Demography and mortality patterns of removed brown bears in a heavily exploited population

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Abstract: Harvesting wild animals can affect demographic parameters and life history traits of surviving individuals. Most brown bear (*Ursus arctos*) populations currently experience low levels of hunting. We characterized mortality patterns in a heavily exploited transboundary brown bear population in Slovenia, Central Europe. Overall, 927 brown bears were reported removed from 1998 to 2008. Most (97%) removals were human caused including removals from hunting (59% of removals), management removals of problem individuals (18%), and vehicle collisions (16%). Median age of bears removed in Slovenia was 2.3 years, and 78% of bears removed were <4 years old. Removal was male-biased overall (59%), mainly due to the high percent (49%) of young (<4 years old) males removed during hunting, a possible consequence of sex-related differences in bear behavior and harvest regulations. However, the effect of sex-biased removal was less than expected based on removal data, and it appears a different harvest regimen in neighboring Croatia and sex-biased dispersal of young bears buffered the demographic effects of selective harvest in Slovenia. We also observed that annual proportion of females in harvests increased with harvest intensity. More males were removed among younger classes, whereas females started to dominate above the age of 8 years. About 20% of the brown bear population was removed annually by legal harvest; this is one of the highest harvest rates reported for this species.

Key words: brown bear, demography, Dinaric Mountains, harvest, hunting, mortality, Slovenia, survival rate, *Ursus arctos*

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Many large carnivore populations have decreased substantially or have been extirpated, especially in human-dominated landscapes like parts of Europe (Breitenmoser 1998, Zedrosser et al. 2001) and North America (Berger et al. 2001). Most surviving populations have more recently received protection, which enabled them to increase in abundance and range. Consequently, levels of protection have decreased and some large carnivore populations are again experiencing increased harvest (Breitenmoser 1998, Zedrosser et al. 2001, Boitani 2003). Increased population numbers have often led to increased conflicts with people, but also have provided sustainable harvest opportunities for some populations (Boitani 2003, Rigg and Adamec 2007).

Hunting can affect demographic parameters (Ginsberg and Milner-Gulland 1994, Langvatn and Loison 1999, Whitman et al. 2004, Milner et al. 2007); genetic (Harris et al. 2002) and morphological characteristics (Coltman et al. 2003); habitat use (Wielgus and Bunnell 2000); social structure (Rutledge et al. 2010); and behavior of individuals in the harvested population (Swenson 1999, Frank and Woodroffe 2001, Treves 2009). Such effects are not limited to hunts characterized by intentional selection for certain individuals, but have also been observed in harvesting monomorphic species without intentional selection (Bunnefeld et al. 2009). While it is relatively easy to obtain large sample sizes for game species like ungulates and game birds, studies are more constrained for large carnivores that typically occur at lower densities.

Brown bears (*Ursus arctos*) are a charismatic and highly valued trophy species among hunters (Swenson et al. 2000). They have low reproductive rates and are sensitive to high harvest rates (Zedrosser et al. 2001). Because overharvest is a common concern, analysis and monitoring of bear mortality,

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especially of bears removed through harvest, is important to ensure population viability (Miller 1990, McLellan et al. 1999, Bischof et al. 2009). In general, European brown bears can sustain higher harvest rates than can North American populations (Swenson et al. 2000). For example, 4–8% annual harvest mortalities reported for European countries appear sustainable (Rigg and Adamec 2007, Bischof et al. 2008a, Huber et al. 2008), whereas for North America it has been suggested that most populations can tolerate only 3–5% annual harvest (McLoughlin 2003).

Nevertheless, most brown bear populations in Europe currently experience low levels of harvest (Swenson and Sandergren 1996, Linnell et al. 2002). A notable exception appears to be brown bears in Slovenia, which form the northwestern part of the Dinaric–Pindos population. The high harvest rates of bears in Slovenia have caused concern and have been the subject of criticism (e.g., Kaczensky 2000, Kaczensky et al. 2011); however, the magnitude of this harvest in relation to the population size is unknown. In addition to high harvest quotas, other bear harvest regulations in Slovenia (Adamič 1997, MKGP 2002) could result in the sex and age structure of harvest bears differing considerably from those of the standing population. This is in contrast to the bear population in Scandinavia, where there is low selectivity among harvested bears (Bischof et al. 2008a, 2009). Therefore, there is potential for more pronounced effects of harvest on demographic structure and population dynamics of brown bears in Slovenia.

