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Challenges for transboundary management of a European brown bear population

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ABSTRACT

Pan-European legislation stimulates international cooperation to overarching challenges of large carnivore management across jurisdictions. We present an analysis for current transboundary brown bear (*Ursus arctos*) population management in Croatia and Slovenia. Slovenia's bear management attempts aimed to reduce human-bear conflicts, by limiting the size and distribution of the bear population, with a relatively frequent use of intervention shooting. In contrast, fewer conflicts occur in Croatia and bears have been traditionally managed as a valuable game species, with heavily male-biased trophy hunting. On average 9% of the estimated bear population was removed annually in Croatia and 18% in Slovenia for the years 2005–2010. In Croatia, a greater proportion of adult males were shot than in Slovenia (80% vs 47% of total hunted males, respectively). We model a scenario for the shared panmictic population and two scenarios assuming that Croatian and Slovenian bear populations were spatially closed. When isolated, each countries' policies lead to potentially undesired management directions. The Slovenian bear population showed a stable or slightly decreasing trend that maintained its sex and age structure, while the Croatian bear population showed an increase in size but with a possible lack of older male bear. The panmictic scenario showed that different management policies buffered each other out with the overall combined population trend being slightly increasing with a sustained age/sex structure. The recent geopolitical refugee crisis has led to the partial erection of border security fencing between the two countries. Our data illustrate how the impacts of constructed fencing put in place to address border security issues may also impact the fate of Europe's bear populations and other wildlife species that use shared ecosystems.

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1. Introduction

Managing large carnivores such as brown bears (*Ursus arctos*) represents one of the greatest challenges in biodiversity conservation. This challenge is tied to the nutrient requirements of their large body size and their trophic position requires that individuals need very large home ranges (Duncan et al., 2015). As a consequence, many large carnivore populations function on scales measured in thousands or tens of thousands of square kilometres. In a world where the human footprint is constantly expanding (Venter et al., 2016), and available areas of interconnected habitat are shrinking, this can represent considerable management challenges. In addition to the ecological demands posed by their spatial requirements, there is also a range of issues related to the administrative and political fragmentation of the landscape as individual movements and population distribution areas will inevitably cross multiple jurisdictions. This is especially acute in Europe where countries are relatively small, and where a high degree of autonomy for environmental issues is often further delegated to sub-national levels like cantons, states, regions, counties, provinces, municipalities and protected area administrations. As a result, European populations of species like brown bears stretch across multiple jurisdictional borders. Of the ten brown bear populations in Europe, eight of them span international boundaries, with two spanning four countries and one even spanning a total of nine countries (Chapron et al., 2014).

There is also a range of social, cultural, political, institutional and economic issues that complicate management. Large carnivores often attract very polarized points of view among the public, and as a result, are embroiled in a diverse range of conflicts that include complex interactions between economic and social elements (Redpath et al., 2013). As these elements vary between regions and countries in line with differences in ecological and socio-economic conditions it can make achieving transboundary cooperation in management very difficult. Although Pan-European bodies of legislation like the European Union's Habitats Directive and the Council of Europe's Bern Convention aim to stimulate international cooperation in biodiversity conservation (Fleurke et al., 2014; Linnell et al., 2008; Linnell and Boitani, 2012) there has actually been very little progress in achieving such formalized coordination at any level beyond cooperation between scientists in research and monitoring (Blanco, 2012) in the case of large carnivores. This is despite recent analyses which have conceptually (Kark et al., 2015) and empirically demonstrated the importance of transboundary coordination, for example in the field of population monitoring (Bischof et al., 2016; Gervasi et al., 2016) and comparing divergent management approaches impact shared populations (Bull et al., 2009; Gervasi et al., 2015). Although there is widespread experience in Europe with transboundary cooperation in protected area management (Erg et al., 2012). It would appear that the social and political complexity is a major hindrance towards achieving the much-needed cross-border cooperation of managing controversial species like large carnivores (Kark et al., 2015).

In this study, we present an analysis of brown bear hunting management in Slovenia and Croatia, two countries that share the north-western part of the Dinaric-Pindos bear population of south-eastern Europe. Although both countries have a shared history from the former Yugoslavia era, their independence since 1991 and in minor measure different entry dates (Slovenia, 2004; Croatia, 2013) into the European Union has led to very different bear management regimes in more recent times. Previous work has focused on either one or the other national segments (Huber et al., 2008a; Krofel et al., 2012; Knott et al., 2014; Jerina et al., 2003, 2013) but no studies have yet combined data from both sides of the shared border into a common analysis framework. We first describe how bears are hunted in both countries with respect to hunting rates and age and sex categories of the harvest. We then model the impacts of these harvest management strategies under 3 hypothetical scenarios of each country's portion of the population being either connected or closed.

When this study was initiated the scenarios involving closure seemed rather abstract as there were no serious obstacles to animal movement across the border. However, recent geopolitical developments (the refugee crisis of 2015) have led to the erection of border security fencing between the two countries (Linnell, 2015; Linnell et al., 2016). Although this fencing was designed to stem the flow of refugees it could also impact bear movements. Our dataset does not permit the assessment of these fences impact on bear movements, but our findings do have important relevance to bear conservation in these areas. The goal was to illustrate the impacts of two different management systems and the border fence as a potential absolute barrier to the population connectivity and the need for transnational cooperation, rather than to directly critique the management practices in either of the two countries.

