the discussion. We then carried out a survey of the attitudes of people living in rural Scotland, in an area where wolf reintroduction has been proposed, and of urban residents, and compared the results with attitudes expressed by the media and the stakeholder groups.

2. MATERIAL AND METHODS

(a) *Population modelling*

The dynamics of the red deer population were described using a density-dependent, discrete-time, age- and sex-structured Markov model. The deer population model was parameterized from the long-term individual-based study conducted in the North Block of the Isle of Rum, Scotland (e.g. Clutton-Brock *et al.* 2002). A complete description of the red deer population model can be found in Clutton-Brock *et al.* (2002), Milner-Gulland *et al.* (2004) and as electronic supplementary material to this paper. The model captures the dynamics of population growth on the island of Rum very well and is an acceptable base model for red deer in the Highlands of Scotland more generally (Clutton-Brock *et al.* 2002; Milner-Gulland *et al.* 2004).

We simulated the wolf population using an individual-based model. Our model was a variant of the models used by Haight *et al.* (1998) and Chapron *et al.* (2003), but was updated with respect to the interactions between the wolves and their prey. As previous studies have shown that the social organization of wolves strongly influences their population dynamics and extinction probabilities (Vucetich *et al.* 1997; Haight *et al.* 1998), a detailed approach is necessary to capture the dynamics. The model distinguished individuals by their membership of a wolf pack, which consisted of a dominant breeding pair and one or more cohorts of their offspring (see also Haight *et al.* 1998). The dominant female in each pack bred yearly, producing a single litter. By their first winter, the pups were fully grown. We also incorporated an annual rate of dispersal from the natal pack. A dispersing wolf might then colonize a vacant territory or join a widowed alpha individual of the opposite sex and become a dominant individual. A full description of the modelling philosophy is found in the electronic supplementary material.

As demographic stochasticity is known to affect the population dynamics of small populations, each transition was modelled as a binomial probability. Consequently, the fate of each wolf was determined by drawing a random number (between 0 and 1) and comparing it with the probability that a certain event occurred (e.g. mortality, dispersal).

For simplicity, we assumed that prey kill rates were depressed at low deer densities and were more affected by stochastic factors (e.g. snow conditions; Post *et al.* 1999) at moderate-to-high densities. We consequently chose a type II functional response represented by the disc equation (equation (2.1))

$$k = \frac{aP}{h+P}, \tag{2.1}$$

where k is the *per capita* kill rate (deer killed per wolf per year); P is the deer density; a is the asymptote which the kill rate approaches and h the deer density at which the kill rate reaches half the asymptotic value. By setting h low (0.5 deer km^{-2}), kill rates are relatively constant across a wide range of deer densities, as observed in data from Yellowstone area (Smith *et al.* 2004) and in comparisons across studies (Eberhardt *et al.* 2003). To account for stochastic variation in the kill rate (Post *et al.* 1999; Hebblewhite 2005), we modified the realized kill rates such that (equation (2.2))

$$k' = Ke^{\varepsilon}, \tag{2.2}$$

where k' is the realized *per capita* kill rate and ε is a Gaussian distributed random variable with mean zero and $\sigma = 0.05$. The total number of deer killed by wolves is a function of the number of wolves present and the per capita kill rate. Furthermore, we accounted for the fact that wolves prefer to kill certain age classes by adopting and modifying the approach taken by Fieberg & Jenkins (2005). Thus, wolf-killed deer were distributed among the different age and sex classes by the following formulation (equation (2.3))

$$k_{i,j} = k' \left[\frac{n_{i,j}\mathrm{Sel}_{i,j}}{\sum_{i=1}^{i=2}\sum_{j=1}^{j=14} n_{i,j}\mathrm{Sel}_{i,j}} \right], \tag{2.3}$$

where k' is the realized *per capita* kill rate; $k_{i,j}$ is the number of individuals from sex i and age j that are killed per wolf per year; $n_{i,j}$ is the number of individuals in sex i and age class j; and $\mathrm{Sel}_{i,j}$ is the selectivity constant for sex i and age j individuals (Fieberg & Jenkins 2005). We assumed that the wolves selected juveniles and old females (10 years or more; Smith *et al.* 2004), with the selectivity constant given by Sel_1, which is relative to the selectivity constant for all other age–sex categories (Sel_2).

