Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians

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Summary

1. Where populations are confined to fragmented, human-dominated landscapes, preventing declines and extirpations will often rely on metapopulation management. Spatially-explicit population viability analyses provide tools to evaluate how well the local management efforts can be combined to conserve metapopulations across large areas. Yet, metapopulation models have rarely been combined with tools to assess the cost-effectiveness of different conservation strategies.

2. European bison Bison bonasus only occur in small, fragmented populations, making their long-term survival dependent on establishing a metapopulation across eastern Europe. We parameterized a European bison metapopulation model based on time-series of bison demography and a habitat suitability map to assess the viability of bison populations in the Carpathians and the relative cost-effectiveness of (i) reintroductions, (ii) wildlife overpasses and (iii) anti-poaching measures in establishing a viable bison metapopulation.

3. Our results suggest that the Carpathians could support a viable metapopulation of European bison provided that active efforts are taken to safeguard bison and connect isolated herds. With such steps, our model forecasts that bison numbers could increase substantially over the next 100 years as local populations increase and bison recolonize parts of the Carpathians.

4. Reintroductions appear to be the most cost-effective approach for establishing a viable bison metapopulation among our scenarios, especially when coupled with wildlife overpasses to improve connectivity among herds. The most promising region for a bison metapopulation in the Carpathians was south-eastern Poland, Ukraine and northern Romania. We identified several candidate regions for reintroductions and wildlife overpasses, especially in the border region of Romania and Ukraine. Site-specific assessments of both habitat suitability, and the costs and benefits of a large bison population, should target those regions.

5. Synthesis and applications. Our results highlight how careful conservation planning can identify solutions to preserve large mammals in human-dominated landscapes. Choosing the most effective option from a range of management strategies is a central challenge for wildlife managers. We have shown that incorporating cost-effectiveness analyses into metapopulation models can elucidate the relative value (gain per unit cost) of different conservation management options, allowing decision makers to choose cost-effective options to preserve large mammals. Our model projections also provide hope for establishing a viable free-ranging European bison population in the Carpathians, one of the last relatively wild areas in Europe.

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Introduction

Population declines and extirpations now occur at rates several times faster than the species losses they often foreshadow but are often overlooked in the wider biodiversity crisis (Ceballos & Ehrlich 2002; Gaston & Fuller 2008). With about 75% of the planet’s land surface already transformed by humans (Ellis & Ramankutty 2008), habitat conversion is clearly the largest driver of these population declines and the extinction debts they incur (Rogers et al. 2009). Large mammals are particularly at risk from habitat conversion as they often require large tracts of intact habitat (Maehr, Noss & Larkin 2001; Morrison et al. 2007). As a result, many large carnivores and herbivores today only persist in small, fragmented populations (Woodroffe 2000; Gordon & Loison 2009).

Over-exploitation represents a second formidable threat to large mammals as they are attractive targets for poachers seeking meat, trophies or medicinal animal parts. Large mammals are also persecuted because they conflict with land use (Morrison et al. 2007; Gordon & Loison 2009). Due to slow reproductive rates, large mammals lack demographic resiliency; consequently, they are particularly vulnerable to poaching and the loss of only a few individuals can doom small populations (Milner-Gulland & Bennett 2003; Linkie et al. 2006). Moreover, over-exploitation and poaching tend to be widespread in times of political and institutional instability, as during armed conflicts or revolutions (Jedrzejewska et al. 1997; Stephens et al. 2001; Dudley et al. 2002).

The collapse of the Soviet Union in 1991 is an example of such an event. As states moved from central-planning to market-oriented economies, corruption increased (TI, 2010), law enforcement was weakened, the infrastructure for nature protection eroded and illegal resource use increased (Henry & Douhovnikoff 2008; Kuemmerle et al. 2009). Poaching also increased substantially causing, for example, population collapses in saiga antelopes Saiga tatarica (Milner-Gulland et al. 2001) and Siberian tigers Panthera tigris altaica (Carroll & Miquelle 2006). This is worrying, because eastern Europe and the former Soviet Union are among the few regions in the world where large mammals still roam freely (Morrison et al. 2007). Several species persist there that were extirpated long-ago from most of the western Europe (DeVries 1995; Breitenmoser 1998).

Although poaching threatens large mammal populations in regions of eastern Europe, the post-socialist period has also brought a decreasing intensity of land use and declining rural populations (Ioffe, Nefedova & Zaslavsky 2004; Müller et al. 2009). Millions of hectares of farmland were abandoned as the region’s agricultural sectors collapsed and farmland was privatized (EBRD & FAO, 2008; Kuemmerle et al. 2008). As vast areas essentially rewild, some large mammals are extending their range westward in response (Enserink & Vogel 2006). Recent land use changes could afford substantial opportunities to conserve large mammals and restore their ecological roles. However, the fate of currently unused farmland remains uncertain and competing land use claims are likely (Verburg & Overmars 2009). To capitalize on this unique conservation opportunity, we urgently need to understand how recent threats like poaching interact with the opportunities afforded by newly available habitats to affect the persistence of large mammal populations.

European bison Bison bonasus L. only occur now in eastern Europe (Pucek et al. 2004; Krasinska & Krasinski 2007). The species were extirpated from the wild during the early 20th century with only about 50 bison surviving in zoos. Thanks to captive breeding followed by a reintroduction programme, today roughly 2600 wild bison are distributed in about 30 herds across eastern Europe (Krasinska & Krasinski 2007; Raczyński 2008). Despite these important conservation achievements, European bison face an uncertain future. All contemporary herds are small (only six herds exceed 100 bison) and isolated (Perzanowski, Olech & Kozak 2004; Pucek et al. 2004). Genetic diversity of the European bison population is low, with 90% of the combined gene pool provided by only seven founders (Pucek et al. 2004; Tokarska et al. 2009). The resulting effective population size of free-ranging bison appears to be too small to ensure long-term viability (Olech & Perzanowski 2002; Perzanowski & Olech 2007). In addition, poaching and trophy hunting have increased during the post-socialist period, especially in Ukraine where herds have declined substantially or been extirpated (Parnikoza et al. 2009).

The long-term persistence of European bison depends upon increasing the size of more herds to greater than 100 animals and connecting herds to establish a large bison metapopulation of several thousand animals (Pucek et al. 2004). To meet these conservation goals we need to know what determines the viability of contemporary bison herds, how local poaching affects metapopulation viability, which areas are becoming suitable for re-establishing herds and where active reintroductions should occur to link existing herds. Spatial metapopulation viability analysis is well-equipped to answer such questions (Akçayak 2000) and has been used to assess population viability in large mammals (e.g. Carroll & Miquelle 2006; Hamel et al. 2006; Linkie et al. 2006). Metapopulation models can also provide important insights into the cost-effectiveness of different conservation management strategies, for example, to design reserve networks (Moilanen & Cabeza 2002; Haight & Travis 2008), to minimize habitat protection costs (Haight et al. 2002a) or to optimize population management (Haight et al. 2002b; Lindsey et al. 2005). Yet, no study to date has analysed how different conservation strategies could affect the
metapopulation viability of European bison, or any other large mammal, in eastern Europe.

