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The potential impacts of changes in bear hunting policy for hunting organisations in Croatia

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Abstract The brown bear (Ursus arctos) in Croatia is currently being managed through trophy hunting, with quotas allocated to local hunting organisations. Human-bear conflict is present at a low level, but any losses are compensated by the hunting organisations that benefit from bear hunting. Attitudes towards bears are generally positive, and the bear population appears stable, or even increasing. Croatia's current bear hunting policy relies upon both the ecological sustainability of the quotas and the economic sustainability of the hunting organisations. To address the first of these pillars of current policy, we used a two-sex matrix model of the bear population to investigate the biological sustainability of current hunting levels. The model suggests that if the annual allocated quota were fully realised, the population would suffer a considerable decrease over 10 years. A likely explanation for the mismatch between this result and the observed stability of the population is that the bear population size is underestimated. To address the second pillar, we quantified the current structure, costs and benefits of bear hunting to hunting organisations through an interview survey with hunting managers. We found that bear hunting is a substantial component of hunting organisations' income, supporting the other activities of the organisation. Croatia's recent accession to the EU will require changes in their bear

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D. Huber · S. Reljić · V. Kereži Biology Department, Faculty of Veterinary Medicine, University of Zagreb, Zagreb, Croatia management system, potentially stopping bear trophy hunting. Therefore, we assessed the changes in hunting organisations' budgets in the absence of bear hunting. Our results demonstrate that a loss of bear trophy hunting would result in a substantial loss of income to the hunting organisations. Moving bear hunting and compensation mechanisms from local management and responsibility to a more centralised system without trophy hunting, as suggested by EU legislation, will lead to considerable uncertainties. These include how to make centralised decisions on population targets and offtake levels for population control, given the uncertainty around population estimates, and on compensation payments given the loss of the current system which relies heavily on local income from trophy hunting, local relationships and informal monetary and non-monetary compensation.

Keywords Brown bear · *Ursus arctos* · Trophy hunting · Cost–benefit analysis · Population modelling

Introduction

Many species are coming into conflict with a growing human population, and this is thought to be one of the most challenging problems facing conservation today (Redpath et al. 2013). These human–wildlife conflicts can be direct costs to the communities who live with wildlife, such as attacks on humans, crop damage and depredation of livestock, or indirect costs, such as financial and time costs in preventative measures (Thirgood et al. 2005). It is the communities surrounding wildlife habitat that must bear the cost of living with wildlife, and it is important to manage any ensuing conflict in a way that minimises the impacts of wildlife on the local communities (Nyhus et al. 2005). Reducing conflict is particularly challenging for predators because they are generally wide-ranging and therefore difficult to adequately conserve solely within protected areas (Linnell et al. 2005). In cases where conservation success has resulted in the recovery of predator populations, conflict can be particularly problematic because communities may have lost traditional methods of reducing the impact of the predators. Often it is more insightful to frame the issue not as a conflict between humans and wildlife but between conservationists and the communities who must live with the outcomes of conservation success (Redpath et al. 2013). This is particularly the case in areas of Europe where carnivore populations are recovering from low numbers, such as in the Republic of Croatia (Huber et al. 2008a, b).

This study uses the brown bear (Ursus arctos) in Croatia as a case study of the relationship between local people and a species that has the potential to cause conflict. Currently, in Croatia, the bear is managed as a game species, with 10-15 % of the population allocated for trophy hunting annually. The current bear population in Croatia is estimated to be about 1,000 individuals (Kocijan and Huber 2008), and it is believed that the bear population is increasing under this management strategy (The Croatian Parliament 2005; Huber et al. 2008a, b). The bear is accepted and valued by local communities (Majić et al. 2011), with poaching occurring very rarely (Reljić et al. 2012). Damage caused by bears is compensated by the hunting organisations that profit from hunting, and the members of these organisations are predominantly local people, hence they have an interest in ensuring harmonious relationships.

The brown bear historically inhabited the majority of Eurasia and North America (Huber et al. 2008a). In Europe, the brown bear has undergone a severe range and population reduction as a result of persecution and habitat loss, leaving remnant populations across the continent. The Croatian bear population is part of the main Dinaric–Pindos population with an estimated 3,070 individuals, and is within the Northern Dinaric sub-population which covers Southern Slovenia, Croatia, Bosnia and Herzegovina (Kaczensky et al. 2012). The population is contiguous in the mountainous, forested areas between these countries.

Croatia acceded to the European Union (EU) on 1 July 2013. Under EU legislation, the brown bear is a strictly protected species, and trophy hunting and disturbance are prohibited (Swenson et al. 2000; Council of the European Union 1992). This Directive, better known as the Habitats Directive, provides a window for more flexible management through derogations (Art. 16e). The removal of a "limited number" of individual animals may be allowed. Slovenia, which joined the EU in 2004, has moved from a trophy hunting management scheme to population management through culling (which is permitted by the same derogations in order to reduce human–wildlife conflict) and government compensation for bear damage, rather than local compensation by the hunting organisations. Following Croatia joining the EU, management of the bear population will change. EU

authorities assume that the default position will be full protection, which would mean the complete abandonment of hunting and other related activities and would have associated impacts on the hunting organisations that currently benefit from commercial trophy hunting. It is realistic to expect that Croatia will continue some form of bear hunting using the above-described derogations, which may lead to a similar management approach to that currently in place in Slovenia.

Brown bears are managed in a variety of ways in non-EU European countries. They are managed as game species in Bosnia and Herzegovina (Swenson et al. 2000), while in Serbia and Macedonia, they are currently protected. Some countries like Norway have small populations recovering from over-hunting, and hunting is strictly controlled by the government with population targets closely monitored through genetic analysis of hair and scats (Swenson 2012). Sweden, an EU member state, holds the majority of the Scandinavian trans-boundary population, estimated to be 3,298 bears in 2008, with an annual harvest quota, culled in order to reduce human-wildlife conflict, of 233 bears in the same year (7 % of the population; Kindberg et al. 2011). Finland, also an EU member state which uses culling as a last resort to reduce conflict between people and bears, has an estimated population of 920 bears (Swenson et al. 2011) and an annual harvest quota regulated by the government (which in 2005-2006 was 81 bears; The Ministry of Agriculture and Forestry 2007).

Croatia's current bear hunting policy is based upon both the biological sustainability of the quotas and the economic sustainability of the hunting organisations (Fig. 1). To address the first of these pillars of current policy, we used a two-sex matrix model of the bear population to investigate the biological sustainability of current hunting levels, parameterised using data from animals hunted in 2009/2010. We ran the model using both the allocated and actual quotas, and calculated the expected population trend. We compared the results to the observed stable or positive population trend under the current bear hunting profile in Croatia, and drew inferences about the potential for bias in current bear population estimates.