To account for the effect of prey availability on wolf population growth, we assumed that wolf survival was affected by the deer : wolf ratio (equation (2.4))

$$S_i = \frac{s_i P}{g+P}, \tag{2.4}$$

where S_i is the realized age-specific survival; s_i is the maximum age-specific survival; g is the deer : wolf ratio at which the survival is half of maximum; and P is the deer : wolf ratio. Although the literature is very limited on whether vital rates in wolves are density dependent or ratio dependent, circumstantial evidence suggests that survival rates are lower when per capita prey availability is low (Fuller *et al.* 2003). We assumed that the survival rates differed between juveniles (s_{juv}), wolves aged 1–6 years (s_{prime}) and older wolves (s_{old}). All parameter values are given in the electronic supplementary material.

To predict the equilibrium numbers of deer and wolves for different levels of hind culling rates, we simulated the stochastic population model in 100 loops, each lasting 100 years (initial trials suggested that 100 time-steps were sufficient to reach equilibrium). In each loop, we first ran the deer model for 50 years without any harvesting or predation to reach equilibrium. Then we released three wolf packs into the system, each consisting of one dominant pair and two subordinates. We scaled deer density to give the number of deer 2000 km^{-2}, the approximate size of the area considered by the 'Trees for Life' project (see below), assuming that dynamics would be similar across the 25 000 km^2 Scottish Highlands if wolves were allowed to colonize the entire area.

(b) *Estimated economic consequences for deer estates*

To investigate the potential economic consequences for the deer estates, we assumed that the estates followed the recommendations from Deer Commission for Scotland aiming for approximately six deer km^{-2}. To reach this management goal, a hind cull is needed in order to control population growth. As the commercial harvest in Scotland is mainly for trophy stags, we assumed £200 profit per stag and £50 loss per hind (Milner-Gulland *et al.* 2004). We then compared the economic outcome for the deer estates prior to and after a wolf reintroduction by varying the harvesting rate for trophy stags.

We did not model the economic consequences for the sheep farming industry, but considered the broad implications of wolf reintroductions for farmers' livelihoods.

(c) *Sensitivity analysis*

We used standardized linear regressions between parameter values and model predictions to determine prediction sensitivity to parameter values—see McCarthy *et al.* (1995) for an illustration of the approach, and Saltelli *et al.* (2000) and Fieberg & Jenkins (2005) for a more general discussion. As information about parameter uncertainty was scarce for most parameters, we used uniform distributions (Fieberg & Jenkins 2005). We then drew 200 sets at random from these distributions and ran the stochastic model 50 times for each set of parameters. Each of the 50×200 simulations were run for 100 time-steps, with population sizes reported for the final time-step, such that sensitivities are reported for the equilibrium only. We then calculated the mean equilibrium deer population size across simulations for each set of parameter values. Using mean population size at time $t=100$ as the dependent variable, we fitted regression models through data scaled to have a mean of zero and a standard deviation of unity (Saltelli *et al.* 2000). If parameters are not strongly correlated, the sensitivity of model prediction to a parameter is the square of the regression estimate for that parameter (Saltelli *et al.* 2000). We looked for evidence of strongly nonlinear sensitivities by fitting quadratic terms ($\beta_1 x+\beta_2 x^2$) into the regression models, but little support was found for the inclusion of these terms. Note that this technique results in unit-less coefficients representing the relative importance of the different parameters (Fieberg & Jenkins 2005).