2. Study area

The Dinaric-Pindos Mountains extend from Slovenia in the north, southwards through Croatia, Bosnia & Herzegovina, Montenegro, Serbia, Kosovo, Albania, the Former Yugoslav Republic of Macedonia and Greece. The overall Dinara-Pindos population size of brown bears in 2014 was in the order of 3000 individuals, making it the second largest in Europe (Chapron et al., 2014). Although Slovenia represents the northernmost tip of this large population, it represents the crucial linkage to the highly threatened population in the Alps (Güthlin et al., 2011). The bear population was greatly reduced by the late 19th and early 20th centuries. However, protective legislation was imposed in the 1930s in each country, and these policies were continued through the Yugoslavia era when the countries were united (Jerina and Adamič, 2008; Huber, 1990; Huber et al., 2008b). Following periods of protection, carefully regulated hunting was initiated, under which the bear populations continued to grow. When the countries separated again in 1991, they continued to harvest bears, although their policies began to diverge. Slovenia's bear management aimed to reduce human-bear conflicts (by limiting the size and distribution of the bear population) to a far greater degree than Croatia's policy which focused more on managing for trophy hunting (Krofel et al., 2012; Knott et al., 2014). This was in part due to Slovenia's earlier EU membership which only permits bear culling under derogations from Habitats Directive in response to conflict, but also due to a higher level of conflicts with land uses like sheep farming that has been heavily promoted by subsidies paid through the EU Common Agricultural Policy after Slovenia joining the EU (Kavčić et al., 2013). Conflict levels in Croatia are much lower (Bautista et al., 2017). Slovenia's current bear range (c. 4000 km^2) borders directly onto Croatia's bear range (c. 10 000 km^2), which in turn is contiguous with that in Bosnia and Herzegovina.

3. Materials and methods

3.1. Data collection

We used registered brown bear removal data from both Croatia and Slovenia (Supplemental file B), covering the six-year period from 2005 to 2010. The removal data consists of all causes of bear mortality as well as cases of taking out the live animals from the population. Once a live animal is taken out from the population it is considered dead for that population. The dataset included: (1) identification number of each bear, (2) cause of removal from the population, (3) date of the event, (4) coordinates of sites where removal occurred, (5) sex, and (6) age of each animal. The age of each removed animal was determined by one of two methods. For most bears, age was determined by counting the cementum annuli in teeth (Matson et al., 1993; Costello et al., 2004) done by Matson's Laboratory LLC, Montana, USA. The second method for ageing was developed by Jerina (Jerina and Krofel, 2012) for the bears that could not be aged using teeth sections, for example, if no teeth were available. The method predicts age based on other information (bear pelt, body weight and other measurements) using regression trees, e.g. (Jerina et al., 2003). For Croatia (total $n = 535$) and Slovenia (total $n = 614$) respectively, 412 and 518 bears ages were determined based on cementum annuli method and 110 and 96 bears were aged using Jerina's method, while 13 and 8 bears remained without age determination. Each case of brown bear removal was recorded according to protocols established in the respective country (Krofel et al., 2012; Bišćan et al., 2016). We have reason to believe that the available material provides a relatively complete picture of legal and accidental anthropogenic mortality.

For each bear, the cause of removal from the population was categorized into one of four categories. “Harvest quota” included animals killed within prescribed legal hunting seasons each year. “Intervention shooting” encompassed all cases of killing problem bears and/or bears that appeared outside of predetermined acceptable bear zones. The category “Traffic kill” included all cases of deaths due to train and road vehicle collisions with bears. The “Other causes” category included all other causes of bear removals that could not be placed in one of the first three categories. It comprised: natural deaths, illegal killings (e.g. poisoning (Reljić et al., 2012)), undetermined causes, accidental and indirect causes of anthropogenic mortality (e.g. drowning in a water well) as well as taking out the live animals from the wild population (orphaned cubs rescued and sent to Kuterevo bear sanctuary, or adults live-captured for augmentation of other bear populations, e.g. in Italy (Groff et al., 2014)).

We measured distances of all bear removal locations from the administrative border between the two countries using the tool “Near” in ArcMap (ESRI). Considering average home range diameters for females to be 21.5 km and for males 40.9 km (Jerina et al., 2012; Krofel et al., 2010), we determined if a given removal was within a home range diameter from the border.

In addition to bear removal datasets, we used data compiled from regular observations of bears on feeding sites to estimate litter sizes and survival probabilities for cubs of the year (COY) in both countries (Supplemental file C). For Croatia, we used data from 2007 to 2011, and for Slovenia from 2004 to 2010. Observations were made two times a year in Croatia (April and October (Bišćan et al., 2016)) and three times a year in Slovenia (May, August and October (Anonymous, 2015)). Data were gathered from 120 sites in Croatia and 167 sites in Slovenia.

3.2. Statistical analysis

All statistical analyses were conducted in R 3.0.3 (R Core Development Team, 2014). To test for differences between proportions we used Two-sample tests for equality of proportions with continuity correction (“prop.test” function (Crawley, 2007)). When testing for differences between two arithmetic means we used the Wilcoxon rank sum test with continuity correction (“wilcox.test” function) when variances between two means were not significantly different or by fitting generalized linear model (GLM) and performing analysis of deviance (“anova” function) when variances were different. Homogeneity and differences between variances of arithmetic means were tested using the Fligner-Killeen test of homogeneity of variances (“fligner.test“ function (Crawley, 2007)). For count data, we used Poisson or quasi-Poisson (if overdispersion occurred) distribution of errors and for proportion data binomial distribution of errors.

3.3. Matrix model parameterization

To investigate the consequences of the current hunting regimes, and to explore a set of contrasting scenarios, we constructed a two-sex, age-classified, density-independent deterministic Leslie matrix model assuming post-breeding census (Crawley, 2007; Skalski et al., 2005; Caswell, 2001; Leslie, 1945). A general density-independent matrix population model can be written as:

$$N_{t+1} = \boldsymbol{A} * N_t \tag{1}$$

where the vector N_t is the number of individuals in the different age and sex classes at time t, and **A** is the (density independent) transition matrix (Caswell, 2001), with total population size n_t being the sum of all age and sex classes across N_t. In our two-sex model, we assumed that all bears died after the age of 20 years, thus distributing males and females respectively across 21 age classes. The transition matrix **A** was parameterized based on demographic rates given in the Supplemental file A, Table A1.