To address the second pillar, we quantify the current structure, costs and benefits of bear hunting to hunting organisations through an interview survey with hunting managers. We describe the institutional structure of the bear hunting management system in Croatia, assess the extent to which bears contribute to the economic viability of hunting organisations and determine which components of the revenues and costs of hunting organisations are directly related to bears, and which are independent of bear hunting.

Next, we consider the potential economic effects on the hunting organisations of a change in brown bear status which precludes trophy hunting. This represents a baseline against which other potential scenarios (e.g. continued hunting for

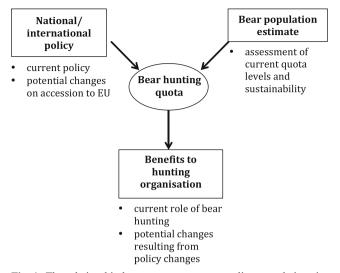


Fig. 1 The relationship between management, policy, population size and economics of bear hunting in Croatia. The *bullet points* show the specific aspects of each area addressed in this paper

conflict reduction, as in Slovenia) can be assessed. We conclude by discussing the other potential local-level effects of the cessation of trophy hunting, including conflict with local communities, and reflect on the wider implications of this case study for conservation of hunted species and wildlife management more generally.

Background: hunting structure in Croatia

The Croatian government is the highest management level in the hunting system and determines the number of bears to be hunted annually. Since 2005, the bear quota has been set at 10–15 % of the total estimated population size (Dečak et al. 2005). This is then individually allocated to each hunting organisation depending on the size of the hunting ground that it controls and its fulfilment of the quota and other obligations in the previous year. Once the quota has been allocated to a hunting organisation, it is their responsibility to ensure that it is fulfilled; organisations that do not fulfil their quota face a penalty of a reduced or denied quota the following year as well as a fine. However, despite these penalties, only 83 of the 100 bears allocated as quota in 2009 and 86 of the 100 bears allocated in 2010 were actually killed.

It is prohibited to hunt females and cubs that are together, and the hunting method itself is controlled (Huber et al. 2008a). Bears are attracted using bait (meat, corn, apples and various wet fodder) and are generally hunted from a hunting stand on a moonlit night. It is important to be able to see the bears clearly so that the trophy price can be more accurately estimated in advance. Other than mothers and cubs, the sex and age (and thus the trophy size) of a hunted bear is not restricted, and neither is the price controlled, allowing hunting managers to negotiate with hunters. Ideally, managers want to sell the largest bears for the highest prices.

The three types of hunting organisations all maintain hunting grounds on which a number of large mammal species are hunted, including bears, wild boar (Sus scrofa), red deer (Cervus elaphus) and roe deer (Capreolus capreolus). Bears are the only game species subject to state-imposed hunting quotas. Both the state and private organisations employ people to manage their hunting grounds, and all hunting is commercial; they sell the rights to shoot a certain number of a given species of game. Local hunting clubs are groups of local people who pay an annual subscription to the club and volunteer their time to manage the hunting grounds (for example, mowing grassland meadows to maintain the habitat or maintenance of hunting structures) in return for being able to hunt; the members who volunteer the most time have priority in the allocation of game available for hunting. Although little of the game on a hunting ground managed by a hunting club is sold commercially, bears and red deer are often exceptions to this because of their value. The hunting organisations must also compensate for any bear damage within the hunting grounds which, particularly with local hunting clubs where claimants are likely to also be members, is often informally settled with goods (e.g. sacks of corn) rather than money. Human-bear conflict in Croatia was reported to be mainly damage to apiaries and automatic feeders for wildlife; however, bears are also known to damage orchards when fruit is ripening, take livestock, damage trees in forest that is managed for timber, damage buildings and cause damage to vehicles though road and rail collisions. These damages are estimated to total €6,000 across Croatia annually (Kaczensky et al. 2012).

Materials and methods

The biological sustainability of trophy hunting

We constructed an age-structured two-sex stochastic matrix model using R version 2.13.1 software (R Core Development Team 2011). Bears experienced survival and fecundity rates as shown in Table 1. Demographic stochasticity was included in the survival rates using a binomial distribution. Environmental stochasticity was introduced through randomly selecting the survival rates and the litter size from a normal distribution with mean and standard deviations taken from the literature (see Table 1). Sensitivity analyses suggested that the model was most sensitive to hunting quota, adult female survival, sub-adult and cub survival above carrying capacity and the inter-birth interval (for details, see Appendix). The model was run over a 10-year projection with 1,000 replications.

Table 1	The parameter	values used	in the	biological	model
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Parameter	Value	Reference
Lifespan	25 years	Schwartz et al. 2003; Huber et al. 2008a
Age of female primiparity below carrying capacity	4 years	Huber, personal observation
Age of female primiparity above carrying capacity	5 years	Støen et al. 2006
Litter size	2.39	Frković et al. 2001
Birth sex ratio	0.5	Bellemain et al. 2005
Harem size	4	Dahle and Swenson 2003d
Inter-birth interval	2.09 years	Zedrosser et al. 2009
Adult female survival	$0.934 {\pm} 0.012$	Bischof et al. 2009
Adult male survival	$0.893 {\pm} 0.018$	Bischof et al. 2009
Cub survival without infanticide below carrying capacity	$0.85 {\pm} 0.1$	Swenson et al. 1997
Cub survival with infanticide below carrying capacity	$0.656 {\pm} 0.197$	Swenson et al. 2001
Cub survival above carrying capacity	0.61 ± 0.1	Swenson et al. 1997
Yearling female survival	$0.823 {\pm} 0.033$	Bischof et al. 2009
Yearling male survival	$0.914{\pm}0.034$	Bischof et al. 2009
Sub-adult female survival below carrying capacity	$0.94{\pm}0.016$	Bischof et al. 2009
Sub-adult female survival above carrying capacity	$0.83 {\pm} 0.1$	Calculated
Sub-adult male survival below carrying capacity	$0.817 {\pm} 0.028$	Bischof et al. 2009
Sub-adult male survival above carrying capacity	0.61 ± 0.1	Calculated

The survival rates here represent mortality from all other causes except hunting mortality, which is included separately in the model

The demographic characteristics of the hunted individuals in 2009 and 2010 were used to determine the age and sex classes targeted for hunting. Details and samples from dead bears (from hunting or other causes) were sent to the Faculty of Veterinary Medicine in Zagreb, including a premolar tooth which is used to determine the age of the bear through cementum aging (Stoneberg and Jonkel 1966; Costello et al. 2004). In 2009 (n=68) and 2010 (n=73), the majority (49.9 %) of the hunted animals were adult male bears 4 years old or older, 13.5 % were older females (4+years old) and 27.6 % were younger males (Table 2).