Here, we analyse the cost-effectiveness of different conservation management options on the viability of European bison populations in the Carpathians in eastern Europe. The Carpathians are among the few regions that could support a wild bison metapopulation (Perzanowski, Olech & Kozak 2004; Perzanowski & Olech 2007) as they provide ample habitat, much of which is currently unoccupied (Kuemmerle et al. 2010b). Our first goal was thus to assess European bison metapopulation viability in the Carpathians given current habitat patterns and herds. Our second goal was to compare the cost-effectiveness of three conservation management activities: (i) reintroductions; (ii) enhancing dispersal ability and (iii) anti-poaching measures, on European bison metapopulation viability.

Materials and methods

The Carpathians

The Carpathians of Central Europe extend over seven countries (Czech Republic, Poland, Slovakia, Hungary, Ukraine, Romania and Serbia), and are Europe’s largest mountain range (210 000 km², Fig. 1). Gentle slopes dominate the topography with elevations ranging from ~100 to 2665 m. The climate is temperate-continental with strong altitudinal gradients in mean annual temperature (9 °C in the plains to < 0 °C on mountain peaks) and precipitation (< 500 to > 2000 mm). There are four distinct zones of potential natural vegetation: foothills (< 600 m) dominated by beech Fagus sylvatica, hornbeam Carpinus betulus and oak Quercus spp; montane mixed forests with beech and fir Abies alba (600 to 1100 m in the north/1400 m in the south), subalpine coniferous forests (up to 1500 m/1800 m) with Norway spruce Picea abies, stone pine Pinus cembra; and alpine vegetation above the treeline (Webster, Holt & Avis 2001). Centuries of land use have created a mosaic landscape of forests, pastures and croplands. Yet, land use intensity remains relatively low so the region still harbours substantial old growth and semi-natural forests and high biodiversity (UNEP, 2007).

The Carpathians provide habitat for viable populations of all European large carnivores (brown bear Ursus arctos, wolf Canis lupus and lynx Lynx lynx, UNEP, 2007) as well as several large ungulates such as red deer Cervus elaphus, fallow deer Dama dama, roe deer Capreolus capreolus and wild boar Sus scrofa. European bison were reintroduced in the Carpathians during the 1960s, and in 2009 the region harboured five free-ranging herds (Pucek et al. 2004; Krasinska & Krasinski 2007): a western and eastern herd in the Polish Bieszczady Mountains (each ~150 animals), one herd in the Slovak Poloniny National Park (9), one herd in the northern Ukrainian Skole district (~15), and one herd in the southern Ukrainian Bukovyna region (~80) (Fig. 1).
As elsewhere in eastern Europe, the collapse of socialism reduced land use intensity and rural populations, allowing some areas of the Carpathians to rewild (Baur et al. 2006; Kuemmerle et al. 2008). All Carpathian countries except Ukraine recently joined the European Union, requiring them to enlarge protected area networks substantially (http://www.natura.org. UNEP, 2007). Together, these trends may represent unique opportunities to conserve large mammals and establish a Carpathian metapopulation of European bison.

**METAPOPULATION MODEL**

To analyse metapopulation viability of European bison in the Carpathians, we used the software RAMAS GIS 5.0. First, the programme analyses habitat structure to derive patches that can harbour populations and to characterize species’ dispersal ability. Secondly, a demographic matrix model is linked to each patch, allowing for spatial structure in population viability analyses and spatial variability in population dynamics (Akc¸akaya 2000, 2005).

We adopted the ecoregion defined by the Carpathian Ecoregion Initiative (Webster, Holt & Avis 2001), buffered by 30 km to include adjacent forests, but excluded the Serbian Carpathians as no bison exist there and the Danube River prevents dispersal. Habitat suitability (HS, scaled between 0 and 1) data were available from our previous research (Fig. 1b, Kuemmerle et al. 2010a). High-quality bison habitat in the Carpathians is characterized by a landscape mosaic including high forest cover, interspersed grasslands and low human impacts. We aggregated the HS map from its original 100 m resolution to 500 m using a median filter.

RAMAS GIS uses the continuous HS map to delineate a landscape that distinguishes patches of suitable habitat (i.e. with the potential to host a population) from background unsuitable habitat (i.e. matrix). We used HS thresholds of 0.5 and 0.6 representing the 25th and 50th percentile of the HS values within the contemporary bison ranges, respectively, to identify patches of suitable habitat. We clustered suitable cells into a single population if they were less than 2 km apart (see Appendix S1 Supporting Information). We derived separate patch maps for both spatial resolutions (100 and 500 m grain). To model the permeability of the background matrix for European bison dispersal (i.e. movements between two separate populations), we modelled a cost surface that incorporated both matrix quality and dispersal barriers (Akc¸akaya 2005) such as settlements, water bodies and major roads (Fig. 1c–e, see Appendix S1 Supporting Information).

To model bison population dynamics, we developed an age-structured matrix model (Caswell 2001) with annual time steps. We focused on the female segment of the population because: (i) male survival exerts only a minor influence on population viability of large ungulates (Gaillard et al. 2000); (ii) only about 50% of all male European bison participate in breeding (Daleszczyk & Bunевич 2009) and (iii) the sex ratio in larger herds is even (Krasinska & Krasinski 2007; Mysterud et al. 2007). Ungulate life cycles can be well-described by age-classes (Gaillard et al. 2000). We used a Leslie matrix model with 20 age-classes divided among calves (year 1), juveniles (2,3) and prime-aged adults (4,…, 20), as well as a senescent adult class (21 and older). Average vital rates for these four sets of age-classes were available from previous studies (Krasinski 1978; Gill 1998; Krasinska & Krasinski 2007; Daleszczyk & Bunевич 2009) (Table 1). Using the matrix model, we estimated λ and conducted elasticity analyses to identify key determinants of population growth (see Appendix S1 Supporting Information).

Density dependence in vital rates of ungulates is well-documented (McCullough 1975; Gaillard et al. 2000) and has been observed in both European (Mysterud et al. 2007) and American bison Bison bison (Plumb et al. 2009). We estimated carrying capacity (K) at 0.4 bison km\(^{-2}\) (=0.2 females km\(^{-2}\)) for the Carpathians, and included habitat quality when calculating K (see Appendix S1 Supporting Information for details). Only habitat patches that could support at least five females were deemed suitable habitat, corresponding to the smallest known free-ranging herds (Pucek et al. 2004). We assumed density-dependent recruitment (Fowler 1981) and adjusted growth rates using a Ricker-type function with a maximum finite rate of increase (\(R_{\text{max}}\)) of 1.19. Density dependence was based on all (female) individuals (see Appendix S1 Supporting Information).