As a first step, we ran 1000 simulations of this transition matrix to estimate a stable sex and age structure (42 classes in total) for a fictive non-hunted bear population using the add-on library "popbio" (Stubben and Milligan, 2007) in R, applying the "eigen.analysis" function. Given the sex and age structure, we adjusted according to the actual proportions of females and males in the Slovenian part of the population (Skrbinšek et al., 2008). For the Croatian part, we didn't have sound estimates of female:male ratio in the population and we wanted to have the same initial sex structure ratios so the effects of modelling would be comparable. A population vector N_0 then was established by distributing the population size n_0 proportionally across 42 classes from the simulated and adjusted non-hunted age and sex structure.

After establishing a stable initial non-hunted population structure our next step was to implement hunting mortality, based on registered data in both countries for the period 2005–2010. The average annual hunting mortality (H_t) vector was comprised of female and male hunting mortality for each age class (42 integers) and divided by a number of data collection years ($n_y = 6$). H_t vectors were formed for both countries separately and combined. These vectors were used to test various scenarios.

$$H_t = \frac{\left(H_f + H_m\right)}{n_y} \tag{2}$$

H_t was subtracted from the population vector N, in order to obtain estimates of the post-hunting population size and sex and age structure. Hunting mortality was expressed as real numbers and assumed being constant across 5-year iterations (n.years) of the simulated population's development. In cases where results of subtraction for particular sex and age classes were below zero, final values in the subtracted vector were transformed to 0. These cases could appear in older age classes which were represented as a minor proportions in the total population size. We simulated 1000 iterations of the process and recorded population size and structure after each iteration of 5 years.

The matrix model was used to forecast the population development regarding the differences in management practices in terms of total size, and sex and age structure in Croatia and Slovenia. The importance of using hypothetical scenarios is to understand how differences in management between the two countries combined with potential effects of a border fence may affect the population and which parameters are most influential in driving the differences in projections. In the first scenario, we assumed closed but shared panmictic Croato-Slovenian brown bear population. This scenario served as a baseline for comparison and represented the period before the border fence was erected. In the second and third scenario, we assumed that the Croatian and Slovenian bear populations were separated and closed, i.e. with no migration or dispersal of bears across the borders, corresponding to a "reality" where the border fence became an absolute barrier. We also tested what would be the minimum population size that would be sustainable ($\lambda = 1$, reproductive female:male ratio less than 6:1) with an implementation of the current management practices in Croatia and Slovenia conjointly. The results of each scenario were summarized through three output metrics: the overall population growth rate (λ), differences in the reproductive female:-male sex ratio (reproductive female proportion), and the sex and age structure's deviation from the initial population. Reproductive female:male sex ratios were obtained by summing the final frequencies for all reproductive age classes separately for females and males. As a maximum ratio of reproductive females and males that would not affect population growth because of the lack of the males in the population we took 6:1, based on the assumption that one male can on average successfully mate with a maximum of 6 females in one mating season (Steyaert et al., 2012).

Average annual lambda for each of 1000 iterations at the end of 5-years period (n.years) was approximated according to the equation where n denotes population size:

$$\lambda = \left(\frac{n_{n.years}}{n_0}\right)^{\frac{1}{n.years}} \tag{3}$$

3.4. Sensitivity analysis

The sensitivity analysis (Nilsen et al., 2005) is a standard procedure to acquire the impact (positive or negative) of implemented demographic parameters in the model to the variable of interest (population size and average lambda in our case). To run it, we developed a new matrix model which used sex and age composition results obtained by the matrix model for initial population structure. For each of the 16 parameters tested (Table 3), we set an arbitrary minimum and maximum value and run the model for 1000 simulations. From the results gained for each parameter, we took values of 2nd and 4th quantiles as a minimum and maximum range values, respectively. We standardized results for each parameter to be directly comparable. Then we tested the correlation of the parameters with two variables, final population size and population growth rate (lambda) by setting two GLMs, one for each explanatory variable. The final model was run for 10000 simulations.

Scripts, for free software environment for statistical computing and graphics "R", to perform described modelling process and model sensitivity analyses can be found in Supplemental files D and E.

4. Results

4.1. Removals and hunting quotas

A total of 535 bears were removed in Croatia and 614 in Slovenia during the six-year period from 2005 until 2010. Total removal included both quota hunting and recorded removals due to all other causes. On average 89 bears per year were removed in Croatia and 102 in Slovenia, and there was a higher (χ-sq. = 28.43, df = 1, p«0.0001) mean annual offtake in Slovenia (18.3% of the estimated population size) than in Croatia (8.9%) (Table 1). In addition, the quota filling (number of hunted bears relative to planned quota) was also (χ-sq. = 142.35, df = 1, p«0.0001) higher in Slovenia (102.7%) than in Croatia (74.7%).

There was a significant difference between the two countries in the proportions of removals from the different categories (Anova; df = 3, p«0.0001; Fig. 1). It was mainly caused by the difference in intervention shooting (Croatia 5.2% and Slovenia 16.6%; χ-sq. = 35.77, df = 1, p«0.0001) while there was no difference between the proportion of hunting mortality in Croatia and Slovenia (χ-sq. = 1.47, df = 1, p = 0.23). However, combined hunting mortality and intervention shooting, which together represent intentional human-caused killing, was a more frequent cause of mortality in Slovenia than in Croatia (Croatia 73.4% and Slovenia 81.3%; χ-sq. = 9.60, df = 1, $p < 0.01$). There was also a difference between mortality from traffic accidents and removals from other causes, but to a lesser extent than for intervention shooting (χ-sq. = 4.02, df = 1, $p < 0.05$, and χ-sq. = 5.18, df = 1, $p < 0.05$, respectively). Both causes were more frequent in Croatia.