Two hunting scenarios were run using the population model, firstly assuming the allocated quota was all hunted (100 bears annually, the annual quota over the period 2008– 2012), and secondly using the mean realised hunting from 2009 to 2010 (Table 2). In order to explore the effects of potential bias in estimates of the brown bear population size for estimated hunting sustainability, a range of initial population sizes from 500 to 2,500 individuals was used. The model was run over a 10-year projection with 1,000 replicates, and the population trend over this period was reported.

Model parameterisation

Carrying capacity The Brown Bear Management Plan (Huber et al. 2008a) set out biological and social carrying capacities for bears in Croatia, as 1,100 and 900, respectively, based on best estimates of the current and potential bear population size. The

biological carrying capacity was determined using current bear density estimates (Huber et al. 2008a; Kocijan and Huber 2008). Since we are exploring the possibility that the current population size, and thus densities calculated using this population estimate, may be over- or under- estimated, it follows that the carrying capacities stated above would similarly deviate from their true value. Therefore, the same percentage difference between the stated biological carrying capacity (1,100 bears) and the maximum estimate of the current population size (1,000 bears; Kocijan and Huber 2008) was used to calculate an equivalent biological carrying capacity for each initial population size used in the model runs.

Age structure In the model, bears could be cubs (<1 year), yearlings (1 to <2 years), sub-adults (2 to <4 years) and adults (4+years; Table 2). Following Dahle and Swenson (2003a, c), but adjusted for maturity happening 1 year earlier in southern Europe, the cub and yearling age classes (<2 years) were assumed to be dependent on their mothers. The 2- to <4-year age classes were sub-adult, when the offspring are independent of their mothers but not yet breeding adults (age classes 4+).

Demographics of initial population The model was run with an initial population size of 1,000 and hunting at a level that allowed the population to stabilise at the biological carrying capacity. The mean age and sex structure over 150 years from the point of population stability and over 1,000 replicates was

Table 2 Percentage of huntedbears in 2009 ($n=68$) and 2010	Sex	Age (years)	% of hunted bears		Total quota hunted	Mean actually hunted	
(n=73) within each age category, used to generate the sex/age			2009	2010	Mean		
structure of the bears hunted each year within the model, the total quota hunted scenario (to the	Male	<1	0.0	0.0	0.0	0	0
		1 to <2	1.5	6.8	4.2	4	3
nearest bear, $n=100$) and mean		2 to <3	13.2	15.1	14.2	14	10
actually hunted (to the nearest bear, $n=72$)		3 to <4	7.4	11.0	9.2	9	7
(cai, ii /2)		4+	57.4	42.5	49.9	50	35
		Total	79.5	75.4	77.4	77	55
	Female	<1	0.0	0.0	0.0	0	0
		1 to <2	2.9	2.7	2.8	3	2
		2 to <3	0.0	5.5	2.7	3	2
		3 to <4	4.4	2.7	3.6	4	3
		4+	13.2	13.7	13.5	13	10
Data from the University of Zagreb		Total	20.5	24.6	22.6	23	17

determined and used as the initial population structure in the final model runs.

Survival rates Swenson et al. (2001) show that infanticide is a key factor in cub mortality. Therefore, we varied cub survival rates in order to mimic the effect of reduced survival as a function of male mortality, following Swenson et al. (1997):

$$S_r = p\left(r_{t-1} \times \frac{h_M}{MA}\right) + q\left(r_{t-1} \times \left(1 - \frac{h_M}{MA}\right)\right) \tag{1}$$

where *r* denotes the cub age class, *p* is the survival rate with infanticide for cubs, *q* is the survival rate without infanticide for cubs, *MA* is the total number of adult males and h_M is the number of males hunted. Survival rates for all other age–sex classes follow Bischof et al. (2009).

The survival of females that had reached senescence (25 years old) was set to 0 since this is the expected lifespan of a European brown bear (Schwartz et al. 2003; Chapron et al. 2009).

Fecundity rates Two fecundity functions were used: one for male fecundity ($F_{\rm m}$) and one for females ($F_{\rm f}$). The mating system of brown bears has been described variously as both promiscuous and polygamous for both sexes; however, studies agree that males roam to find females, and females generally mate with most males they meet during the breeding season, a strategy possibly developed to reduce infanticide by any of the resident males in the area (Steyaert et al. 2012; Dahle and Swenson 2003b; Bellemain et al. 2006). We approximated this mating system to a harem system with the harem size relating to the expected number of female ranges within a single male's range during the breeding season. $F_{\rm m}$

and $F_{\rm f}$ were calculated using the equations below (Lindstrom and Kokko 1998):

$$F_{\rm m} = \frac{\frac{L}{2i} n_{\rm f}}{n_{\rm m} + n_{\rm f} h^{-1}}$$
(2)

$$F_{\rm f} = \frac{\frac{L}{2i} n_{\rm m}}{n_{\rm m} + n_{\rm f} h^{-1}}$$
(3)

where $n_{\rm f}$ is the number of breeding females, $n_{\rm m}$ is the number of breeding males, *L* is the litter size, *i* is the inter-birth interval and *h* is the harem size. Reproductive productivity reduces by 7.5 % in females aged 16 to 19 years old, and by 15.2 % in females aged 20 years and above (following Schwartz et al. 2003).

Density dependence The age of primiparity for the Croatian bear population has been recorded at 4.3 years, with a single recording of a female reproducing at 3 years (Djuro Huber, personal observation; Frković et al. 2001). The philopatric behaviour of female bears has been shown to lead to delayed primiparity at high bear densities (Støen et al. 2006; Ordiz et al. 2008); therefore, density dependence was included in the model by delaying onset of reproduction to 5 years when the population was above carrying capacity.

Brown bears demonstrate sex-specific dispersal with male sub-adults dispersing away from their natal range and female sub-adults generally remaining philopatric, often establishing their range within their mother's home range (Sæther et al. 1998; Støen et al. 2006; Zedrosser et al. 2007). We therefore assumed that when carrying capacity is reached, it is primarily sub-adult bears that disperse, with a higher dispersal of males than females, and that survival of dispersing bears is low, due to their movement out of 'desirable' areas into 'undesirable' areas where it is legal for all bears to be shot (Huber et al. 2008a).