We analyzed structure and mortality patterns of brown bears removed in Slovenia during 1998–2008. Our objectives were to (1) determine sex and age structure of removed bears and possible temporal changes in this structure, (2) estimate relative importance of different causes of removal relative to total removal and explore patterns among sex and age classes, (3) examine potential differences in demographic structure of removed bears in relation to cause of removal, and (4) estimate proportion of population removed annually by harvest.

Study area and methods

Study area and brown bear management in Slovenia

Brown bears live mainly in the Dinaric Mountains, southern Slovenia (45°30′–46°15′N, 13°30′–15°15′E). The landscape is predominantly karstic with high plateaus and intermediary valley, ridges, and peaks. Dinaric plateaus are mainly covered with the silver fir (*Abies alba*)–common beech (*Fagus sylvatica*) association (the Omphalodo fagetum plant community). Human density is 54 people/km^2; however, most settlements are in valley bottoms and higher elevation areas are sparsely populated (Perko and Orožen Adamič 1998). Large unfragmented forests and primary roads are generally oriented parallel to mountain ridges; this reduced fragmentation has facilitated brown bear range expansion (Jerina and Adamič 2008a). These forests extend south to the Gorski Kotar region of Croatia. Slovenia encompass the northwestern part of the larger transboundary Dinaric–Pindos brown bear population, including its edge, and the Slovenian part of the bear population continues uninterrupted into neighboring Croatia.

By the late 19th century, brown bears were nearly extirpated in Slovenia, with only 30–40 bears remaining in 2 forest patches near the Croatian border (Simonič 1994). Since the 1940s, bear numbers and distribution increased due to conservation measures. An important measure was the establishment of a Core Bear Protective Area (CBPA) of 3,500 km^2 within the Dinaric Range in 1966, where bear hunting was strictly regulated (Simonič 1994). In contrast, bears outside this area (mostly dispersing individuals) experienced higher harvest rates (Kryštufek and Griffiths 2003, Jerina et al. 2003). Thus, the present distribution of brown bears in Slovenia is mainly a function of past management regimes, habitat characteristics, and human infrastructure.

In general, bear density decreases northward from Croatia, especially outside the Core Bear Protective Area (Jerina and Adamič 2008a, Krofel et al. 2010a). The number of brown bears in Slovenia was estimated in 2007 at 394–475 animals with densities up to 19 bears/100 km^2 in the core area (Skrbinšek et al. 2008). Population dynamic for Slovenian bears during the study period was reconstructed using virtual population analysis method (Roseberry and Woolf 1991, Klopčič et al. 2010) based on data from removed bears in 1998–2008. This method is based on the number and age of removed animals, which are then used to reconstruct the minimal number of animals that lived in a specific year. We also incorporated different scenarios of non-recorded mortality and calibrated them with the population size estimation from 2007 genetic study (Skrbinšek et al. 2008). According to this reconstruction, the estimated number of bears in Slovenia during the study period varied between 278 and 451, was steadily increasing until 2005, and since then was more or less stable (Jerina and Adamič 2008b, K. Jerina et al. unpublished data).

In Slovenia, the most important current bear management practices are harvest and supplemental feeding. Legal harvest encompasses: (1) hunting, which is geographically and temporally restricted and has a prescribed structure according to bear weight categories (described below), and (2) management removals of conflict bears, which are prescribed for bears that cause repeated conflicts with people and are not limited by the hunting season or by age or reproductive status. The quota of bears harvested during the hunting season (Oct 1 through Apr 30) is prescribed according to the 3 body mass categories: <100 kg (at least 75% of prescribed harvest), 100–150 kg (maximum 15% of harvest), and >150 kg (maximum 10% of harvest). It is illegal to shoot females with offspring; however, it is legal to shoot dependent young. Bear hunting can occur only from an elevated platform, usually located at a feeding site, and the shooter must be accompanied by another hunter who shares responsibility for assessing body mass of the bear. To decrease probability of error in estimating body mass, hunting is only allowed under good visibility (i.e., during the day or in moonlight).