Variability in environmental conditions (e.g. changes in winter severity or forage availability) can have strong effects on fecundity and survival of European bison (Krasinska & Krasinski 2007; Mysterud et al. 2007) and we therefore randomly sampled all vital rates from log-normal distributions with means taken from the Leslie matrix and SD available from the literature (Table 1). Environmental conditions in the Carpathians vary along latitudinal and elevation gradients and we therefore modelled covariation in environmental stochasticity among two populations as a negative exponential function of the distance between these populations (see Appendix S1 Supporting Information).

Dispersal rates (% of source population migrating to a target patch) between patches were based on a negative exponential function (Akc¸akaya 2005). We parameterized low, medium and high dispersal scenarios. We also included density dependence in dispersal rates and assumed maximum dispersal distances of ~90–100 km (see Appendix S1 Supporting Information).

Our base metapopulation model included the four contemporary Carpathian bison herds with 2009 population numbers (see above), assuming even sex distribution and stable age distributions (inferred from the matrix model). At the time of writing, no exchange was occurring among herds except for the Slovak and western Bieszczady herds that we consequently modelled as a single population. Our base model also included an additional herd of 10 female bison to be reintroduced in northern Romania in 2010 (Fig. 1b). We estimated average poaching rates in the Ukrainian populations at 20% of the population annually (see Appendix S1 Supporting Information). We used 1000 replications and a simulation period of 100 years.

**SENSITIVITY ANALYSES**

To assess how robust our metapopulation model was to uncertainty in parameter estimates, we compared model runs for the two different HS thresholds (HS = 0.5 and HS = 0.6) and the two spatial resolutions of the habitat map (100 and 500 m, for a 150 x 150 km\(^2\) subset...
of the study region). We also varied mean demographic rates (by −5%, −2%, −1% and +1%), environmental stochasticity (SD of demographic rates by −20%, −10%, +10% and +20%), carrying capacity (by −25%, −10%, +10% and +25%) and \( R_{\text{max}} \) (−10%, 5%, +5% and 10%). We compared metapopulation runs for our low, medium and high dispersal scenarios. Finally, we compared model runs using time horizons of 100 and 200 years, and 1000 and 10 000 model replications.

**MANAGEMENT SCENARIOS**

We considered three European bison conservation management options: (i) reintroductions; (ii) enhancing dispersal ability via wildlife overpasses; (iii) anti-poaching strategies. We assumed reintroductions of 10 female bison (mixed age group, no calves, distributed among age classes so as to approximate the stable age distribution of our matrix model) and a sufficient number of bulls to ensure reproduction. We selected all patches that had a carrying capacity of at least 50 female bison (Pucek et al. 2004) and that included a protected area of at least 50 km², and we modelled reintroductions for each patch separately. Wildlife overpasses can substantially enhance habitat connectivity for large mammals (Gloyne & Clevenger 2001; Van Wieren & Worm 2001). Based on the network of permanent barriers and the metapopulation map, we selected 11 locations for potential wildlife overpasses. We then recalculated dispersal rates without these barriers, and ran the metapopulation model separately for each potential overpass. To assess the effect of anti-poaching strategies on metapopulation viability, we reduced poaching levels from 20% in the base model to 10% and 5% in each of the Ukrainian populations separately. Finally, we assessed the effect of combining different conservation management options.

To compare among our scenarios, we extracted the probability that metapopulation size will remain below 1000 female bison during the simulation period of 100 years (\( P_{\text{1000}} \)). We chose this threshold, because a minimum \( N_c \) of 50 has been suggested for European bison (Pucek et al. 2004) and the ratio of \( N_c \) to \( N \) is as low as 0.07 for American bison (Frankham 1995), and likely to be even lower for European bison due to high inbreeding (Olech & Perzanowski 2002; Pucek et al. 2004; Traill, Bradshaw & Brook 2007). We also extracted total bison population (TBP), metapopulation occupancy (MO) and the number of herds exceeding 100 animals (i.e. 50 females, N50) for each scenario. For all these measures, we calculated confidence intervals based on the Kolmogorov–Smirnov test statistics and 1000 replicate runs (Akçakaya 2005).

The cost-effectiveness of all scenarios was compared by first calculating the increases in metapopulation viability for each scenario relative to our base model and second dividing these increases by the cost of a scenario (in 1000€). We assumed a cost of 250 000 € for a reintroduction project, based on the costs of previous European bison reintroduction projects in the Carpathians in which we have been involved (for the herds in Poland, Slovakia and Romania). The average cost for a wildlife overpass was estimated at 2 000 000€ based on a European-wide assessment of wildlife crossing structures (Bank et al. 2002; Trocme et al. 2003) as well as cost estimates from Canada (Gloyne & Clevenger 2001; Huijser et al. 2009). Safeguarding a herd from poaching was estimated at 20 000€ for one ranger per year (i.e. salary, initial costs for a jeep and equipment and running costs) and we assumed one ranger for herds with a \( K < 25 \) female bison, two for herds with \( K < 50 \), three for herds with \( K < 100 \) bison and four for herds with \( K > 100 \). We assumed reducing poaching levels to 5% would be twice as costly as reducing poaching levels to 10% and that anti-poaching measures would be necessary for 20 years.

**Results**

We identified potential habitat for 151 European bison populations in the Carpathians using a HS threshold of 0.5. If fully utilized, these habitats together could support up to a total carrying capacity of 8038 female bison. Large patches were frequent in the Ukrainian and Romanian Carpathians (Fig. 2), where the three largest potential populations occurred (578 and 510 bison in Ukraine, and 421 in south-western Romania). In contrast, almost all potential populations in the Polish and Slovak Carpathians were small (<100 individuals), except for the Bieszczady Mountains in south-eastern Poland where four habitat patches could support a combined population of 401 bison (Fig. 2).

Our more realistic base model predicted more modest increases in the Carpathian metapopulation of European bison up to an eventual average final abundance of 1015 female bison (95% CI: 715–1436) after 100 years (Fig. 3). European bison colonized 23 new patches, mainly during the first half of our simulation. With barriers inhibiting dispersal into much of the Carpathian range in our base model, we observed a mean metapopulation occupancy of only 18%. On average, 1568 bison were poached or harvested in Ukraine. Nevertheless, the extinction risk of the European bison metapopulation was relatively low, with a probability


Fig. 2. (a) Potential European bison populations and their carrying capacities (K) and (b) histogram of K.
Fig. 3. (a) Metapopulation trajectory and metapopulation occupancy of the base model (i.e. current habitat and herd distribution, HS = 0.5, medium dispersal). (b) Relative changes in metapopulation trajectories and occupancy when varying vital rates (age matrix means), environmental stochasticity (age matrix SD), carrying capacity and the maximum intrinsic growth rate ($R_{\text{max}}$).
of <5% that bison numbers will remain below 700 animals (and <1% for <570 bison) during the next 100 years. The probability that the bison metapopulation will not reach 1000 female animals ($P_{1000}$) during the next 100 years was 53%. Six herds exceeded 100 animals (N50) in our base model at the end of our simulation period.