4.2. Hunting bag composition

The proportions of male bears in hunting mortality was higher (χ -sq. = 29.09, df = 1, p«0.0001) in Croatia (77%, n = 365) than in Slovenia (59%, n = 397; Fig. 2). Within the hunted male category, the proportion of adult males over 3 years of age was also larger in Croatia, 80% (n = 281) versus 47% (n = 230) in Slovenia (χ -sq. = 61.09, df = 1, p«0.0001). In contrast, there was no difference (χ -sq. = 0.28, df = 1, p = 0.60) between the proportion of males removed in non-quota categories between Croatia (45% males, n = 170) and Slovenia (48% males, n = 217). The proportion of males in the total reported removals was higher (χ-sq. = 16.81, df = 1, p«0.0001) in Croatia (67% males, n = 535) than in Slovenia (55% males, n = 614) as well.

We found a significant difference (df = 1127, p«0.0001) between the average age of all bears in the total reported removals in Croatia 4.4 ± 0.15 years (all means ± 1 SE, n = 522) and in Slovenia 2.9 ± 0.12 years (n = 606). There was also a difference (df = 754, p«0.0001) between the average age of bears shot in quota hunting in Croatia, 5.2 ± 0.17 years (n = 363) and in Slovenia 3.1 ± 0.14 years (n = 392). There was no difference (W = 15579.5, p = 0.16) between the average age of bears that died from all non-quota causes in Croatia 2.5 ± 0.22 years (n = 159) and in Slovenia 2.5 ± 0.24 years (n = 214), as well as (W = 4570, p = 0.85; W = 395.5, p = 0.22) between the average age of bears killed in traffic collisions and from other causes in Croatia (2.1 ± 0.24 years, n = 102; 2.8 ± 0.68 years, n = 30) and in Slovenia (2.9 ± 0.44 years, n = 91; 3.3 ± 0.61 years, n = 22), respectively. A difference was found (W = 575, p«0.0001) between the average age of bears shot in intervention shooting in Croatia 3.7 ± 0.38 years (n = 27) and in Slovenia 2.0 ± 0.27 years (n = 101). Furthermore, differences in average ages between different sexes in quota hunting and non-quota removals for each country and across countries were tested (Table 2).

Table 1
Total annual brown bear removals, planned and filled harvest quota in Croatia and Slovenia from 2005 till 2010.

Year	CROATIA				SLOVENIA			
	All removals	% of N	Planned quota[a]	Filled quota	All removals	% of N	Planned quota[a]	Filled quota
2005	51	5.1	80	31	95	17.0	67	73
2006	82	8.2	70	49	126	22.6	100	94
2007	58	5.8	70	50	108	19.4	100	89
2008	115	11.5	70	64	92	16.5	75	76
2009	109	10.9	100	86	85	15.2	70	70
2010	120	12.0	100	86	108	19.4	75	98
Total	**535**		**490**	**366**	**614**		**487**	**500**
Average		**8.9**				**18.3**		

N = estimated population size.
[a] Planned quota in Slovenia includes hunting mortality and intervention shooting of bears. In Croatia, it includes only hunting mortality.

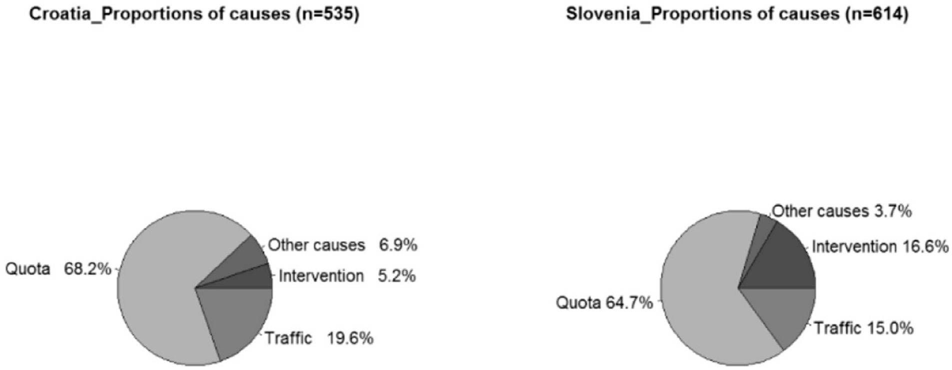

Fig. 1. Proportions of four different causes of reported removals in Croatia and Slovenia.

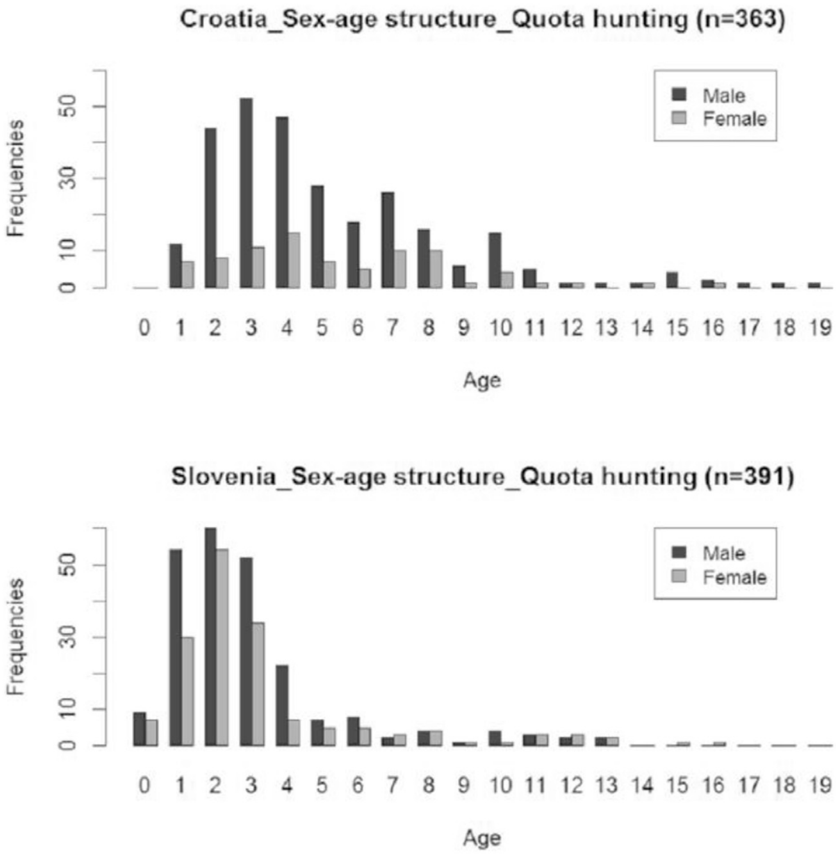

Fig. 2. Sex and age structure of hunted brown bears in Croatia and Slovenia for 2005–2010 period.