(d) *Assessing rural and urban attitudes to wolf reintroductions*

The rural survey was carried out in the Glen Affric area of Scotland. This area was chosen because it borders the area of the Trees for Life project, which aims to reforest 2380 km^2 of the Scottish Highlands with the ultimate aim of rewilding the area, including reintroduction of wolves and other recently extirpated large mammals (http://www.treesforlife.org.uk/tfi.acti.html). Consequently, this rural population is particularly sensitized to issues regarding wolf reintroduction. We carried out a geographically stratified random sample with hand-delivered questionnaires, obtaining a 65% response rate and 126 usable responses. The urban sampling was carried out opportunistically at leisure centres and shopping centres in Inverness and Edinburgh, producing a sample of 226 respondents. The attitude scores were calculated using a 5-point Likert scale of responses to nine attitudinal questions based on Kellert's typologies of attitudes to wolf reintroductions (Kellert 1986). Cronbach's alpha was used to test the reliability of the resulting ordinal scale (Pate *et al.* 1996). The Factiva search engine (http://www.factive.com) was used on 23 June 2005, searching UK local and national newspapers excluding republished news, pricing and marketing data, obituaries and sports news. A Boolean 'OR' search was done for 'wolf or wolves' as free text in the headline and lead paragraph. Articles were then individually screened for relevance and content assessed using the same categories as those used to characterize advantages and disadvantages of reintroduction in the questionnaire (Goulding & Roper 2002). Key informant interviews were carried out with representatives of stakeholder groups, and informants were asked to fill in the questionnaire from the point of view of their organization. Attitude scores were then inferred for the organization as a whole.

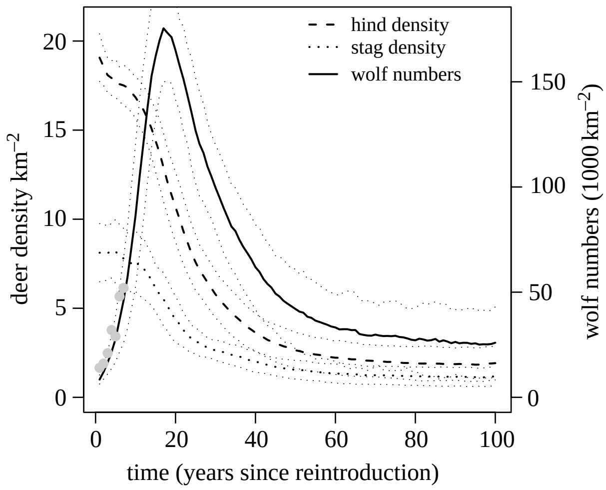

Figure 1. Predicted transient dynamics following the introduction of wolves into Scotland. The dashed line represents hind (3 years or more) densities, the dotted line trophy stag (more than 5 years) densities, and the solid line wolf densities. Standard deviations (thin dotted lines) around the lines do not include cases when wolves went extinct. The grey points are wolf densities in the northern range of Yellowstone National Park following the wolf reintroduction in 1995 (from Smith *et al.* 2003).

3. RESULTS

(a) *Population modelling*

At the start of the simulation, red deer numbers were at equilibrium, either hunted or unhunted depending on the scenario under examination. Three wolf packs, each consisting of one dominant pair and two subordinates, were introduced into the system at time $t=1$. After an initial decrease in deer numbers and an increase in wolf numbers, wolf numbers rapidly declined to a mean equilibrium value of 25 wolves per 1000 km^2 (s.d.= 17)—a value similar to those recorded in unmanaged wolf populations in the Bialowieza Forest, Poland (20–49 wolves per 1000 km^2; Jedrzejewski *et al.* 2002). An equilibrium density of approximately seven deer km^{-2} (s.d.=3.2) was reached *ca* 60 years after the initial release (figure 1). The deer : wolf ratio (approx. 288) is