Our metapopulation model was relatively robust to small changes in mean survival and fecundity (Fig. 3b). Decreasing survival and fecundity did not affect patch colonization substantially, but local extinctions became more common, leading to reduced mean patch occupancy. Altering environmental variability also did not affect projections substantially (Fig. 3b). In contrast, varying $K$ had a marked effect, with faster colonization and higher patch occupancy for lower $K$ and vice versa (because dispersal is density-dependent, Fig. 3b). Finally, our metapopulation model showed marked sensitivity towards changes in $R_{max}$, with up to 50% higher abundances when increasing $R_{max}$ by 10%. Colonization also occurred faster and more patches were occupied for higher $R_{max}$ values (Fig. 3b). The three dispersal scenarios resulted in markedly different metapopulation occupancy patterns (Fig. 4). All accessible patches (27) were colonized in the high dispersal scenario vs. 13 patches in the low dispersal scenario (19 in the base model) with corresponding differences in the estimated final population sizes (1304 and 773 in the high and low dispersal scenarios respectively). Extending our base metapopulation model to 10 000 replications or 200 years did not affect the average trajectory, but more replications decreased SE.

Increasing, the HS threshold from 0.5 to 0.6 reduced the number of potential populations from 151 to 114 patches and these patches were substantially smaller than in the base model, resulting in a total potential carrying capacity of 4449 bison. Predicted average abundance after 100 years decreased from 1015 to 673 bison although patch occupancy remained similar. Extinction risk rose markedly for an HS threshold of 0.6 (e.g. 98% probability of $P_{1000}$ after 100 years compared with 53% in the base model; only five herds could exceed 100 animals in this scenario). In contrast, changes in the spatial resolution of our habitat map had little effect.

Our base model identified 26 unoccupied habitat patches that satisfied our criteria for reintroductions (i.e. $K > 50$ and protected area $> 50$ km$^2$, Fig. 5). Modelling reintroductions for each patch separately resulted in a median decrease of 47% in $P < 1000$ (probability of female bison population $< 1000$ after 100 years), an average increase in TBP of 32%, a mean increase in MO (mean occupancy) of 24% and a mean increase in N50 (number of herds larger 100 animals) of 34%. However, these viability estimates varied among the reintroduction scenarios with SD of 18%, 22%, 19% and 29% for $P_{1000}$, TBP, MO and N50 respectively. Thirteen patches occurred in Ukraine (Fig. 5). Implementing anti-poaching measures for each of these 13 patches separately only improved viability slightly, except for the largest patch and the patch containing the Bukovyna herd (e.g. reducing $P_{1000}$ by 53% and resulting in higher patch occupancy). Reducing poaching levels to 10% instead of 5% did not affect viability estimates substantially.
Constructing wildlife overpasses, however, was predicted to affect metapopulation viability greatly, reducing mean P1000 by 29% and increasing TBP, MO and N50 by 29%, 35% and 17% respectively. The effects of adding overpasses also varied substantially (e.g. 0% to 53% decrease in P1000).

Based on these results, the cost-effectiveness ranking of our scenarios (see below), as well as expert knowledge (i.e. regarding the placement of wildlife overpasses), we modelled nine scenarios that combined different management options: three scenarios each for combining (i) one reintroduction and one anti-poaching measure; (ii) one reintroduction with one overpass and (iii) multiple reintroductions (one scenario each for two, three and four reintroductions). Combining reintroductions and anti-poaching efforts did not increase metapopulation viability substantially compared with reintroductions alone (e.g. <5% decrease in P1000, <10% increase in MO). In contrast, combining even a single wildlife overpass with one reintroduction strongly increased metapopulation viability compared with reintroductions alone (e.g. up to P1000 of 0%, 30% increase in TBP, 50% increase in N50). Multiple reintroductions had the strongest effect on metapopulation viability, increasing TBP up to 224%, MO up to 110% and N50 up to 267%.

The potential distribution of bison in the Carpathians varied substantially among the different scenarios (Fig. 6). Wildlife overpasses and reintroductions both allowed European bison

![Fig. 6. Metapopulation occupancy for three reintroduction scenarios (first row), three anti-poaching scenarios (second row), three wildlife overpasses (third row) and three combined scenarios (bottom row). Patches where management options were implemented are marked ⊗.](image-url)
to colonize much habitat, but colonization rates were higher and more patches were colonized following reintroductions. Our results also showed that the southern and north-western Carpathians are dissected strongly by dispersal barriers (i.e. many patches close to source populations remained uncolonized), whereas in northern Romania, introducing a single herd led to the predicted colonization of most habitats. Anti-poaching activities increased the probability of colonization of adjacent patches, but only if large patches were protected (Fig. 6).

Reintroductions emerged as the most cost-effective option to increase population viability in our comparisons of the cost-effectiveness of different bison conservation strategies (Fig. 7), accounting for 20 or more of the 25 most cost-effective scenarios across all viability measures. Reintroductions in Calimani National Park (northern Romania, scenario R19), the Cindrel Mountains in southern Romania (R24) and in Magurski National Park (Poland, R4) were the most cost-effective reintroduction scenarios (see Supporting Information). Wildlife overpasses could also improve viability substantially, especially when combined with reintroduction projects, but tended to be costly. Coupling a reintroduction project in northern Romania with an overpass to connect this region to neighbouring Ukraine emerged as the most cost-effective combined scenario (see Appendix S2 Supporting Information). As the costs of anti-poaching strategies scaled with patch size in our model, protecting herds from poaching emerged as the least cost-effective management option (e.g. anti-poaching strategies for the largest patches in Ukraine increased viability substantially, but the cost-effectiveness of conservation management remained low due to the high costs of anti-poaching strategies).

Fig. 7. Cost-effectiveness of different European bison conservation management options regarding four metapopulation viability measures: (a) risk of total population < 1000 female bison after 100 years, (b) total female bison population after 100 years, (c) metapopulation occupancy and (d) number of populations exceeding 100 animals (>50 female bison) after 100 years (markers = median of viability change compared with the base scenario of all scenarios with the same conservation management strategy; whiskers = ±1SD; all values measure improvement relative to the base model).
Discussion

Habitat loss and over-exploitation threaten large mammals worldwide. Preserving their populations in increasingly human-dominated landscapes is thus a grand challenge of conservation biology. European bison, Europe’s largest land mammal and last surviving large grazer, today only occur in small and isolated herds. Our results show that conservation management could increase bison numbers and the connectivity among herds substantially. Conservation goals are met in many of our scenarios, suggesting that the Carpathians could support a viable metapopulation provided that the steps are taken to expand and protect existing herds. The collapse of socialism and subsequent EU expansion has reduced human presence and enhanced nature protection in some parts of the Carpathians. Despite increased poaching in the post-socialist period, we may be facing a ‘hot moment’ for implementing the first comprehensive plan to sustain the European bison metapopulation. Our model suggests that reintroductions, the main conservation strategy during the last decades, is the most cost-effective approach for establishing such a metapopulation, especially when reintroducing several herds or when coupling reintroductions with wildlife overpasses to improve connectivity among herds.