Table 2
Average age between sexes in quota hunting and non-quota removals for each country and across countries.

		CROATIA		SLOVENIA		
		Average age	n	Average age	n	Comparison
Quota	Females	5.3±0.34	82	3.2±0.24	161	p«0.0001***
	Males	5.2±0.20	281	3.0±0.16	230	p«0.0001***
	Comparison	p=0.43		p=0.82		
Non-quota	Females	3.1±0.36	67	3.1±0.38	105	p=0.25
	Males	2.1±0.28	73	2.0±0.28	102	p=0.36
	Comparison	p<0.05*		p<0.05*		

4.3. Spatial distribution of bear removals

On average, females and males were removed further away (df = 414, p«0.0001 and df = 692, p«0.0001) from the administrative state border (Fig. 3A) in Croatia (32.9 ± 2.57 km, n = 152 and 46.6 ± 2.15 km, n = 356) than in Slovenia (15.7 ± 0.59 km, n = 263 and 18.0 ± 0.63 km, n = 337), respectively. The average distances of female removals from the administrative state border were shorter than for males in both countries (Croatia: df = 507, $p < 0.001$; Slovenia: W = 39949.5, $p < 0.05$). A total of 73% of removed females and 97% of males in Slovenia and 52% of females and 55% of males in Croatia were removed within their respective average female (21.5 km) and male (40.9 km) home range (HR) diameter from the state border (Fig. 3B).

4.4. Scenario results for Croatia and Slovenia under conditions of panmixia and isolation

When modelling a combined Croatian and Slovenian transboundary population (Figure A3) the model resulted in an increase in population size for about 25% after 5 years with the average lambda value of $\lambda = 1.046$ (95% distribution range 1.033–1.057, Fig. 4). The initial proportion of reproductive females after 5 years changed from 62.8% to 70.5% (χ-sq. = 11.41, df = 1, $p < 0.001$) and the population structure (Table A3) showed differences from the initial state ($p < 0.01$) but with no serious lack of older males in the population. The ratio of reproductive females and males was 2.4:1.

The minimum population size that would be sustainable regarding total number and sex and age structure of removed bears from the population, at the same rates as in the study period, was 960 for a panmictic scenario. In this scenario, two conditions should be met: $\lambda = 1$ and reproductive female:male ratio less than 6:1.

In the scenario where Croatia was modelled as a separate and closed country (Figure A4) after a 5-year modelling period, the population size increased by about one and a half times from the initial population size with an average population growth rate $\lambda = 1.084$, (95% distribution range of predictions 1.071–1.097). The initial proportion of reproductive females after 5 years changed from 62.8% to 69.7% (χ-sq. = 5.87, df = 1, $p < 0.05$) and the ratio of reproductive females and males was 2.3:1. Modelled population structure regarding sex and age categories showed significant differences from the initial population structure ($p < 0.01$), especially with respect to a lack of males older than 10 years of age in the population. The closed Slovenian population scenario (Figure A5) showed a stable or slightly decreased population size after a 5-year period with an average lambda value of $\lambda = 0.998$, (95% distribution range 0.985–1.010). The initial proportion of reproductive females after 5 years did not change significantly (from 62.7% to 70.7%; χ-sq. = 3.72, df = 1, p = 0.054) and the population structure did not show the difference from the initial population structure (p = 0.75). The ratio of reproductive females and males was 2.4:1.

4.5. Sensitivity analysis results

Among 16 tested parameters (Table 3) the highest positive impact on the final population size, in both countries combined and Croatia and Slovenia separately, was associated with initial population size (0.65–0.68) and litter size (0.35–0.38),

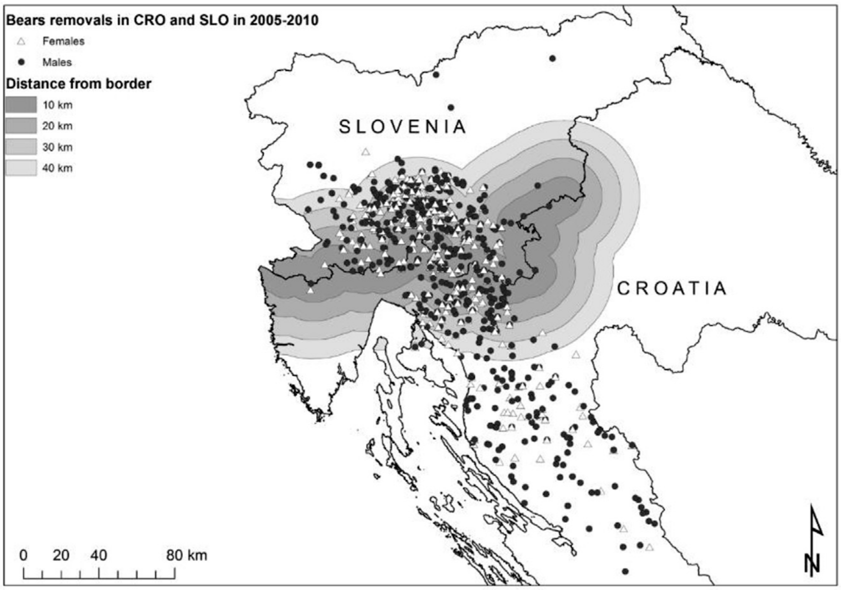

Fig. 3A. Locations of all recorded bear removals in Croatia and Slovenia in the 2005–2010 period. Males are marked with black circles and females with white triangles. Each grey-scaled zone represents distance increments of 10 km from the administrative border between countries.