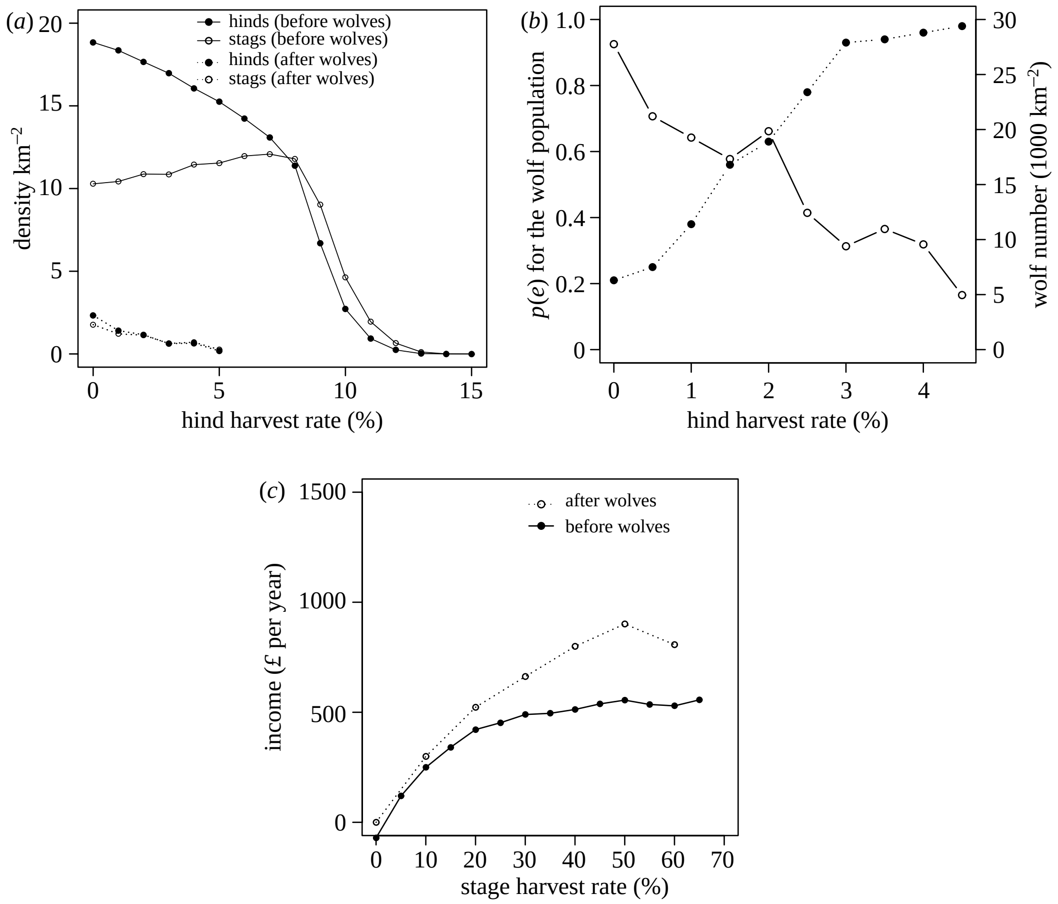

Figure 2. Ecological and economic consequences of wolf reintroduction. (*a*) Estimated trophy stag (5 years or more) and hind (3 years or more) densities before and after wolf reintroduction for a given hind harvest, when stags are unharvested. (*b*) Estimated wolf population density (solid line and open circles) and extinction probabilities for the wolf population (dotted line and filled circles) at different hind culling rates. (*c*) Estimated annual revenue at equilibrium for a 10 000 ha estate from culling trophy stags (5 years or more) when the income is set to £200 for a stag and −£50 for culling a hind, at different culling rates for stags and an unmanaged wolf population. In the situation with no wolves, hinds are culled at approximately 11%, the rate needed to keep the deer population at roughly six deer km^{-2}. In the situation with wolves, no hinds are culled.

consistent with those reported by Fuller *et al.* (2003). Initial conditions (deer density and number of wolf packs released) affected the time needed to reach equilibrium and the peak wolf population, but not equilibrium density.

Although the equilibrium reached was unaffected by the initial conditions, the equilibrium deer numbers are strongly dependent on hind culling rates (figure 2*a*). This in turn affected the viability of the wolf population. When we simulated the model without any deer harvesting, the wolf population went extinct in *ca* 19% of the simulations. With increasing hind culls, the probability that the wolf population went extinct increased dramatically. In general, the red deer population could not support a harvest greater than 4–5% of females as well as a viable wolf population (figure 2*b*). Our simulations thus suggest that the viability of the wolf population is strongly dependent on the prey density.

In our simulation, the deer and wolf populations attained point equilibria, and there was no indication of any long-term autocorrelation in the dynamics (autoregression coefficients (mean (5th and 95th percentiles)): AR(1)-coef: 0.20 (−0.28–0.53), AR(2)-coef: 0.07 (−0.33–0.37)). There is a specific range of conditions when cycles between predators and prey do not occur, with the prey population growth rate and density dependence on the prey population growth rate being the important factors. We suspect that because most female red deer in the Highlands only reproduce every second year (Clutton-Brock & Coulson 2002), the growth rate of the red deer population is not high enough to generate cycles.