Our metapopulation models suggest that even without management intervention, the Carpathian population of European bison could, if allowed, increase substantially during the 21st century (about fivefold in our base model). Much of this increase depends upon their ability to recolonize more of their former range (Fig 6), which requires local populations to rise markedly (dispersal was density-dependent in our model). Barriers to dispersal exclude bison from much of the Carpathians and inhibit animal movements and thus genetic exchange among herds. Even aside from these difficulties, the probability that bison numbers in our base model reached the conservation goal of 1000 female bison (N_e ~ 50) was only 47% and average abundance (1015) was only slightly higher than this goal. This is troublesome in light of the uncertainty we face in the ecological and social carrying capacity (i.e. acceptable population levels in landscapes managed for both, land use and conservation) of European bison (Krasinska & Krasinski 2007). Active conservation management will therefore be necessary to establish and sustain such a metapopulation. The most promising management option to expand the range of European bison in the Carpathians and boost population numbers. Several large but currently unoccupied habitat patches exist that include protected areas. These are obvious starting points for reintroductions, especially in northern and southern Romania. These areas also contain relatively few dispersal barriers, potentially allowing bison to recolonize larger areas of unoccupied habitat. Our metapopulation model also suggests that because the ongoing reintroduction project in Romania occurs in an isolated patch of habitat, further reintroductions will be necessary if bison are to recolonize other Romanian patches (Fig. 6). Any strategy focused solely on reintroduction though, would confront the disadvantage that barriers (mainly highways) inhibit exchange among herds.

Wildlife overpasses, properly placed to improve connectivity, substantially improved the viability of the European bison metapopulation in our models. Moreover, overpasses would be likely to prove crucial for allowing bulls to disperse among herds, fostering genetic exchange and thus preventing further erosion of genetic diversity. Wildlife crossings now provide movement corridors for many wildlife species while increasing traffic safety, often outweighing the relatively high construction costs (Gloyne & Clevenger 2001; Van Wieren & Worm 2001). Infrastructure is currently being developed in much of the region as most Carpathian countries have joined the EU (UNEP, 2007). Given the importance of this region as a hotspot of large mammal diversity and the fact that wildlife crossings only increase the total cost of a road project by 7–8% (Bank et al. 2002), maintaining and improving ecological corridors in the Carpathians should be a priority (UNEP, 2007; Huck et al. 2010).

In our models, reactive anti-poaching strategies emerged as less cost-effective than reintroductions and overpasses in improving metapopulation viability. High poaching rates in Ukraine, however, represent real threats that should not be ignored. Poaching reduced patch colonization and dispersal rates substantially in our models. Field evidence also suggests that poaching rates may have increased further since the last census (2009), potentially threatening the existence of the Ukrainian herds. This is particularly worrisome considering that Ukraine emerges as a key area in all our models, connecting the northern and southern Carpathians. The root causes of poaching in Ukraine are corruption, an inadequate legal framework, weak law enforcement and poverty. Ironically, many trophy hunts are carried out under the guise of precautionary culling (e.g. of sick animals, Parmikoza et al. 2009). Addressing poaching will therefore not only require adequate law enforcement (which we modelled), but also a combination of legal measures including improved species’ protection status, capacity building through education and local participation and long-term conservation programmes. Our analyses demonstrate that relatively large numbers of bison could be harvested without substantially affecting metapopulation viability. As substantial demand for European bison trophies exist, sustainable harvesting could generate conservation funds, mitigate human-wildlife conflict and complement rural incomes.

Our results clearly suggest that the Carpathians could harbour a viable metapopulation of European bison, and that moderate efforts of conservation management could suffice to establish and sustain such a metapopulation. The most promising strategy appears to be reintroducing subpopulations, particularly in the border region of Romania and Ukraine. The addition of a few strategic wildlife overpasses (e.g. bridging north-south running highways in the eastern Carpathians) would further benefit not only the European bison but also large mammals and Carpathian biodiversity generally. Human pressures in many rural areas of the Carpathians have declined following the collapse of socialism and protected area.
networks and infrastructure expand in the new EU countries. This suggests that we may be facing particularly a favourable time to implement these conservation management options and establish a bison metapopulation.

Our metapopulation model was based on demographic parameters derived from long-term (>40 years) studies of bison population dynamics and a HS map derived from a comprehensive set of bison locations (Kuemmerle et al. 2010a). Sensitivity was high towards changes in \( R_{\text{max}} \). Yet our \( R_{\text{max}} \) estimates were very similar for both herds we assessed and nearly identical to two independent assessments (Mysterud et al. 2007; Daleszczyk & Bunevich 2009). Varying carrying capacity and the HS threshold affected our results noticeably and in similar ways. Though we calculated \( K \) based on available winter forage and our estimate agreed closely with estimates from the Białowieża Forest and the \( K \) of wood bison \emph{Bison bison} in North America (see Appendix S1 Supporting Information), we cannot fully rule out uncertainty in this parameter. The main goal of our scenario simulation was to compare conservation management options. Changes in \( K \) would only affect absolute bison numbers, and not our main conclusions. Varying dispersal rates also affected our results markedly. We carefully parameterize our dispersal functions using available field observations and our base model resulted in realistic occupancy patterns. Dispersal is likely to be density-dependent, yet no Carpathian bison herd is currently at carrying capacity. Dispersal rates and matrix permeability therefore remain weakly understood and further research along these lines is urgent. If dispersal rates were lower than assumed in our base model, we expect the importance of additional reintroductions to increase, whereas the effectiveness of wildlife overpasses would increase if European bison dispersal was higher than assumed in our base model. Finally, we did not model predation explicitly. Predation of European bison by brown bears in the Carpathians has been rare (five reported cases since the 1960s). Romania harbours large populations of bears, and it is possible that predation will increase as bison are released there and more animals approach senescence. How this would affect metapopulation viability is unknown.