The Minister for Environment and Spatial Planning annually prescribes the number of bears to be harvested, primarily based on expert opinion, bear population trend data, and number of human–bear conflicts. The harvest quota is then allocated among bear management regions (inside or outside the CBPA), and further allocated among smaller hunting-management regions to maintain a viable bear population in the CBPA and to limit population expansion in other areas, except potentially within designated corridors toward Italy and Austria (MKGP 2002). If the harvest quota is exceeded in any area, the quota in an adjacent area is correspondingly reduced. Permission for management removals of conflict bears is issued on a case-by-case by the Environmental Agency of the Republic of Slovenia upon recommendation from the Slovenia Forest Service (SFS); removed conflict bears are included in the harvest quota.

Data on removed bears

According to national legislation, all removals of brown bears from the wild must be recorded. Based on national legislation, information on any dead or wounded bear, regardless of cause, must be reported within 12 hours of detection. Similarly, it is compulsory to search for all wounded bears (due to shooting or vehicle collision) using a trained dog, until the animal is located or it is concluded with high probability that the animal will survive. Since 1994, data on bear removals have been maintained by the SFS and include sex, estimated age (using cementum annuli, Craighead et al. 1970), and body measurements along with date, location, and cause of removal. Data quality is strictly controlled by SFS officials, who inspect each removed bear and conduct body measurements. When cause of death can not be determined by SFS personnel, carcasses are inspected by the National Veterinary Institute.

We refer to bears in their first year of life as cubs and bears in their second year as yearlings. When calculating bear age we assumed all bears were born on 31 January. We categorized causes of removal as: hunting, management removals of conflict bears, illegal killings, traffic accidents (animals that died in vehicle collisions on road or railway), found dead (animals that died from natural causes or cases when cause of death could not be determined), removed to sanctuary (orphaned cubs taken to captive facility), and live captures for export (bears captured and translocated to other countries for reintroduction or population augmentation). For bears found dead, we made no attempt to distinguish between natural- and human-caused mortality because carcasses were often decayed or consumed by scavengers to the point where we could not reliably determine specific cause of death. We believe that most bears that died from natural causes were found and recorded (as described in Discussion).

Analyses of bear removal

We used data on all bears removed during 1998–2008. Bears were grouped by year (hereafter: annual removal). Annual removal varied considerably among years (e.g., 56 and 116 individuals in 2001 and 2002, respectively; Fig. 1).

We tested variables (annual removal, sex ratio, relative importance of causes of removal) for serial correlation with a 1-year lag and found no indication among years ($r = -0.17$–0.36; $P = 0.30$–0.76, $n = 10$). We tested for temporal trends in the arcsine

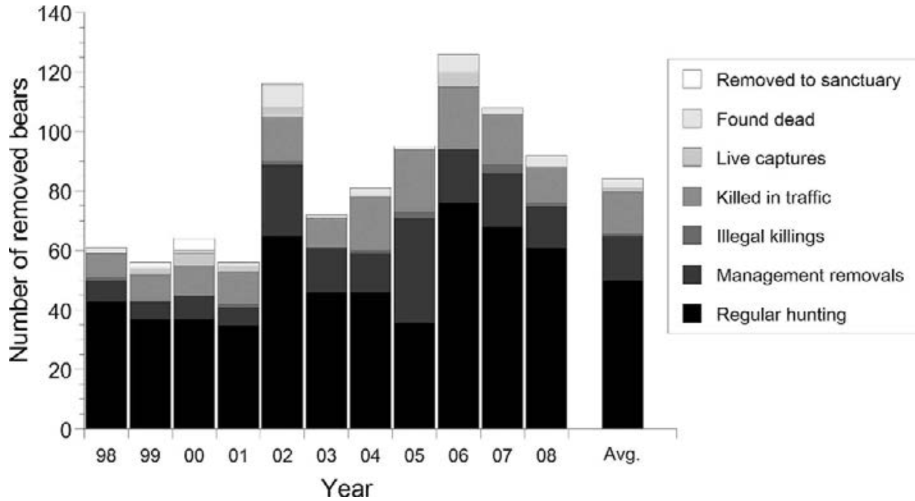

Fig. 1. Number of brown bears removed annually (*Ursus arctos*) in Slovenia, 1998–2008, by type of removal (*n* = 927). The last column represents average removal during the study.

transformed proportion of females among removed bears using linear regression, controlling for annual removal. The same method was used to analyze temporal trends of relative importance of main causes of mortality (i.e., hunting, management removals, and traffic accidents).