Structure and economics of bear hunting

Semi-structured interviews with hunting organisations were used to gather information about the structure and economics of the current bear management system and the future of bear trophy hunting in Croatia. Hunting organisations with the right to obtain hunting quotas in Croatia can be split into three different categories: the state hunting organisation, private companies and local hunting clubs. Each hunting organisation manages and has the right to hunt the game on one or more hunting grounds. A questionnaire was used to guide the interviews and was sent to the hunting organisation managers in advance to allow collation of the economic information required. We conducted 12 interviews, eight with local hunting clubs, two with private companies, one with a private company that also ran a hunting club and one with the state organisation. Respondents were selected using opportunistic sampling, based upon existing contacts and recommendations from other interviewees.

Hunting organisations gain income from hunting fees (for trophies), selling the meat from hunted species and, for the local hunting clubs, membership fees. For the purposes of this study, only economic information relating to bear hunting has been included. Specific amounts spent on all aspects of hunting ground management, and within that, the amount allocated to bear hunting, were ascertained. Where it was not possible to give an amount for bear hunting, for example, the maintenance of shooting stands, which are for hunting other species as well as bears, an estimated proportion of the cost was given. The cost in time as well as financially was determined for one type of organisation (hunting clubs) since labour is provided as part of hunting club membership. These values were only obtained for the previous year (2010) to ensure that they were as accurate as possible.

The economics of hunting were analysed separately within each category of hunting organisation. Following this, a pooled analysis provided an estimate of potential total costs of accession to hunting organisations. All income from and costs of bear management were identified and then split into those that were dependent on the bear trophy hunting quota available to the hunting organisation, and those that were independent of the quota. All quota-dependent costs were divided by the quota of bears allocated to each hunting organisation to standardise the values between the organisations. Each cost was then assessed to determine whether and how it would change if trophy hunting of bears were prohibited.

Information on every dead bear is supplied to the Faculty of Veterinary Medicine in Zagreb, including the International Council for Game and Wildlife Conservation (CIC) value (CIC 1977) and the mass of meat of trophy-hunted bears. The income from bear hunting was calculated based on the trophy value and the meat sold. The mean CIC points and mean mass of meat of all bears hunted in 2010 were calculated. We used datasets from 2010 for comparability with the economic data, which were collected in May-June 2011. CIC points are determined by the quality of the trophy and are calculated using the size and condition of the pelt. Meat prices are agreed between hunting organisations and butchers. We obtained values and price guidelines for both trophy hunts and the resulting meat from the hunting organisations. The prices were then used to approximate the annual income to the hunting organisations from bear hunting. The costs and income were then used to give insights into the effects that banning bear trophy hunting may have on the hunting organisations and on the wider population.

This paper deals solely with the economics of bear trophy hunting from the perspective of hunting organisations. Therefore, although the total cost of a hunting trip would also include food and accommodation in the local area, these additional benefits to other local businesses are recognised but not investigated here.

Results

The biological sustainability of trophy hunting

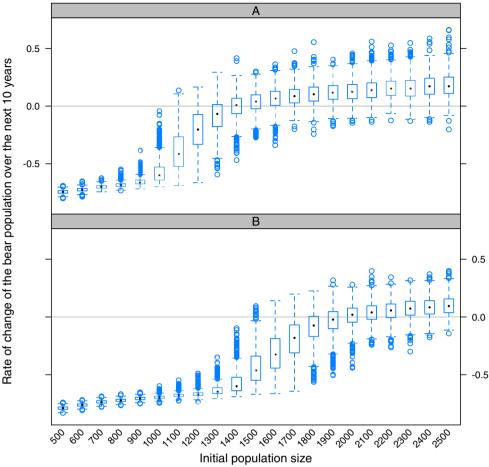
The demographic structure of the modelled population at stabilization showed a bias towards females with a mean of 55 % of the population female, 24 % male and 21 % cubs under 1 year. This structure determined the initial population demographics for both scenarios then explored through the model.

The expected rate of change of the bear population under the hunting quota depends on the initial population size (Fig. 2). Both hunting scenarios, hunting at the mean realised level in 2009 and 2010 (Fig. 2a) and hunting the full quota (Fig. 2b), showed a similar general trend in the rate of change of population size. For smaller bear populations, up to 900 bears for the realised hunting scenario and 1,200 bears in the full quota scenario, there is a decrease of up to 70 % of the population across 10 years of hunting. In both hunting scenarios, the demographic structure of the hunted bears was based on the demographic structure of bears hunted in 2009 and 2010, and was strongly skewed towards male bears (77.5 %, Table 2). This male-biased hunting, along with a female-dominated population, results in breeding males frequently being hunted out of the population when total population sizes are small, thus halting reproduction all together and preventing the population from recovering.

At larger population sizes, although the population still decreases across the modelled 10-year period, the decrease is

Fig. 2 The rate of change of the modelled bear population over a 10-year projection with (a) the mean number of bears hunted in 2009/2010 hunted annually and (b) 100 bears (the current allocated quota) hunted annually, with initial population sizes varying from 500 to 2,500 individuals

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progressively reduced, as there are sufficient males to ensure reproduction. However, it is not until initial population sizes of 1,400 and 2,000 bears, for the realised and full quota hunting scenarios, respectively, are reached that the hunting becomes sustainable and the population sizes stabilise. This implies that the current estimate of 1,000 bears with an increasing population trend in Croatia (Kocijan and Huber 2008) may be an underestimate, as the population is only stable with current hunting levels if it contains at least 1,400 bears (Fig. 2a).

Current and post-accession economics of bear hunting

We identified three categories of expenditure related to bears. The first was the costs that are incurred to maintain the hunting ground regardless of bear hunting, in order to continue to hunt other species. These costs would continue if bear hunting was stopped, and represented 37.8 % of costs. The second category varied depending on the bear quota (20.5 % of costs), and the third category was bear-related but quota-independent, relating to bear damage (41.7 %; Table 3).

Because all three types of hunting organisation sell bear trophy hunting, bear-specific costs and income were consistent between organisation types. Post-accession, it is expected that all bear damage to hunting organisation property and private property will be compensated for by the state, as is the case with the currently protected wolf (Canis lupus; Majić and Bath 2010), and therefore, these costs would be removed from the hunting organisations. Administration of bear hunting is a cost that would be removed entirely if bear hunting ceased. However, with all damage compensated by the government rather than locally, additional administration would be required in reporting these incidents when damage is to hunting organisation property, for example, to feeding stations for other species. The size of this additional cost could not be calculated; however, it serves to increase the loss to the hunting organisations.