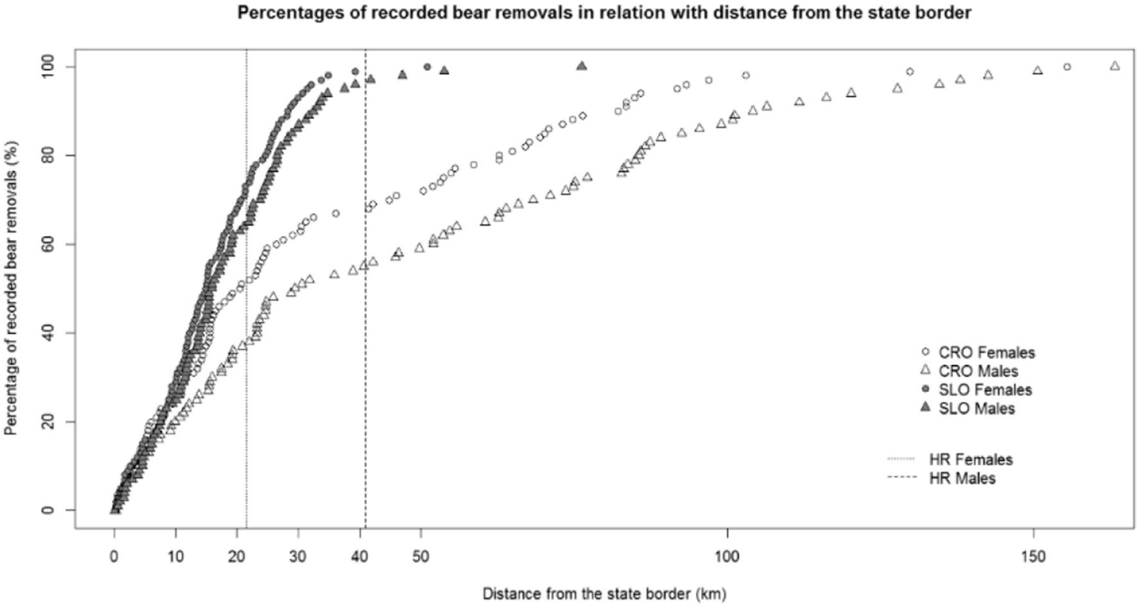

Fig. 3B. Cumulative percentages of all bear removals in relation to the distance from the Croatian-Slovenian border. Vertical lines refer to average female (21.5 km) and male (40.9 km) home range (HR) diameters.

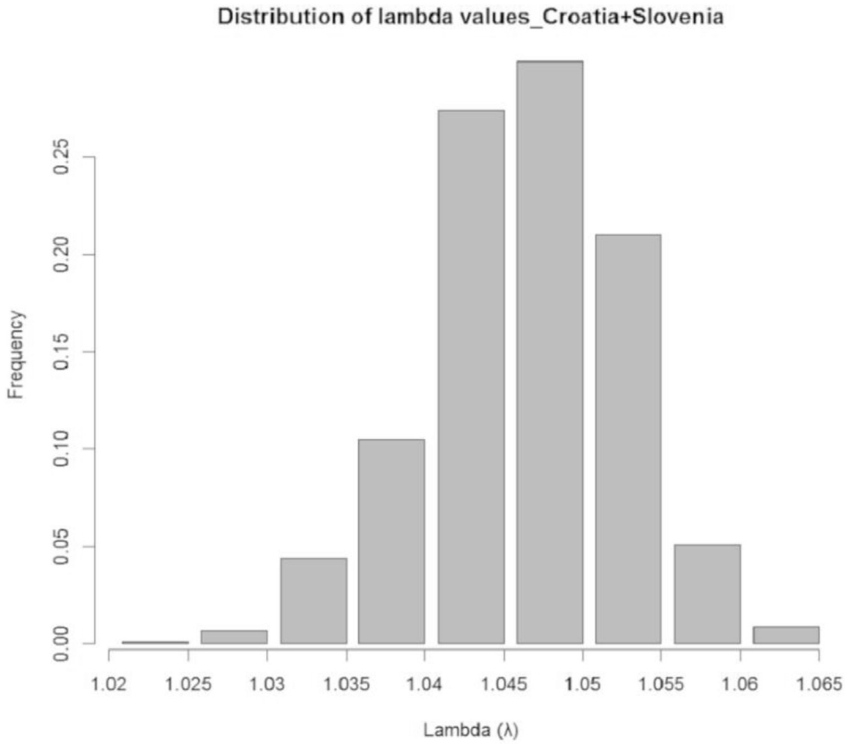

Fig. 4. Distribution of 1000 model run lambda values. Distribution in Fig. 4 is given for joint Croatian and Slovenian scenario (panmixia).

followed by survival rates of adult females, female:male ratio, survival rate of COYs and survival rates of subadult females. Conversely, litter size (0.43–0.54) with a survival rate of adult females (0.38–0.44) had a major positive effect on the average population growth rate (λ). Female:male ratio, initial population size, the survival rate of COYs and survival rates of subadult females all had important positive effects on λ. The parameters with the highest negative impact on both, the final population size and λ, were the inter-litter interval (0.21–0.31) and the loss of the whole litters (0.20–0.29).

Table 3
. Results of sensitivity analyses run for 16 parameters used in the population matrix modelling for Croatia, Slovenia and both countries combined.