We assessed homogeneity of yearly age structures of removed bears using the exact homogeneity test with 10,000 simulations. Data were combined into 3 periods (1998–2000, 2001–04, 2005–08) and 10 age classes (ages 0, 1, 2, 3, 4, 5, 6, 7, 8–11, and >11 years) to ensure that expected frequencies in each period by age class were ≥5 (Zar 1999).

We used generalized linear models (GLM) to test main effects of cause of removal and sex, with annual removal (removed bears/year) and year as covariates and meaningful 2-way interactions on log-transformed age of removed bears. We used logistic regression to explore factors affecting sex of removed bears, including cause of removal, age (ordinal variable: 0, 1–2, 3–7, and >8 years), log-transformed age (covariate), annual removal (covariate), and year (covariate). We used an ordinal variable for age because the sex ratio of bear cohorts varied nonlinearly relative to cohort age. In assigning categories, we considered frequencies and homogeneity of units in candidate categories. We also considered frequencies of units in cross-tabulations so that each class (in crosstab age by cause of removal) contained at least minimum required sample sizes (Zar 1999). Consequently, we retained the 3 largest categories (i.e., hunting, management removals, and traffic accidents) that cumulatively comprised 93% of all bear removals. Remaining causes were combined into the category "other."

For both analyses, we calculated all possible models with algorithm best subsets and selected the models with the lowest Akaike Information Criterion (AIC_c) value (Burnham and Anderson 2002). We explored structure of all candidate models with ΔAIC_c scores lower than 4, calculated Akaike weights, and used them for model averaging to obtain robust parameter estimates (Burnham and Anderson 2002, Johnson and Omland 2004).

Results

During 1998–2008, 927 bears were recorded as removed in Slovenia. Sex was known for 908 (98%) and age for 918 (99%) individuals. All bears were assigned a category of removal cause.

Overall, 97% of recorded removals were human-caused. Most bears (59%) were removed by hunting (Table 1), the dominant mortality source throughout the study (Fig. 1). Legal harvest (i.e., hunting and management removals) accounted for 77% of recorded removals. Vehicle collisions accounted for 16% of removals. Each year, 8–21 bears were killed in vehicle collisions ($\bar{x} = 14$), with an average of 41% of these on railways, 14% on motorways, and 44%

Table 1. Sex and age structure of brown bears removed in Slovenia during 1998–2008 (n = 927) by cause of removal. Values in parentheses indicate median age of bears, assuming all bears were born on 31 January.

Cause of removal	Total bears removed	Percent of all removals (%)	Sex structure			
			Males	Females	Unknown	Percent females
Hunting	550 (2.8)	59.3	349 (2.8)	198 (2.8)	3 (no data)	36.2
Management removals	164 (1.8)	17.7	78 (1.8)	86 (1.8)	0	52.4
Traffic accidents	152 (1.5)	16.4	84 (1.4)	65 (1.8)	3 (0.5)	43.6
Found dead	30 (0.5)	3.2	11 (0.5)	9 (2.3)	10 (0.4)	45
Live captures for export	16 (3.3)	1.7	4 (3.8)	12 (3.3)	0	75
Illegal killings	10 (1.8)	1.1	6 (1.6)	2 (5.1)	2 (3)	25
Removed to sanctuary	5 (0.2)	0.5	2 (0.3)	3 (0.2)	0	60
Total	927 (2.3)	100	534 (2.3)	375 (2.5)	18 (0.4)	41.3

on other roads (in contrast to other roads, motorways are usually 4-laned, with more traffic, faster vehicles, and fenced).

Four models explaining the age of removed bears had ΔAIC_c score less than 4. Parameter values produced by model averaging showed that age of removed bears was best explained by cause of removal, sex, the cause by sex interaction, and to a lesser degree, by year and by annual removal (Table 2). The best model explaining the sex of removed bears included variables cause of removal, age, and annual removal (Table 3). No other model had ΔAIC_c score <4 (the second best model ΔAIC_c score was 6.3). The r^2 values of both final models were low (0.06 and 0.10; Table 2 and 3), meaning that much variation in response variables remained unexplained by these models.

Table 2. Model averaged parameter estimates explaining age (log transformed) of removed brown bears in Slovenia during 1998–2008 (n = 908). We based model selection on Akaike selection criterion and used all top models with ΔAIC_c scores <4 (4 models). One level of each categorical variable served as contrast (estimate = 0) for the remaining levels of that variable. Model R^2 = 0.10; n = 908.