Supplementary food for bears would no longer be supplied as there will be no reason to attract them to the hunting stations, and baiting with meat (done only for bears rather than the other hunted species) is prohibited under EU legislation. Currently, very little money is being spent on the prevention of bear damage because of the relatively positive attitude of local people towards bears. However, when the government is providing compensation, it is likely that a threshold level of damage prevention will be required before compensation will be paid, resulting in an increase in this

	Description	Current	No bear hunting
Expenses (quota-dependent)	Administration Supplementary food Sub-total	-1,201 -6,601 -7,802	
Expenses (on-going)	Salaries	-7,953	-7,953
	Maintenance Sub-total	-6,476 -14,429	-6,476 - <i>14,429</i>
Expenses	Repair damage	-5,938	1,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,
(damage-related)	Prevent damage Compensation	-6,000 -3,956	>-6,000
	Sub-total	-15,893	>-6,000
Income	Trophy value	+36,585	
	Meat value	+3,041	+3,041 ^a
	Sub-total	+39,626	
Total per bear (HRK)		1,501	>-17,388
Total per bear (Euros)		201	>-2,325

Table 3 The economics of bear trophy hunting, shown in Croatian Kuna, per bear per year for the hunting organisations (at the time of the study, 1.00 EUR=7.48 HRK)

We show the current bear-related costs and revenues and the expected change if bear hunting ceases (based on interviews with hunting organisation representatives). Only incomes and costs specifically related to bear hunting are included, for example, 'salaries' refers to the salary for time spent working for bear hunting. The values are shown per bear since the size of the hunting quota allocated to the hunting ground determines the effort invested in bear hunting activities and the quota allocation is not necessarily related to hunting ground size. The *greater than symbol* implies that the losses concerned will be at least the amount shown

^a It is uncertain whether hunting organisations would still receive income from selling the meat of culled bears

cost to protect hunting organisation property. Tasks associated with bear trophy hunting only represent a small proportion of the roles of hunting organisation employees, and therefore, if bear hunting is stopped, it is not expected that this will affect the salaries paid to employees. All maintenance and equipment are related to a variety of hunted species, not specifically bears, and therefore, costs associated with these are expected to remain constant.

The mean trophy size of legally hunted bears in 2010 was 298.10 CIC points (n=68, maximum=545.30, minimum=139.26), and the mean mass of meat from the hunted bears in 2010 was 82.75 kg (n=40, maximum=186 kg, minimum=30 kg). The approximate income per bear to hunting organisations was 39,626 HRK, based on the current state hunting organisation price list for trophy-hunted bears (which is used as a guideline by many other hunting organisations) and the mean value of bear meat per kilogram (obtained from interviews). The value of bear meat is approximately 8 % of the total value of hunted bear. The income from selling bear trophies will be lost when bear hunting becomes illegal, and possibly that from selling the bear meat as well. Local hunting

club membership fees were not included in the economic analysis because the bears are not generally hunted by hunting club members; this suggests that the number of hunting club members would not change with a change in the status of the bear.

Currently, calculated bear-specific income marginally outweighs bear-specific expenditure (Table 3); however, the majority of hunting organisations interviewed stated that overall their organisations had no net profit. The gain from bear hunting therefore appears to subsidise to some extent the costs of running the hunting organisations, compared to other species. If bear hunting is prohibited then, although some of the bear-specific expenditure will decrease, some (for example, salaries and maintenance) will not change. This is because these expenses are required in order to hunt all species, and will need to be continued regardless of the hunting status of the bear. As such, our results suggest that the overall financial loss to hunting organisations would be in the region of an order of magnitude larger than the current gains (Table 3).

It is expected that local hunting clubs will be the most affected type of organisation by the loss of bears from their trophy hunting list because many of the hunting clubs only commercially sell two species, red deer and brown bear, the remainder of the species being primarily for club members to hunt. Much of the payment for hunting these other species is in the form of voluntary labour, and although this reduces the expenditure of the club, the hunting lease and other large financial costs must still be met. The shortfall may have to be compensated for by an increase in membership fees, or an increased cost for hunting the other game species.

Discussion

There is some uncertainty around the current bear population estimate in Croatia. Our model used the provisional available parameters and suggests that for the bear population to remain stable, the maximum proportion of the population which can be hunted annually is 5 %. The current quota level is set at 10 % of the current population estimate (1,000 bears); however, only 6.8 % and 7.3 % of the estimated population was actually hunted in 2009 and 2010. It appears that the current allocated hunting quota for this population is both too high to be sustainable biologically and larger than the demand from hunting organisations. However, the observed population stability suggests that the population estimate is potentially too low. This raises concerns about the ability of the current monitoring system to detect population trends in the species. In the context of a changing management regime, with concomitant concerns about the effects on bear populations, it is vital that accurate population estimates are available in order to ensure that any negative effects on

the population are picked up quickly and with adequate power (Elphick 2008; Kinahan and Bunnefeld 2012).

Accurate population estimates of a cryptic species such as the brown bear are exceedingly difficult to obtain; however, new technologies have been used to produce more accurate estimates in the Scandinavian and Slovenian bear populations. Genetic techniques use capture-mark-recapture analysis with DNA extracted from non-invasive samples of faeces and hair (Kindberg et al. 2011; Swenson et al. 2011; Skrbinšek et al. 2012). This technique also reduces error through double counting, which can be a problem with transboundary populations. Bellemain et al. (2005) also demonstrated that with the cooperation of hunters in collecting bear scat, it is possible to sample much larger areas when determining the population size. These opportunities for collaboration between scientists and hunters may also be lost in the absence of a regulated trophy hunting industry.

Additional research into the population demographics of the Dinaric-Pindos brown bear population and the ecological carrying capacity of the available bear habitat is needed to improve understanding of the dynamics of this population and reduce the uncertainty of the demographic parameters. This population model mainly uses parameters recorded in Scandinavian bear populations, and further research into the true parameter values for the Croatian bears would give a more reliable picture of the effect of hunting on this population. The population model used here assumes a marked decline in sub-adult male and female survival above carrying capacity; however, this is likely to represent both mortality and the dispersal of sub-adult bears into neighbouring Slovenia and Bosnia and Herzegovina, a process that currently is little understood. A study that investigates the rate of dispersal across these country boundaries and the effect of different population management policies on this transboundary population's spatial dynamics would contribute to improving the management of large carnivore populations.

Supplementary feeding of bears may also affect the dynamics of the population since it brings bears into close contact with each other. Adult bears are generally solitary, with male bear territories overlapping those of females with whom they will mate (Dahle and Swenson 2003d). Supplementary feeding sites may allow males access to larger numbers of female bears as they are attracted into a small area. This may allow the fecundity rate of the population to remain high even with very low numbers of males, and hunting to be sustainable at a higher quota level than shown here.