Parameter	CROATIA		SLOVENIA		CROATIA+SLOVENIA	
	Population size in 5 years	Average λ	Population size in 5 years	Average λ	Population size in 5 years	Average λ
Whole litter loss	[b]-0.2101	[b]-0.2890	[b]-0.2016	[b]-0.2710	[b]-0.2004	[b]-0.2418
Interlitter interval	[b]-0.2332	[b]-0.3114	[b]-0.2307	[b]-0.2986	[b]-0.2082	[b]-0.2477
Survival rate of COYs	0.2110	0.2863	0.1960	0.2706	0.1905	0.2432
Survival rate of female yearlings	0.0725	0.1038	0.0702	0.0920	0.0675	0.0862
Survival rate of subadult females	0.2431	[a]0.3289	0.1836	0.2524	0.1823	0.2218
Survival rate of adult females	0.2758	[a]0.3897	[a]0.3059	[a]0.4422	0.2937	[a]0.3785
Survival rate of females at age of 20	−0.0016	0.0036	0.0104	0.0018	0.0006	0.0043
Survival rate of male yearlings	0.0337	0.0488	0.0266	0.0406	0.0254	0.0251
Survival rate of subadult males	0.0423	0.0664	0.0370	0.0544	0.0238	0.0220
Survival rate of adult males	0.0198	0.0335	0.0457	0.0699	0.0124	0.0203
Survival rate of males at age of 20	−0.0024	0.0002	−0.0038	0.0027	0.0029	0.0011
Litter size	[a]0.3862	[a]0.5359	[a]0.3751	[a]0.5110	[a]0.3489	[a]0.4301
Harvest rate	−0.0551	−0.0915	−0.0830	−0.1410	−0.1279	−0.1999
Initial population size	[a]0.6534	0.2034	[a]0.6645	[a]0.3010	[a]0.6759	[a]0.4354
Age of first reproduction	0.0463	0.0646	0.0392	0.0428	0.0321	0.0440
Female:male ratio	0.2294	[a]0.3143	0.2186	[a]0.3068	0.2658	[a]0.3785

[a] Parameters with the most positive effect.
[b] Parameters with the most negative effect.

5. Discussion

The data on brown bear management collected from Slovenia and Croatia demonstrates the contrasting management regimes operating in these two countries. Slovenia operates with a higher harvest rate, a higher degree of quota fulfilment, a far greater proportion of females and young bears among those killed, and a relatively frequent use of intervention killing to remove nuisance bears. Croatia's management regime has a lower harvest rate, lower degree of quota fulfilment, a larger proportion of males and older animals in the bag, and a less frequent use of lethal control of nuisance bears. Due to mentioned differences in management practices, the implemented hunting mortality for each country differs and hence the model accordingly produced different outcomes.

Brown bears are listed on Annex IV of the Habitats Directive in all European Union countries regardless of their population size. This designation requires “a strict protection” of the species. Formally, the only deliberate killing of bears must, therefore, be done under a system of exceptions called derogations. However, different countries apply widely different management practices and interpretations. Lethal control, technically organized as a derogation from protection but largely organized as a form of de facto hunting is practised in Sweden, Finland, Estonia, Slovenia and Croatia. Countries like Slovakia and Bulgaria operate with a more restrictive form of hunter-based removal, while Romania has currently imposed a stop on what was a de facto hunting system. It is therefore not exceptional that different countries operate with different management systems. However, the difference between Slovenia and Croatia is striking given the overall similarities of habitat and their shared social, cultural and political history as part of Yugoslavia until relatively recently. Moreover, both countries share a large proportion of the population due to the transboundary movement of bears.

The major difference between the two countries appears to be in the extent to which bears have become embroiled with conflicts (Bautista et al., 2017). Slovenia's earlier succession to the European Union opened the way for access to agricultural subsidies that were used to stimulate sheep production in bear habitats, initially without any requirements for protective measures. In addition to this economic conflict, bear conflicts have also been instrumentalised in Slovenia as party political symbols of wider socio-political divisions (Kavčič et al., 2013; Kaczensky, 2000; Kaczensky et al., 2001, 2004). The combination of these processes led to bears becoming more associated as a conflict species that led to a reduced tolerance for their presence. Therefore, management practices have aimed to hold their numbers stable, and mainly confine their distribution to a management “core” area along the southern border with Croatia (Jerina et al., 2013). In contrast, there are relatively few conflicts with brown bears in Croatia and they have been traditionally managed as a valuable game species where the sales of hunting trophies have been a major source of financial revenue for local hunting organizations (Knott et al., 2014; Majić et al., 2011). Although bears are excluded from certain areas (such as the islands and coastline), there have been no explicit efforts to limit distribution or population growth, although it is felt that the bear population is at a level which is suitable for the available habitat and for local tolerance (Huber et al., 2008b; Majić et al., 2011).

Our modelling scenarios provided insights into the potential impacts of these different policies. When viewed in isolation the two countries' policies lead to potentially unsatisfactory management directions. The Slovenian population showed a risk of potentially decreasing slowly, while the Croatian population would increase but with potentially dramatic changes in the population structure with a lack of older males. Neither of these two outcomes would be desired by either country. Seeing as both countries have adaptive management systems where quotas are informed by annual monitoring it is unlikely that either country would allow such undesired developments to appear without there being some reactions in terms of quota (e.g. since 2012 Croatia implemented higher quotas and management rules that aim to increase the proportion of females in the bag). Furthermore, the assumption of no density dependence in our relatively simple models would likely no longer apply under the rapid growth scenarios in Croatia. However, the results do illustrate the impacts that the different policies are having on the overall population. When viewed as a single population it appears that the different policies in effect even each other out such that the overall population trend is positive with no larger changes in population structure.

The scenario that treats the population as a single unit has been realistic when considering that most individuals are shot within a home range diameter of the border. There is also plenty of evidence of transboundary movements of individuals from GPS and VHF collared animals (Jerina et al., 2012; Krofel et al., 2010) and from genetics studies (Linnell et al., 2016). The border effect is slightly asymmetric, with a higher proportion of the Slovenian bears being influenced by cross-boundary issues than Croatia's. This is because of the geographical alignment of bear habitat in the two countries. However, it must be remembered that Croatia has an additional border with Bosnia and Herzegovina where bears are also hunted. Unfortunately, due to an almost total lack of information about the status of the population part in Bosnia and Herzegovina and its management, it was not possible to model the impacts. Another potential effect of Slovenia's high harvest rates is that it slows the expansion of bears to the north, which is necessary to ensure the longer-term viability of the reintroduced Alpine population of bears in Italy and Austria (Güthlin et al., 2011; Wiegand et al., 2004).