While our ecoregion-wide assessments is useful for highlighting key areas for the conservation of European bison in the Carpathians, we recommend our model should be run with a larger number of strategies (e.g. systematically varying the number and timing of reintroductions, and the number and age distribution of the animals reintroduced, and target locations) before conservation strategies are implemented. Likewise, fine-scale assessments of habitat quality (e.g. forage availability) and conflict potentials with land use and people in candidate sites for reintroductions and wildlife overpasses should complement our broad-scale assessment. Finally, the costs of conservation management activities we used represent average estimates and will probably vary among countries. Also, our cost-effectiveness analyses did not include the indirect costs of a large bison population (e.g. damage to crops) nor the benefits from such a population (e.g. via trophy hunting). Furthermore, we did not quantify the additional benefits of particular conservation management options such as increased traffic safety and improved ecological corridors in the case of wildlife overpasses. Site-specific cost–benefit assessments that link economic models and metapopulation models should therefore be carried out for the target areas we identified.

Large mammals struggle to survive in human-dominated landscapes around the globe. Our results highlight that incorporating cost-effectiveness analyses into metapopulation models can elucidate the relative value (gain per unit cost) of different conservation management options, allowing the decision-maker to choose cost-effective options to preserve wildlife. While our ecoregion-wide approach does not replace fine-scale habitat assessments and conservation planning, metapopulation models can help us to target conservation actions, and to harmonize conservation planning across large areas and political borders. Our cost-effectiveness analysis of European bison metapopulation viability also shows how careful conservation planning and assessment of different conservation options can enable the establishment of a large metapopulation of this ungulate. Our study thus provides hope for the future of European bison in the Carpathians, one of the last relatively wild areas in Europe, and for restoring the bison’s key ecological role.

Acknowledgements

We would like to thank A. Bar Massada, M. Dubinin, A. Estes, A. Pidgeon and C. Rittenhouse for fruitful discussions; and A.-T. Bashta, O. Chaszkovskyy, L. Halada, J. Kozak, I. Kruthlov and K. Ostopowicz for helping to generate the habitat suitability map. Three anonymous referees and the editors J. Jones and P. Stephens are thanked for very constructive and thoughtful comments on prior manuscript versions. We gratefully acknowledge the support by the Alexander von Humboldt Foundation and the NASA Land-cover and Land-Use Change Program.

References


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**Supporting Information**

Additional Supporting Information may be found in the online version of this article.

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**Appendix S1**: Metapopulation model parameterization.

**Appendix S2**: Additional results.

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Supporting Information for the manuscript:

Cost-effectiveness of different conservation strategies to establish a European bison metapopulation in the Carpathians

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Appendix S1: Metapopulation model parameterization

Overview

To analyze the metapopulation viability of European bison in the Carpathians, we used the software RAMAS GIS 5.0 (Akçakaya, 2005, www.ramas.com). The program and its modeling approach (Fig. S1) have been described in detail in several previous publications (Akçakaya, McCarthy & Pearce, 1995; Akçakaya, 2000, 2001; Akçakaya et al., 2004b). The program has been applied to hundreds of cases involving a wide variety of species, geographic scales, and applications (Akçakaya et al., 2004a).

Fig. S1: Overview of the data sets and analyses used to parameterize the sub-models of the European bison metapopulation model (DD = density dependence).

Habitat structure

HS_THRESHOLDS AND NEIGHBORHOOD DISTANCE

RAMAS GIS uses the continuous habitat suitability (HS) map in several different ways. To delineate populations, it converts the HS map into a binary landscape of patches (i.e., areas that can hold populations) and background (i.e., matrix between such potential populations). It also uses the total or average HS in each population to calculate patch- or population-specific parameters (see below). We analyzed the distribution of HS values of areas currently inhabited by European bison in the Carpathians and used HS thresholds of
0.5 (approximately the first quartile of the HS distribution) and 0.6 (approximately the median of this distribution) to derive two patch maps (Fig. S2).

Groups of suitable habitat cells occurring in close proximity (defined in RAMAS via the so-called neighborhood distance) were considered as one patch because the program assumes that one panmictic population inhabits each such patch. We used a neighborhood distance of 2 km based on observed average foraging distance and home range radius in the Carpathians. To test the effect of changes in spatial resolution in the habitat suitability map on our habitat structure, we derived separate habitat patch maps for both spatial resolutions (100 m and 500 m) for each HS threshold (HS = 0.5 and HS = 0.6).

Fig. S2: Distribution of habitat suitability values inside the ranges of the five European bison herds in the Carpathians (Kuemmerle et al., 2010). Whiskers mark the 10th and 90th percentile of all HSI values.

**COST SURFACE APPROACH AND DISPERSAL BARRIERS**

We used a cost surface approach to model the permeability of the background matrix for European bison dispersal (i.e., movements between two separate populations). This approach uses a friction surface, where each gridcell value represents the relative cost of dispersing through that cell, to calculate the least-cost pathway from one population to another (Eastman, 1989). Thus, cost surface analysis allows incorporating matrix quality and dispersal barriers when evaluating the connectivity among populations (Akçakaya, 2005). To derive a friction surface for our study region, we used the inverse habitat suitability index as a proxy for dispersal cost for all areas outside habitat patches and linearly scaled habitat suitability from 1 (HS >= 0.5) to 10 (HS = 0). Areas with HS > 0.5 outside habitat patches (i.e., habitat patches smaller 25 km² that may function as stepping stones) were assigned the base cost of 1. We considered four types of dispersal barriers: settlements, lakes, rivers, and roads (Fig. 1). Settlements were derived from the CORINE 2000 land cover map (CLC2000, 100 m resolution, www.eea.europa.eu/data-and-maps) and from digital topographic maps (1:200,000) in the case of Ukraine, which is not covered by CLC2000. Digital maps of lakes and streams were available from the Pan-European River and Catchment Database (version 2.1, http://ccm.jrc.ec.europa.eu). We
extracted all lakes larger than 15 ha and stream segments with a stream order index (SOI) of four or larger, because we assumed ponds and narrow creeks did not to represent dispersal barriers for bison. A digital road network was available from the ESRI Data and Maps Kit 2008 and we used all highways (level 0) and major roads (level 1 and 2). We assumed all settlements, lakes, highways, and large rivers (SOI > 4) to represent full dispersal barriers. Although rare, European bison have been observed to cross major roads and smaller rivers (SOI = 4 in our case) and we specified a dispersal cost value of 200 for such landscape elements (see Fig. 1, main document). In other words, dispersing through 200 cells of high-quality habitat (HS >= 0.5) is equally costly than dispersing through 20 cells of low-quality habitat (HS = 0) or one partial barrier. We did not consider topography as a factor limiting dispersal because bison inhabit higher elevations and steeper slopes in the Caucasus than those occurring in the Carpathians (Pucek et al., 2004; Krasinska & Krasinski, 2007). Once the friction map was available, we calculated least-cost, edge-to-edge distances between all patches (Akçakaya, 2005).