(b) *Estimated economic consequences for deer estates*

Model results suggest that a wolf reintroduction would be economically beneficial for deer estates through a reduction in deer numbers and hence the removal of the requirement to cull hinds in order to meet the Deer Commission's management objectives (figure 2*c*). However, it would reduce the number of stags available to hunters (figure 2*a*). If we assume £200 profit per stag and £50 loss per hind, we estimate that in the presence of wolves an estate would make £800 yr^{-1} 10 km^{-2} from culling 40% of stags and not hinds, while without wolves it would make £550 yr^{-1} 10 km^{-2} from culling 40% of stags and 11% of hinds, the appropriate hind culling rate required to meet management objectives (i.e. approx. 6 deer km^{-2}; see also Milner-Gulland *et al.* 2004). We have not accounted for the possibility that trophies may increase in size because deer would be at lower densities in the presence of wolves, and thus that an individual trophy may achieve higher returns.

Table 1. Sensitivity analysis of the equilibrium population size of deer to parameters in the wolf model. (The first three parameters relate to wolf predation on deer and the remaining parameters to wolf demography. We report sensitivities of parameters of the wolf model only because the sensitivities of red deer population size to model parameters have been reported elsewhere (Milner-Gulland *et al.* 2004). Sensitivities were estimated using standardized linear regression of model results obtained by extensive parameter perturbation.)

description of parameter	parameter name	β	p-value	$\sim r^2$
asymptotic kill rate (deer/wolf)	a	−0.417	<0.001	0.174
deer density at ½a	h	0.126	0.003	0.016
selectivity constant of juveniles and old females (10 years or more)	Sel_1	−0.116	0.005	0.013
juvenile survival	s_{juv}	−0.010	0.815	0.001
adult survival	s_{prime}	−0.563	<0.001	0.318
deer : wolf ratio when adult wolf survival = one-half maximum value	g	0.153	<0.001	0.023
probability that a dispersing wolf settles	p_{settle}	−0.458	<0.001	0.209

(c) *Sensitivity analyses*

Red deer equilibrium numbers in the presence of wolves are dependent primarily on the rate at which wolves kill deer when deer are abundant (a), adult wolf survival rates (s_{adult}) and the probability that a dispersing wolf is successful in establishing a territory (p_{settle}; table 1). The other parameters in the wolf population model had a less strong effect on the deer equilibrium numbers. Unfortunately, all parameters with large sensitivities have large confidence intervals in the literature, so until further research provides more accurate estimates we should interpret the results in terms of the essential features of the predicted dynamics rather than focusing on exact numbers.

(d) *Assessing rural and urban attitudes to wolf reintroductions*

Attitudes to reintroductions of wolves and other extirpated components of the British fauna varied between rural and urban samples. Urban respondents had a mean attitude score of +5.3 on a scale of −18 to +18, while rural respondents had a significantly lower score of +1.9 (figure 3). The lower score for the rural population was due to the negative attitudes of the subsample of farmers (mean score −4.7). When offered a choice of scenarios, 43% of respondents favoured the reintroduction of a range of species, including wolves, into the wild; 35% favoured reintroductions into fenced eco-parks; 8% favoured reintroductions of species other than wolves (e.g. beavers) and 14% favoured no reintroductions of any species. Of the rural population, 23% felt that deer control was the major advantage of wolf reintroductions, with the potential for tourism ranking second (21% of respondents). Of urban respondents, 19% felt that tourism would be the major benefit, but they also saw a range of other advantages that were not highlighted by the rural community, including preserving Scotland's heritage and restoring the balance of nature. The major concern of the rural population was loss of livestock (54% of respondents), while the urban population was predominately concerned about the potential of wolves to harm humans (35% of respondents). The attitudes of people other than farmers reflected media coverage of the wolf issue; a search of UK national and local newspapers using Factiva revealed that 54% of articles mentioning wolves had a positive message and 19% were negative. The attitudes of stakeholder organizations ranged from −16 (National Farmer's Union for Scotland) to +18 (Trees for Life), with the Mammals Trust UK (+7) closely matching the mean urban attitude, and the Scottish Countryside Alliance (−4) being close in attitude to the farmer sample.