Explanatory variable	Estimate	SE
Cause of removal		
Hunting	0	
Management removals	−0.060	0.057
Traffic accidents	−0.180	0.059
Other	−0.090	0.088
Sex		
Females	0	
Males	−0.120	0.037
Sex x cause of removal		
Hunting x females	0	
Management removals x males	0.074	0.057
Traffic accidents x males	−0.117	0.059
Other x males	−0.127	0.088
Year	0.001	0.009
Annual removal	0.000	0.001

The percent of females among all removed bears was 41%; the percent was lower in hunting (36%) and higher in traffic accidents (44%) and management removals (52%; Table 1). The absolute difference overall between males and females removed was 159 animals. Most of this difference was due to hunting (151 more males than females removed), followed by traffic accidents (males − females = 19), illegal killings (males − females = 4), and bears found dead (males − females = 2). Among other causes, females prevailed. Median age was highest for bears removed from hunting (2.8 years), followed by the management removals (1.8 years), and traffic accidents (1.5 years). The GLM model contained a significant interaction of sex by cause of removal, indicating that the group most exposed to the traffic accidents were young males (median age = 1.4 years).

Sex ratios among removed bears differed among age classes. Among removed cubs, the sex ratio was close to unity (males:females = 1:1.02; n = 117). The proportion of females first decreased with age, averaging 37% at years 2–4, but then increased and exceeded the proportion of males at age 8 (Fig. 2). The oldest removed male was 14 years and the oldest removed female was 21 years. Among all bears removed in Slovenia, 78% were removed before reaching 4 years of age (80% of males and 75% of females). Median age at removal was significantly lower for males (2.3 years) than for females (median = 2.5 years; β males versus females = −0.120; P = 0.001; Table 2). The sex differential was largest during ages 1–3 years (males removed = 62% [n = 350], females removed = 38% [n = 211]). Mortality within different causes varied with age (Fig. 3). For example, hunting was lowest among cubs (18%),

Table 3. Parameter estimates and test statistics for the top logistic regression model explaining sex (males = 0, females = 1) of removed brown bears in Slovenia during 1998–2008 ($n = 908$). We based model selection on Akaike selection criterion. The second best model had ΔAIC_c scores >6. One level of each categorical variable served as contrast (estimate = 0) for the remaining levels of that variable. LCL = lower 95% confidence level, UCL = upper 95% confidence level. Annual removal refers to number of bears removed/year. Model *Nagelkerke* $R^2 = 0.06$; $n = 908$.

Explanatory variables	Estimate	SE	Odds ratio	LCL	UCL
Cause of removal					
Hunting	0				
Management removals	0.594	0.186	1.811	1.259	2.605
Traffic accidents	0.208	0.200	1.232	0.833	1.822
Other	0.655	0.311	1.926	1.046	3.545
Age category					
Cubs	0				
1–2	−0.197	0.222	0.822	0.532	1.270
3–7	−0.415	0.240	0.660	0.413	1.057
≥8	0.618	0.326	1.854	0.980	3.510
Annual removal	0.007	0.003	1.007	1.000	1.013

increased until age 3 (79%), and gradually declined thereafter.

Annual removal varied from 56 (2001) to 126 (2006) bears (Fig. 1). Annual removal increased over the study ($\beta = 5.6$; $P = 0.01$; $n = 11$). Proportion of females among removed bears varied annually from 34–49% and increased across years ($\beta = 0.0015$; $P = 0.002$; $n = 11$) and with annual removal ($\beta = 0.012$; $P = 0.007$; $n = 11$; Table 3). However, in a linear regression model that controlled for the effect of annual removal, time (year) did not affect the proportion of removed females (partial $r = 0.33$; $P = 0.35$; $n = 11$). Neither proportion of removals being management removals nor proportion of hunting and traffic accidents were associated with total annual removal or year ($r = 0.07$–0.40; $P = 0.22$–0.88; $n = 11$). Age structure of removed bears among periods was similar ($\chi^2 = 25.05$, 18 df; $P = 0.12$).