Demographic model

VITAL RATES

Vital rates were available from long-term monitoring of European bison population dynamics from the Białowieża Forest that hosts the oldest and largest free-ranging bison herds (Krasinski, 1978; Krasinska & Krasinski, 1995, 2007; Gill, 1998). The proportion of breeding females was estimated at about 40% once bison populations stabilized (Mysterud et al., 2007; Daleszczyk & Bunevich, 2009) and we therefore used a fecundity rate of 20% for our female-only model (offspring sex ratio is close to 1:1, Daleszczyk & Bunevich, 2009). Mean mortality rates for calves, juveniles, and adults were estimated separately for males and females based on population records from 1960 – 2005 for the Polish herd, and 1971 – 2005 for the Belarusian herd (Daleszczyk & Bunevich, 2009). Mortality rates were overall relatively similar among the two herds (with the exception of calf mortality, see Daleszczyk & Bunevich, 2009) and we chose the higher values to be conservative. Mortality rates for senescent females were not available and we therefore reduced the adult survival rate until 99% of senescent females did not exceed 25 years of age (the maximum recorded longevity of a free-ranging female bison was 27 years, Krasinska & Krasinski, 2007).

MODEL ELASTICITY

We carried out an elasticity analysis of our matrix model by evaluating changes in the finite rate of population growth at equilibrium (i.e., the dominant eigenvalue $\lambda$) in response to proportional changes in vital rates (Caswell, 2001). We systematically altered
all vital rates from 50% to 150% (at 1%-increments), derived $\lambda$, and plotted an elastogram (Kohlmann, Schmidt & Garcelon, 2005). We varied only one parameter at the time and did not allow survival rates to exceed one.

Our age-structured matrix model had an intrinsic growth rate ($\lambda$) of 1.097. Elasticity of $\lambda$ was highest for changes in calf and juvenile survival, followed by adult survival (Fig. 3). Elasticity of individual age classes in our model towards changes in survival rates was strongest for younger age classes, and decreased as animals approached senescence, where zero elasticity occurred. Similarly, the elasticity from changes in fecundity was strongest for younger age classes. Note that the sum of elasticities across reproductive age classes was higher (0.58) than the elasticity sum of non-reproductive age classes (0.32), thus following the general pattern of large ungulates (Gaillard, Festa-Bianchet & Yoccoz, 1998; Gaillard et al., 2000). As expected for a long-lived animal, elasticity of survival rates was always higher than the elasticity of fecundity for a given age class (Fig. S3).

![Elastogram of our age-structured European bison population model](image)

**Fig. S3:** Elastogram of our age-structured European bison population model. Each line depicts changes in the population growth rate ($\lambda$) when systematically varying one matrix element (i.e., survival rate or fecundity). Darker colors refer to younger age classes. The steeper the slope of a particular line, the more sensitive the population model reacts towards changes in this parameter.

**DENSITY DEPENDENCE**

Ecological carrying capacity for European bison has so far not been assessed quantitatively, because most herds are small, have only recently started to approach such...
limits, or receive additional feeding in winter (Krasinska & Krasinski, 2007). Indications of density dependence (switch to alternative food sources, increased dispersal, decreasing fecundity, etc) were found at densities of 0.5 – 0.6 bison / km² in the Białowieża Forest, where the population may have exceed carrying capacity in recent years (Krasinska & Krasinski, 2007; Mysterud et al., 2007). For the Carpathians, we estimated a carrying capacity of 0.4 bison / km² (= 0.2 females / km²) based on available winter forage (~150kg of dry mass / ha) and average forage intake of adult bison (~ 6kg/day equaling about 1 ton per winter) (Perzanowski et al., 2005). This density coincides well with estimations of American bison carrying capacity in Yellowstone and Wood Buffalo National Park (Plumb et al., 2009), with long-term densities of European bison in the Białowieża Forest in the presence of other ungulates (Jedrzejewska et al., 1997), as well as with social carrying capacities that have been suggested for European bison in Central Europe (Krasinska & Krasinski, 2007). To consider habitat quality in the calculation of carrying capacity (K), we derived K for each patch j as (Eqn. S1):

\[ K_j = \frac{PHS_j \times (TA*0.2)}{THS} \]  

where PHS determines the total habitat suitability of a patch, TA the total area of all patches in the landscape, and THS the total habitat suitability of all patches in the landscape. Thus, carrying capacity of a patch (K) is a simple, scalar function of the total habitat suitability in that patch, with the multiplier determined by the estimate of an overall, range-wide average of 0.2 females per km². We only considered habitat patches that could support a population of at least 10 European bison (5 females) at carrying capacity, equivalent to the smallest free-ranging bison herds (Pucek et al., 2004). Patches that could not support this minimum population size were absorbed into the background matrix. We assumed scramble-competition density dependence that is typical for ungulates (Fowler, 1981; Bonenfant et al., 2009) and that assumes all animals of a population are affected similarly by decreasing resources as populations reach carrying capacity (Akçakaya, 2005). While density dependence in European bison populations has a marked effect on fecundities, no density dependence in mortality rates was found (Mysterud et al., 2007) and we therefore kept survival rates density independent. RAMAS GIS models scramble density dependence by adjusting recruitment rates based on a Ricker-type (i.e. logistic) function. To estimate the maximum finite rate of increase (Rₘₐₓ), we calculated R as \( \frac{N(t+1)}{N(t)} \) (where N is the female population size) based on population records from the Białowieża Forest (Krasinska & Krasinski, 2007). R was calculated separately for the Polish and Belarusian herds for each year with available data from 1960 – 2006 (n= 46 and n= 26, respectively).
We then fitted a linear regression model of $R$ vs. $N(t)$ to each herd (Fig. S4), and derived the intercepts that are an estimation of $R_{\text{max}}$ for each herd. Intercepts were very similar (1.21 and 1.18, respectively) and we used the mean value ($R_{\text{max}} = 1.19$) for our metapopulation model. This is nearly identical to earlier, independent (based on fecundity rates) estimations of $R_{\text{max}}$ (Mysterud et al., 2007) and coincides well with estimated maximum fecundity rates (Daleszczyk & Bunevich, 2009). Density dependence was based on all (female) individuals in a herd.

**Metapopulation model**

**STOCHASTICITY**

We incorporated environmental stochasticity by randomly sampling all vital rates from a log-normal distribution with means taken from the Leslie matrix and standard deviations available from prior work in the Bialowieża Forest (Table 1, main document). We used standard deviations for the female population segment only (Daleszczyk & Bunevich, 2009) and we used the same values for reproductive and senescent adult survival, because separate standard deviations were not available.