4. DISCUSSION

Deer management in Scotland is relatively unusual compared to most countries where wolves exist. In both North America and Scandinavia, there is a culture of deer hunting for meat as well as for trophies (Milner *et al.* 2006), with a clear objective of maintaining deer populations for human use. Our results suggest that it is not viable to maintain anything other than a very low level of hunting in the presence of an unmanaged wolf population (see also Nilsen *et al.* 2005; White & Garrott 2005; Nelson & Mech 2006). Conversely, the UK's focus on stag hunting for trophies means that wolf introduction could make deer estates more profitable by removing the need to cull hinds to meet the Deer Commission for Scotland's management objectives. The potential lack of conflict between hunters and wolves in the Highlands makes Scotland a particularly interesting case study, as disagreement between stakeholders has generated substantial controversy over carnivore reintroductions and recolonizations in Scandinavia, France and the United States (Ericsson & Heberlein 2003; Naughton-Treves *et al.* 2003; White & Garrott 2005).

Our model apparently captures the dynamics of one expanding wolf population well—the early recolonization phase closely followed the observed patterns in the northern range in Yellowstone National Park (figure 1; see Smith *et al.* (2003) for numbers from Yellowstone), although the peak density reported here is higher. Other reintroduced or recolonizing wolf populations, however, have experienced long lag phases at low numbers, the reasons for which are sometimes clear and sometimes less obvious (Wabakken *et al.* 2001; Boitani 2003). This result is not particularly surprising, as populations are often limited by life-history and stochastic events during the initial stage of population expansion. In our model, the viability of the wolf population was also highly dependent on the prey base, further highlighting the dichotomy in outcomes, which is also reported in the literature (see also Vucetich *et al.* 1997).

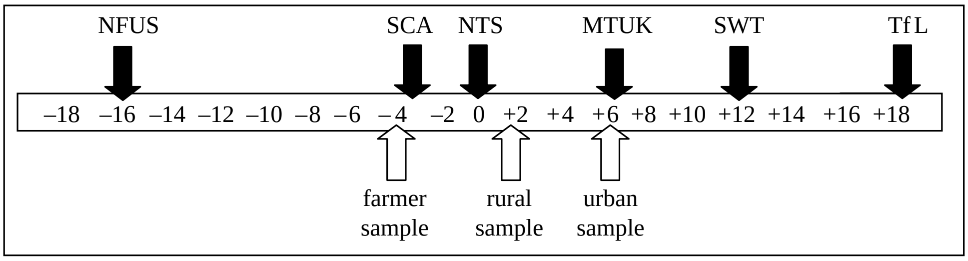

Figure 3. Attitudes of stakeholders to the reintroduction of wolves into the Scottish Highlands. A positive score represents a positive attitude and a negative score a negative one. The rural sample includes farmers, the farmer sample is farmers alone and the urban sample contains only urban responses. NFUS, National Farmers Union for Scotland; SCA, Scottish Countryside Alliance; NTS, National Trust for Scotland; MTUK, Mammals Trust UK; SWT, Scottish Wildlife Trust; TfL, Trees for Life. These attitudinal scores are from questionnaires filled in by the key informants within the organizations, who were asked to represent the organization's point of view in their responses. However, they represent unofficial opinion rather than the stated policy of the organizations.

Compared with current deer densities in the Highlands, our simulations suggest that the deer density in some areas will be reduced by more than 50% following a wolf reintroduction, even in the absence of any excessive hind cull. Is it probable that a wolf reintroduction in the Scottish Highlands will have such a dramatic effect on deer densities? Empirical evidence suggests that wolves often affect deer population dynamics lowering overall population density (Hebblewhite *et al.* 2002; Jedrzejewski *et al.* 2002; Nelson & Mech 2006). However, in an extensive review of the literature on predation control, Ballard *et al.* (2001) found that only a limited set of studies reported a clear effect of predator removal on deer densities and surplus available for human exploitation, mainly because the wolves predominantly killed old and sick individuals. However, most of these studies concerned white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) that often twin every year and thus reproduce at a much higher rate than the Scottish red deer which can produce a maximum of a single calf every other year. We may therefore expect wolves to have a greater effect due to the lower reproductive rate of the prey species. This is really a question about whether communities are structured by top-down or bottom-up processes (Sinclair & Krebs 2002). Most studies indicate that both processes are likely to act simultaneously to various degrees (McLaren & Peterson 1994; Testa 2004; Vucetich & Peterson 2004). On Isle Royale, while wolves do indeed affect the population dynamics of moose (*Alces alces*), climatic factors such as snow conditions are moving the system between periods of top-down and bottom-up control (Vucetich & Peterson 2004). Hence, the degree to which wolves affect deer density is determined by a range of factors which are difficult to quantify *a priori*, but given our current understanding, our model results seem reasonable.