The economic benefits to the hunting organisations of bear hunting appear to be substantial, with losses from hunting other species offset against the income received from bear hunting. The motivations of hunting organisations, particularly the local hunting clubs, do not however appear to be economic since they do not aim to profit overall from their hunting activities. Other benefits to the local communities, such as maintaining traditional hunting practices, may be more important in the overall motivation for the hunting organisations; however, the cost of maintaining the hunting grounds will need to be met.

It is uncertain whether hunting organisations will be able to sell the meat of culled bears if the method of hunting continues to involve meat bait since it is illegal to sell bear meat in the EU if the bear has been fed meat. The loss of this income would further increase the hunting organisation's financial deficit, although meat sales are currently a small proportion of overall income.

The wider community currently benefits further from bear hunting, for example, through providing accommodation and food for hunters during their trips. The impact of the possible change in hunting policy on these businesses has not been addressed here, but it is important to recognise that the changes will affect more than just the hunting organisations (Sharp and Wollscheid 2009). Although most of the hunting organisations we interviewed were only allocated one or two bears in the quota, each bear hunt may translate into a trip of several days to the area.

Tolerance of local communities for large carnivores has been linked to management that empowers the local community to respond to conflict with lethal control (Linnell and Boitani 2012). The legislation in the Habitats Directive does not allow commercial hunting of bears, although it does permit the use of culling in order to reduce human-wildlife conflict, and therefore may not completely remove the ability of local communities to respond to conflict in this way. Human-predator conflict, although seemingly directly between humans and the predator species, is generally fundamentally human-human conflict between parties that have opposing views concerning the management of the predator in question. As a result, typically the first, and often most challenging, step towards conflict management is to initiate engagement between the stakeholders (Redpath et al. 2013). The conflict management system currently in place in Croatia negates the need for these complicated negotiations since the victims of the conflict are often members of the hunting organisations, removing a step in the conflict resolution framework.

Conflict with wolves, a predator that was hunted historically but is now strictly protected in Croatia, is compensated through a government scheme (Majić and Bath 2010). Compensation is commonly used in an attempt to mitigate the costs of living with wildlife, which are generally disproportionately borne by farmers and local communities (Nyhus et al. 2005). The current compensation agreement for damage by bears in Croatia between hunting organisations and the local communities is highly successful because there is a consistent source of funds (ultimately from the trophy hunters), and the hunting organisations are considered to be an important part of the local community (particularly the local hunting clubs) thus ensuring quick, often informal, payments with little incentive to exploit the system. The cessation of commercial bear hunting, as required by the EU, will necessitate a change in this compensation policy since the hunting organisations will no longer gain financial benefits from bears, and it is likely that it will follow a similar scheme to that of the wolf. This will lose the benefits of the current, locally administrated system, may take longer to verify damage and pay legitimate claims and be more vulnerable to exploitation. Anecdotal evidence from one interview shows that the government compensation scheme for wolf depredation of livestock is already being exploited, with a bear attack on six sheep being reported as a wolf attack in order to get compensation from the government rather than the hunting organisation.

Furthermore, current bear behaviour, such as visiting supplementary feeding sites and hunting deer calves (although this is more documented in Scandinavia than Croatia; Huber et al. 2008a; Swenson and Andrén 2005), may be perceived as additional conflict in future when the bears are no longer a game species. These conflicts are more difficult to mitigate than damage to property or depredation because they are too difficult to quantify and therefore to determine appropriate compensation. All listed events of potential conflict, along with the loss of bear trophies and meat as a source of income, may lead to increased poaching of bears (Reljić et al. 2012).

Changes in hunting policy can have substantial effects on both the ecology of the species and the socio-economics of the hunting itself. In Colorado, a state-wide limitation was imposed on the hunting of mule deer in 1999 with the intention of increasing the deer population and improve the proportion of adult males in the population. This was undoubtedly successful in both of these aims; however, the fawn/female ratio declined after the limitation was introduced, possibly as a result of density dependence and compensation from the increase in adult males. There was also a loss in revenue from licenses of US\$7.86 million (this does not take into account possible loss of revenue to other businesses) and a drop in the number of hunters (Bergman et al. 2011). Prior to changes in hunting policy, many systems would benefit from an assessment of both the socioeconomic and biological sustainability of the current and proposed management, as we have done here for the Croatian bear population.

Decisions for wildlife management and conservation are always made under uncertainty, and it is now widely acknowledged that socio-economic incentives and behaviour of resource users are just as important as ecological knowledge to achieve long-term sustainability (Bunnefeld et al. 2011; Langford et al. 2011). Predicting the change in any interlinked social-ecological system, such as hunting, is challenging, and in this study, we contribute to the understanding of some aspects of the economic and ecological factors and their associated uncertainties. Future management in many parts of Europe will have to answer questions about social, economic and ecological sustainability of policy change and how to make decisions under uncertainty in population estimates, poaching levels, people's willingness to accept wildlife that potentially create conflicts and the best spatial scale to implement policies. Recent developments in wolf management policy in Europe, generally towards protection, have triggered a shift in conservation planning, from a state-led to a population approach, resulting in endorsed guidelines (by the European Commission's DG Environment and the Bern Convention Standing Committee) outlining coordinated, flexible and pragmatic policies for managing wolves at a population scale (Linnell and Boitani 2012). This integrated, European-wide approach to large carnivore management may lead the way for flexible policies, which can assess both the socio-economic and ecological aspects of carnivore management, and encourage cooperation and coordination between countries with trans-boundary carnivore populations.

Conclusions

We do not intend to imply that trophy hunting is an appropriate management option for all brown bear populations. However, there is strong evidence that this system is more beneficial for the Croatian population and the communities who share its range than a protectionist strategy would be. It is essential to consider both the economic and biological perspective when making management decisions because a policy in which wildlife pays for itself not only reduces perceived conflict between people and wildlife but can also result in a long-lasting, effective management scheme. However, such policies rely upon accurate population estimates. This research also demonstrates the potential for population models to highlight monitoring inaccuracies, particularly for difficult-to-census populations such as this transboundary bear population.