At the time of initiating this analysis, and for the period from which data was drawn, there were no barriers to bear movement between Croatia and Slovenia. The summer of 2015 dramatically changed this as the Slovenian government responded to the refugee crisis by building a fence along the international border with Croatia. In its current form, there are apparently some openings that allow bear movement. However, if the refugee crisis increases the fence could be extended over the entire border between the countries and this would very likely cut the population into two halves (Linnell, 2015; Linnell et al., 2016). The result of this would be that the two countries could no longer count on their neighbours' management to buffer the impacts of their national policies. For Slovenia, this implies that there will be a need to kill fewer bears, and to show greater caution (and high precision) with management because they are managing a smaller (and effectively isolated) population such that the role of stochastic events becomes greater. For Croatia, it implies that they will need to increase their harvest of females if they wish to prevent rapid population growth but at the same time decrease harvest of older males. However, Croatia has the advantage of having a larger population with a high degree of connectivity to the wider Dinaric population. In this context, our modelling scenarios provide an illustration of the potential impacts of border security fencing. These impacts should provide considerable weight when evaluating the legality of these hastily erected structures (Trouwborst et al., 2016).

The objectives of pan-European legislative instruments such as the Bern Convention and the Habitats Directive is to encourage countries to work together on conservation activities that cannot be achieved in isolation. Unfortunately, neither instrument has formal mechanisms in place to enforce this goal, apart from a set of guidelines for population-level management which were introduced in 2008 (Linnell et al., 2008). However, Slovenia and Croatia since 2007 have initiated a series of meetings between their respective management agencies and are taking steps to coordinate management. Decisions are still made separately in each country but with a respect on annual reports from the neighbouring country.

Although the vast majority of the human-induced mortality documented in this study was under direct management control (through quotas) it is important to highlight the importance of traffic induced mortality in both countries. Both countries have made dramatic investments in their transport infrastructure (especially highways) in the last 25 years. The problem with bear mortality has been highlighted for more than two decades (Kaczensky et al., 1996, 2003). In contrast to border security fencing, the mortality and fragmentation impacts of transport infrastructure can be mitigated through the use of green bridges and other crossing structures (Kusak et al., 2009; Gužvica et al., 2014). Unfortunately, there has not been a uniform integration of such structures into highways and consequentially there will continue to be both fragmentation and mortality effects on the population. The same applies to the illegal killing of bears. Although there were only a few documented cases in our material (Reljić et al., 2012), it represents an underestimate of the total extent of the problem. Collecting such data is always very difficult. While at present there is little evidence that the issue is widespread, management must show an awareness of its potential to have dramatic impacts, e.g. (Kaczensky et al., 2011) if public opinions (Majić et al., 2011) should change.

One of the weakest aspects in our models concerned the lack of local estimates of key demographic parameters. Although basic data on COY and yearling rates could be obtained from the feeding site counts (Supplemental file C) all other parameters had to be borrowed from Scandinavia. Existing comparisons of data indicate that the two populations have broadly similar life-histories (Krofel et al., 2012), including when it comes to body mass and growth which is often a key determinant of other life history traits (Swenson et al., 2007). Collecting demographic data requires a huge investment of resources using radio-telemetry but is essential if locally adapted and precise parameter estimates are needed for management. The sensitivity analysis (Table 3) identifies the key parameters with the highest impact on the population. Unfortunately, data on cub/yearling survival and interbirth intervals are among the most technically demanding of parameters to quantify. Newer indirect approaches using non-invasive genetic data may provide good estimates of population size which was identified as a key parameter (Skrbinšek et al., 2012). While it is not unreasonable to assume that the Scandinavian data provides a general idea of the approximate value of key parameters, there are some differences in habitats between the two regions, both natural and anthropogenic. Probably the most important among the latter is the widespread use of supplementary feeding in the Dinaric population, the effect of which is only poorly understood (Kavčić et al., 2013; Kavčič et al., 2015; Garshelis et al., 2017).

However, important parameters such as inter-birth intervals and infanticidal rates will be very hard to quantify, which will inevitably lead to uncertainties. The only way to deal with these is to exercise caution in management interventions and to closely monitor population development and adaptively respond hunting quotas to undesired developments.

6. Conclusions

Our study has a number of general conclusions valid for the conservation of large carnivores and other wildlife globally. Firstly, it illustrated how two neighbouring countries can differ in the way they manage a shared population. Secondly, our results showed how population connectivity can even out such differences. Because this is due to a fortunate coincidence rather than careful planning it underlines the need for countries sharing populations to formalize the ways they coordinate the management of their shared responsibilities. Failure to do so could just as easily have led to mutual disturbance of each other's goals (Gervasi et al., 2015). The fact that most bears occurred close to the border also underlines how crucial it is to cooperate in routine matters such as census to avoid double counting individuals that occur on both sides of the border (Bischof et al., 2016; Gervasi et al., 2016). Finally, the data shows how dramatic the impacts of constructed border security fencing can potentially have on the isolated segments that remain within national borders if management regimes are not adjusted. Combined, these three points underline how the fate of Europe's bear populations are influenced by socio-economic (agricultural and transport policies and public attitudes) and political (at national and international scales) factors far more than ecological factors.

Data availability

All relevant data are uploaded as Supplemental files (A, B, C, D and E) to the manuscript and available on Mendeley Data repository.

Ethics

On October 17, 2012, Committee on Veterinary Ethics at the Faculty of Veterinary Medicine, University of Zagreb, Croatia issued confirmation letter (Klasa: 640—01/12-17/3; Ur. br.: 251-61-01/139-12-19) about ethical acceptability and scientific justification in performing sample and data collection for the production of this manuscript.

Conflicts of interest

The authors have declared that no competing interests exist.

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Appendix A. Supplementary data

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