Environmental conditions in the Carpathians vary along latitudinal and elevation gradients and we therefore did not assume that environmental stochasticity would affect all population similarly across the entire ecoregion. RAMAS GIS models co-variation in environmental stochasticity ($C_{ij}$) among two populations $i$ and $j$ as a negative exponential function of the distance between these populations ($D_{ij}$) (Eqn. S2):

$$C_{ij} = -e^{-\frac{D_{ij}}{b}}$$

**Eqn. S2**
We estimated the coefficient $b$ based on annual time series of mean minimum winter temperature (Julian day 1 - 59) as a measure of winter severity. We calculated mean minimum temperature from the E-OBS European-wide daily gridded climate surfaces (Haylock et al., 2008), that were derived for 1950 – 2008 at a resolution of 0.25 degrees using a comprehensive set of climate stations and provide climate grids. We sampled 1,000 random locations from the Carpathian ecoregion and calculated Pearson’s correlation coefficient ($\hat{C}$) between each pair of time-series as well as the distance between each pair of locations. The denominator $b$ was then estimated by minimizing (Eqn. S3):

$$\text{Min} \rightarrow \sum (C_y - \hat{C}_y)^2$$

Eqn. S3

where $C$ was calculated using Eq. 3. This yielded a coefficient $b$ of 2100 (i.e., correlation of ~0.6 at distances of 1,000 km). We also included demographic stochasticity in our model by drawing the number of survivors and dispersers from a binomial distribution and the number of calves from a Poisson distribution, thereby avoiding bias at small population sizes due to fractional survivors or dispersers (Akçakaya, 2005).

DISPERSAL

Dispersal refers to the movement of animals from a source to a target patch. Studies examining European bison are scarce, and the few existing ones suggest that solitary males account for most dispersal events, especially across longer distances. Female and mixed groups are characterized by high site fidelity and almost all dispersal events involving females are less than 10 - 15 km, with a maximum reported dispersal distance of approximately 50 km (Perzanowski and Januszczak, in prep., Krasinska & Krasinski, 2007). No study has explicitly assessed European bison dispersal in the Carpathians, although movement patterns of radio-collared female bison suggest maximum individual movements of approximately 30-40 km (measured within one population, Perzanowski, Woloszyn-Galeza & Januszczak, 2008). Density dependency in dispersal is well-documented for American bison populations (Larter & Gates, 1990; Fuller, Garrott & White, 2007; Plumb et al., 2009). There is evidence that density-driven dispersal behavior also exists in European bison populations (Krasinska & Krasinski, 2007), meaning that current dispersal rates could be low, because most populations are well below carrying capacity. Moreover, whereas all reported dispersal events measure Euclidian distances, our metapopulation use cost-distances to incorporate matrix quality and barriers.

RAMAS GIS calculates dispersal rates ($M = \%$ of source population $i$ migrating to a target patch $j$) between patches based on the least-cost distance between them using a negative exponential function (Eqn. S4, Akçakaya, 2005).
To reflect uncertainty in our knowledge about European bison dispersal, we parameterized three dispersal functions representing low, medium, and high dispersal scenarios (Fig. S5, Table S1).

Fig. S5: High, medium, and low dispersal scenario. All dispersal scenarios had a maximum dispersal (cost) distance of 500, equaling about 90-100 km in standard-quality matrix.

We modeled density dependence by linearly scaling dispersal rates in relation to population size (full dispersal at carrying capacity; dispersal rate of zero at N=0). We assumed a maximum dispersal cost distance of 500 for all dispersal scenarios, corresponding to a Euclidian distance of ~90-100 km.

Table S1: Dispersal rates (% of female source population migrating to a target patch) for the three different dispersal scenarios at cost distances of 5 (~ 2-3 km in standard-quality matrix), 100 (~ 20-30 km) and 400 (~50-60 km).

<table>
<thead>
<tr>
<th>Cost distance</th>
<th>Low dispersal</th>
<th>Medium dispersal</th>
<th>High dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>2%</td>
<td>5%</td>
<td>10%</td>
</tr>
<tr>
<td>100</td>
<td>0.25%</td>
<td>1%</td>
<td>3%</td>
</tr>
<tr>
<td>400</td>
<td>0.02%</td>
<td>0.1%</td>
<td>0.5%</td>
</tr>
</tbody>
</table>

**BASE MODEL AND POACHING**

We included the four contemporary Carpathian bison herds with 2009 population numbers, assuming even sex distribution. Herd sizes for these populations were: Western Bieszczady / Slovak herd ~ 80 female bison, Eastern Bieszczady herd ~ 75 females, Skole herd ~ 7 females, and Bukovynska herd ~ 40 females. We distributed animals among the age classes according to the stable age distribution of our matrix model. We
also included an additional herd of 10 female bison to be reintroduced to the Vanatori Neamt National Park (northern Romania, Fig. 1b, main document). These bison were at the time of writing acclimatized in an enclosure and their release was scheduled for summer 2010.

Poaching and trophy hunting of European bison have recently been widespread in the Ukrainian Carpathians (Parnikoza et al., 2009). To estimate poaching rates, we pooled all Ukrainian European bison populations and reconstructed population trends between 1995 (maximum population size) and 2009 by iteratively adjusting harvesting rates until the projected population numbers matched observed numbers (Parnikoza et al., 2009). This yielded a mean annual poaching rate of 20% of the total population (excluding calves) that we implemented in our base model for all populations in the Ukrainian Carpathians.

References


Supporting Information for the manuscript:

Cost-effectiveness of different conservation strategies to establish a European bison metapopulation in the Carpathians

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Appendix B: Additional results

Fig. S1: Different European bison conservation scenarios: Patches where reintroductions were modeled (R1-R29, left). Patches where anti-poaching strategies were assessed (AP1-AP13, right). Locations where wildlife overpasses were assessed (O1-O11, bottom).
Table S1: Cost-effectiveness of different conservation management scenarios to establish a European bison metapopulation in the Carpathians. Cost-effectiveness denotes the relative increase in a viability measure compared to the base scenario divided by the cost of the management strategy (in 1,000€). Four types of scenarios were considered: reintroductions (R1-29), anti-poaching measures (reduction to 10% = AP1-13, reduction to 5% = AP14-26), wildlife overpasses (O1-11), and combinations of reintroductions and anti-poaching measures or overpasses. As viability measures, we used the probability of the metapopulation remaining below 1,000 female bison (P1000), total bison population (TBP), metapopulation occupancy (MO), and the number of herds exceeding 100 animals (i.e., 50 females, N50) at the end of the simulation period (2100). Numbers in **bold** denote the ten most cost-effective scenarios for each viability measures.

<table>
<thead>
<tr>
<th>Scenario (ID)</th>
<th>Cost-effectiveness [%/1,000€]</th>
<th>Cost-effectiveness rank</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P1000</td>
<td>TBP</td>
</tr>
<tr>
<td>Reintroduction (R1)</td>
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</tr>
<tr>
<td>Reintroduction (R2)</td>
<td>0.001</td>
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<tr>
<td>Reintroduction (R3)</td>
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<td>Reintroduction (R4)</td>
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</tr>
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<td>Reintroduction (R6)</td>
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<td>Reintroduction (R7)</td>
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<td>Reintroduction (R9)</td>
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