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Appendix

Table 4	The range of values tested for each parameter in the sensitivity
analyses	

Parameter	Minimum	Maximum	Selected value
Adult female survival	0.82 ^a	1.0 ^b	$0.934{\pm}0.012^{c}$
Adult male survival	0.82 ^a	1.0 ^b	$0.893 \!\pm\! 0.018^{c}$
Cub survival without infanticide	0.25 ^b	0.9601 ^d	$0.85^{e}\pm0.1$
Cub survival with infanticide	0.25 ^b	0.77	$0.656 {\pm} 0.197^{\rm f}$
Cub survival above carrying capacity	0.25 ^b	0.77	$0.61^{d} \pm 0.1$
Yearling female survival	0.72^{a}	1.0 ^{b, e}	$0.823 {\pm} 0.033^{c}$
Yearling male survival	0.72 ^a	1.0 ^{b, e}	$0.914{\pm}0.034^{c}$
Sub-adult female survival	0.7 ^e	1.0 ^b	$0.94{\pm}0.016^c$
Sub-adult female survival above carrying capacity	0.7 ^e	1.0 ^b	$0.83 {\pm} 0.1^{1}$
Sub-adult male survival below carrying capacity	0.7 ^e	1.0 ^b	$0.817 {\pm} 0.028^{\circ}$
Sub-adult male survival above carrying capacity	0.4^{1}	0.8^{1}	$0.61 {\pm} 0.1^1$
Litter size	1.7 ^g	3.0	2.39 ^h
Inter-birth interval	1.75	3.0	2.09^{i}
Harem size	2.65 ^j	5.56 ^j	4 ^k
Proportion of population hunted	0.0	0.1	_
Carrying capacity	825	3,000	—
Initial population size	500	2,500	-

^a Wiegand et al. (2004)

^b Chapron et al. (2009)

- ^c Bischof et al. (2009)
- ^d Sæther et al. (1998)
- ^e Swenson et al. (1997)
- ^fSwenson et al. (2001)

^g Dahle and Swenson (2003b)

- ^h Frković et al. (2001)
- ⁱZedrosser et al. (2009)
- ^j Jerina et al. (2003)

^k Dahle and Swenson (2003d)

¹No value for this parameter exists in the literature so a reasonable value was chosen in line with current understanding of bear biology

 Table 5
 Results of a sensitivity analysis to which a generalised linear model was fitted with the mean population size over the final 10 years of each 100-year run as the dependent variable and the demographic parameter values as explanatory variables

Parameters	Standardised beta
Sub-adult female survival above carrying capacity	0.0834***
Proportion of population hunted	-0.0772**
Initial population size	0.0743**
Sub-adult male survival above carrying capacity	0.0729**
Adult female survival	0.0666**
Inter-birth interval	-0.0610*
Cub survival above carrying capacity	0.0522*
Cub survival without infanticide below carrying capacity	-0.0360
Carrying capacity	0.0314
Harem size	0.0287
Sub-adult male survival below carrying capacity	0.0199
Yearling male survival	0.0159
Litter size	0.0157
Adult male survival	-0.0034
Sub-adult female survival below carrying capacity	-0.0029
Cub survival with infanticide below carrying capacity	-0.0012
Yearling female survival	0.0011

The demographic parameter values were selected randomly for each of 1,000 iterations from uniform distributions with the minimum and maximum values shown in Table 4. The table shows the standardised beta for every parameter in the model and their significance *P < 0.01, **P < 0.05, ***P < 0.01

References

- Bellemain E, Swenson JE, Tallmon D, Brunberg S, Taberlet P (2005) Estimating population size of elusive animals with DNA from hunter collected feces: four methods for brown bears. Conserv Biol 19:150–161
- Bellemain E, Zedrosser A, Manel S, Waits LP, Taberlet P, Swenson JE (2006) The dilemma of female male selection in the brown bear, a species with sexually selected infanticide. Proc R Soc B 273:283–291
- Bergman EJ, Watkins BE, Bishop CJ, Lukacs PM, Lloyd M (2011) Biological and socio-economic effects of statewide limitation of deer licenses in Colorado. J Wildlife Manage 75:1443–1452
- Bischof R, Swenson JE, Yoccoz NG, Mysterud A, Gimenez O (2009) The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. J Anim Ecol 78:656–665
- Bunnefeld N, Hoshino E, Milner-Gulland EJ (2011) Management strategy evaluation: a powerful tool for conservation? TREE 26:441–447
- Chapron G, Wielgus R, Quenette P-Y, Camarra J-J (2009) Diagnosing mechanisms of decline and planning recovery of an endangered brown bear (*Ursus arctos*) population. PLoS One 4:e7568
- CIC (International Council for Game and Wildlife Conservation) (1977) The game-trophies of the world: international formula for the measurement and evaluation of trophies, Vol. 1.0. Parey, Hamburg, 160 pp

- Costello CM, Inman KH, Jones DE, Inman RM, Thomson BC, Quigley HB (2004) Reliability of the cementum annuli technique for estimating the age of black bears in New Mexico. Wildl Soc Bull 32:169–176
- Council of the European Union (1992) Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. OJ L 206, 22 Jul 1992, p. 7
- Dahle B, Swenson JE (2003a) Family breakup in brown bears: are young forced to leave? J Mammal 84:536–540
- Dahle B, Swenson JE (2003b) Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. J Anim Ecol 72:660– 667
- Dahle B, Swenson JE (2003c) Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effects on offspring. Behav Ecol Sociobiol 54:352–358
- Dahle B, Swenson JE (2003d) Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. J Zool 260:329–335
- Dečak Đ, Frković A, Grubešić M, Huber Đ, Iviček B, Kulić B, Sertić D, Štahan Ž (2005) Brown bear management plan for the Republic of Croatia. Ministry of Agriculture, Forestry and Water Management, Zagreb, 90 pp
- Elphick CS (2008) How you count counts: the importance of methods research in applied ecology. J Appl Ecol 45:1313–1320
- Frković A, Huber D, Kusak J (2001) Brown bear litter sizes in Croatia. Ursus 12:103–106
- Huber D, Jakšić Z, Frković A, Štahan Ž, Kusak J, Majnarić D, Grubešić M, Kulić B, Sindičić M, Majić Skrbinšek A, Lay V, Ljuština M, Zec D, Laginja R, Francetić I (2008a) Brown bear management plan for the Republic of Croatia. Ministry of Regional Development, Forestry and Water Management, Directorate for Hunting and Ministry of Culture, Directorate for the Protection of Nature, Zagreb
- Huber D, Kusak J, Majić-Skrbinšek A, Majnarić D, Sindičić M (2008) A multidimensional approach to managing the European brown bear in Croatia. Ursus 19:22–32
- Jerina K, Debeljak M, Džeroski S, Kobler A, Adamič M (2003) Modelling the brown bear population in Slovenia. A tool in the conservation management of a threatened species. Ecol Model 170:453–469
- Kaczensky P, Chapron G, von Arx M, Huber D, Andrén H, Linnell J (2012) Status, management and distribution of large carnivores bear, lynx, wolf and wolverine—in Europe. Istituto di Ecologia Applicata, Rome, 72 pp
- Kinahan A, Bunnefeld N (2012) Effectiveness and cost efficiency of monitoring mountain nyala in the Bale Mountains National Park, Ethiopia. Endang Species Res 18:105–114
- Kindberg J, Swenson JE, Ericsson G, Bellemain E, Miquel C, Taberlet P (2011) Estimating population size and trends of the Swedish brown bear Ursus arctos population. Wildl Biol 17:114–123
- Kocijan I, Huber D (2008) Conservation genetics of brown bears in Croatia. Final report. Project gaining and maintaining public acceptance of brown bear in Croatia. BBI-Matra/2006/020 through ALERTIS, 17 pp
- Langford WT, Gordon A, Bastin L, Bekessy SA, White MD, Newell G (2011) Raising the bar for systematic conservation planning. TREE 26:634–640
- Lindstrom J, Kokko H (1998) Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. Proc R Soc B 265:483–488
- Linnell JDC, Boitani L (2012) Building biological realism into wolf management policy: the development of the population approach in Europe. Hystrix 23:80–91
- Linnell JDC, Nilsen EB, Lande US, Herfindel I, Odden J, Skogen K, Andersen R, Breitenmoser U (2005) Zoning as a means of mitigating conflicts with large carnivores: Principles and reality. In: Woodroffe R, Thirgood S, Rabinowitz A (eds) People and wildlife: Conflict or coexistence? Cambridge University Press, Cambridge