Wolves are likely to spread from their area of initial release throughout the Highlands and this will impact on wildlife other than deer. Many impacts are likely to be positive; the presence of wolves may reduce predator control costs on grouse moors through intra-guild interactions (Palomares & Caro 1999), and reduced deer densities may lead to increased rates of natural forest regeneration, lower densities of deer ticks that spread Lyme disease (but see Perkins *et al.* 2006) and potentially elevated breeding success of some passerine species (Fuller & Gough 1999). The reintroduction of wolves into the greater Yellowstone area has also shed some light on this important issue. Ten years after the reintroduction, several studies have reported effects on prey abundance (White & Garrott 2005; but see also Vucetich *et al.* (2005) for an opposing result), carrion availability for scavengers (Wilmers & Getz 2004) and regeneration of cottonwood and *Salvia* spp. (Ripple & Beschta 2003). Again, the evidence suggests that wider ecosystem-level effects are likely to occur but are difficult to quantify *a priori*.

Wolf predation on sheep will cause conflict. Our model does not consider the impact of wolves on sheep. This is for two reasons: first, a one prey–one predator model has substantially fewer parameters than a two prey–one predator model, especially if the prey interacts through a shared food resource as is the case with sheep and deer in Scotland. Given the existing parameter uncertainty, including sheep would substantially weaken model predictions. Second, the dynamics of the Scottish sheep farming industry are currently changing rapidly, making it difficult to parameterize this part of the model. In the Highlands of Spain, where sheep roam freely as much as they do in Scotland, wolf predation is responsible for 80% of natural sheep mortality (Blanco 2000). If, as it seems probable, wolf predation on sheep in Scotland were at a similar level, it would reduce flock sizes. So, why are sheep farmers not more strongly opposed to wolf reintroduction? Part of the reason may be that, on average, little or no profit is made directly from sheep by Highland farmers—profits accrue through subsidies. For example, the average profit per sheep farm in the Highlands in 1999–2000 was £24 300, of which £24 500 was through subsidies (SEERAD 2001). In other words, without subsidies, the average sheep farm made an operating loss. If farmers are given economic compensation for wolf-killed sheep, the conflict potential need not be too high. Traditionally, farmers have been paid per sheep, although EU policy is now changing towards paying farmers for maintaining grazing irrespective of flock sizes. Such a policy is likely to facilitate the reintroduction of wolves. However, the tolerance of wolves is not always related to economic compensation (Naughton-Treves *et al.* 2003), and the emotional consequences to sheep farmers experiencing wolf predation should not be ignored. Furthermore, wolf predation on sheep would be controversial from an ethical and animal rights perspective, and disagreement could arise between stakeholders wishing to reduce sheep stocking rates for environmental reasons and those aiming to advance social and animal welfare (Waterhouse 1996).

Given current global threats to biodiversity, the re-establishment of extinct species into depauperate natural communities in areas of low human population density is a potentially useful conservation tool. However, attempts to do this will always be contentious, costly and impact local communities. These communities need to support and benefit from any reintroductions to reduce risks of disruption or sabotage to any reintroduction. Fear of wolves can be a major hindrance to reintroductions (Røskaft *et al*. 2003), although attacks on people by non-rabid wolves are virtually non-existent (with the exception of India; see Rajpurohit 1999). Killing of domestic dogs can also be a concern (Naughton-Treves *et al*. 2003; Kojola *et al*. 2004), which can only partly be addressed by education of dog owners.

Our study suggests that the Scottish public, with the exception of farmers, has a generally positive view of reintroductions, including wolves. It is instructive to note, however, that farmer attitudes are less negative than might have been expected, and substantially less negative than the attitudes expressed by their representative organization. However, unless reintroductions are well planned, such attitudes may change in a more negative direction when people actually experience wolf predation (Ericsson & Heberlein 2003). In this paper, we have suggested one advantage of the reintroduction of wolves—solving some of the difficult issues surrounding deer management in Scotland. We have also shown that the public is quite positive towards wolf reintroduction, which is a prerequisite for a successful reintroduction programme.

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