- Majić A, Bath AJ (2010) Changes in attitudes towards wolves in Croatia. Biol Conserv 143:255–260
- Majić A, Marino A, Huber D, Bunnefeld N (2011) Dynamics of public attitudes toward bears and the role of bear hunting in Croatia. Biol Conserv 144(12):3018–3027
- Nyhus PJ, Osofsky SA, Ferraro P, Madden F, Fisher H (2005) Bearing the costs of human-wildlife conflict: The challenges of compensations schemes. In: Woodroffe R, Thirgood S, Rabinowitz A (eds) People and wildlife: Conflict or coexistence? Cambridge University Press, Cambridge
- Ordiz A, Støen O-G, Swenson JE, Kojola I, Bischof R (2008) Distancedependent effect of the nearest neighbour: spatiotemporal patterns in brown bear reproduction. Ecology 89:3327–3335
- R Core Development Team (2011) R version 2.13.1. Available at: http:// www.r-project.org/
- Redpath SM, Young J, Evely A, Adams WM, Sutherland WJ, Whitehouse A, Amar A, Lambert RA, Linnell JDC, Watt A, Gutiérrez RJ (2013) Understanding and managing conservation conflicts. TREE 28:100– 109
- Reljić S, Srebočan E, Huber D, Kusak J, Šuran J, Brzica S, Cukrov S, Prevendar-Crnić A (2012) A case of a brown bear poisoning with carbofuran in Croatia. Ursus 23:86–90
- Sæther B-E, Engen S, Swenson JE, Bakke Ø, Sandegren F (1998) Assessing the viability of Scandinavian brown bear Ursus arctos populations: the effect of uncertain parameter estimates. Oikos 83:403–416
- Schwartz CC, Keating KA, Reynolds HV, Barnes VG, Sellers RA, Swenson JE, Miller SD, McLellan BN, Keay J, McCann R, Gibeau M, Wakkinen WF, Mace RD, Kasworm W, Smith R, Herrero S (2003) Reproductive maturation and senescence in the female brown bear. Ursus 14:109–119
- Sharp R, Wollscheid KU (2009) An overview of recreational hunting in North America, Europe and Australia. In: Dickson B, Hutton J, Adams B (eds) Recreational hunting, conservation and rural livelihoods. Blackwell Science, Hoboken
- Skrbinšek T, Jelenčič M, Waits L, Kos I, Jerina K, Trontelj P (2012) Monitoring the effective population size of a brown bear (*Ursus arctos*) population using new single-sample approaches. Mol Ecol 21:862–875
- Steyaert SMJG, Endrestøl A, Hackländer K, Swenson JE, Zedrosser A (2012) The mating system of the brown bear *Ursus arctos*. Mammal Rev 42:12–34
- Støen O-G, Zedrosser A, Wegge P, Swenson JE (2006) Socially induced delayed primiparity in brown bears Ursus arctos. Behav Ecol Sociobiol 61:1–8
- Stoneberg RP, Jonkel CJ (1966) Age determination of black bears by cementum layers. J Wildl Manage 30:411–414
- Swenson JE, Sandegren F, Söderberg A, Bjärvall A, Franzén R, Wabakken P (1997) Infanticide caused by hunting of male bears. Nature 386:450–451
- Swenson JE, Gerstl N, Zedrosser A, Dahle B (2000) Action plan for the conservation of the brown bear (*Ursus arctos*) in Europe. Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) Nature and Environment No. 114
- Swenson JE, Sandegren F, Brunberg S, Segerström P (2001) Factors associated with loss of brown bear cubs in Sweden. Ursus 12:69–80
- Swenson JE, Andrén H (2005) A tale of two countries: Large carnivore depredation and compensation schemes in Sweden and Norway. In: Woodroffe R, Thirgood S, Rabinowitz A (eds) People and wildlife: Conflict or coexistence? Cambridge University Press, Cambridge
- Swenson JE, Taberlet P, Bellemain E (2011) Genetics and conservation of European brown bears Ursus arctos. Mammal Rev 41:87–98
- Swenson JE (2012) A new management policy for brown bears in Norway. International Bear News 21(2):21–22

- The Croatian Parliament (2005) The hunting act. The Croatian Parliament, Zagreb
- The Ministry of Agriculture and Forestry (2007) Brown bear management plan for Finland.
- Thirgood S, Woodroffe R, Rabinowitz A (2005) The impact of humanwildlife conflict on human lives and livelihoods. In: Woodroffe R, Thirgood S, Rabinowitz A (eds) People and wildlife: Conflict or coexistence? Cambridge University Press, Cambridge
- Wiegand T, Knauer F, Kaczensky P, Naves J (2004) Expansion of the brown bear (*Ursus arctos*) into the eastern Alps: a spatially explicit population model. Biodivers Conserv 13:79–114
- Zedrosser A, Støen O-G, Sæbo S, Swenson JE (2007) Should I stay or should I go? Natal dispersal in the brown bear. Anim Behav 74:369–376
- Zedrosser A, Dahle B, Støen O-G, Swenson JE (2009) The effects of primiparity on reproductive performance in the brown bear. Oecologia 160:847–854