Discussion

Most brown bear mortality in Slovenia was human-caused, and harvest rates appeared to be higher than in any other European study. For example, based on the 2007 population estimate (Skrbinšek et al. 2008), annual mortality due to legal harvest and total human-caused mortality represented 20% and 24% of the December population, respectively. Removal rates varied annually but generally increased in time, together with population growth. Using population reconstruction (see Study Area for details), the harvest rate in 2007 was similar to other years during the study (average = 20%; range for individual years: 14–26%) and considerably higher than the 4–8% annual harvest mortalities reported in other European countries with legal harvest (Rigg and Adamec 2007, Bischof et al. 2008a, Huber et al. 2008). Variation in data quality and extent of illegal killing makes comparisons difficult; however, high human-caused removal rates in Slovenia suggests potential for more pronounced effects on bear demography and behavior than in other populations.

In spite of the high rate of human-caused mortality, bear abundance in Slovenia appeared to be increasing (Jerina et al. 2003, Jerina and Adamič 2008b), while several other brown bear populations with lower human-caused mortalities were stable or declining (e.g., Mace and Waller 1998, Linnell et al. 2002, Wakkinen and Kasworm 2004, Chapron et al. 2009; but see Mace et al. 2012). This is partly a result of low natural mortality and high reproduction rate of bears in Slovenia. This may be the result of environmental factors connected to the southern latitude, high proportion of females in the population, intensive supplemental feeding, and decreased age of primiparity. Natality calculated according to data from bear monitoring through systematic observations at feeding sites (>6,700 bears observed at 352 locations in 1994–2008) was estimated at 71.5–82.8 bears born/year or 20% (95% CI = 19–22%) of the estimated population (Jerina et al. 2005, K. Jerina, unpublished data). In addition, net influx of bears from Croatia may be an important factor enabling high removal rates, and further studies are

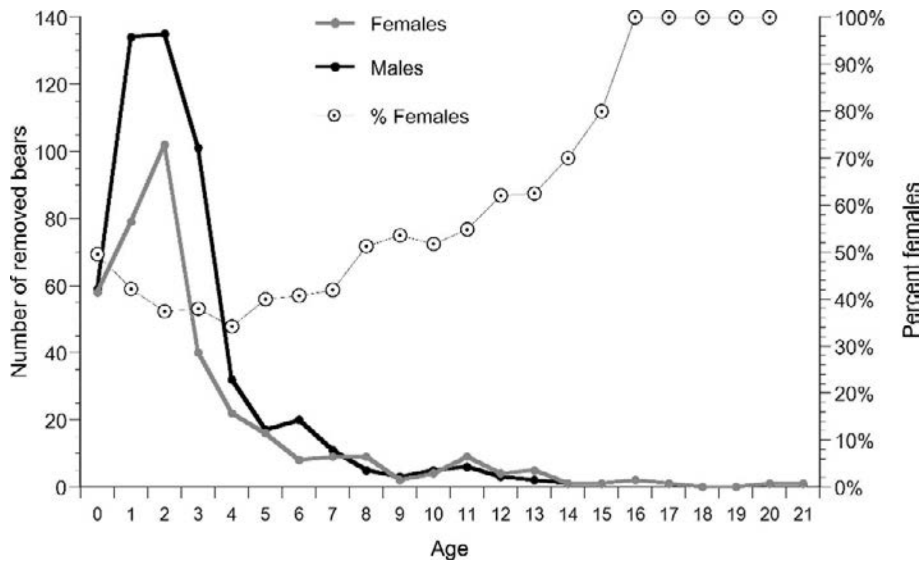

Fig. 2. Number and proportion of removed male and female brown bears by age in Slovenia, 1998–2008 (n = 918). Proportions of females shown are moving averages of 3 years (age − 1, age, age + 1), except for youngest and oldest animals (0 and 21 years), for which year-specific data are shown. Age refers to the bears removed in that year of life, e.g. age 0 represent bears <1 year old.

needed to evaluate its contribution to the population dynamics.

Demography of removed bears

Data acquired with hunting statistics are often biased to certain sex or age groups (Bischof et al. 2008a). We believe that bias of removal data in Slovenia is relatively small due to: (1) high rate of human-caused bear mortality (because of high harvest rates and also frequent vehicle collisions); (2) consistent reporting of dead bears, which is prescribed by law; and (3) good coverage of terrain due to high density of hunters, foresters, hikers, amateur speleologists, mushroom-pickers, and others afield (Jerina and Adamič 2008a). Considering high harvest quotas, legislation which prevents keeping trophies of bears that were removed without being reported, and intensive peer control among

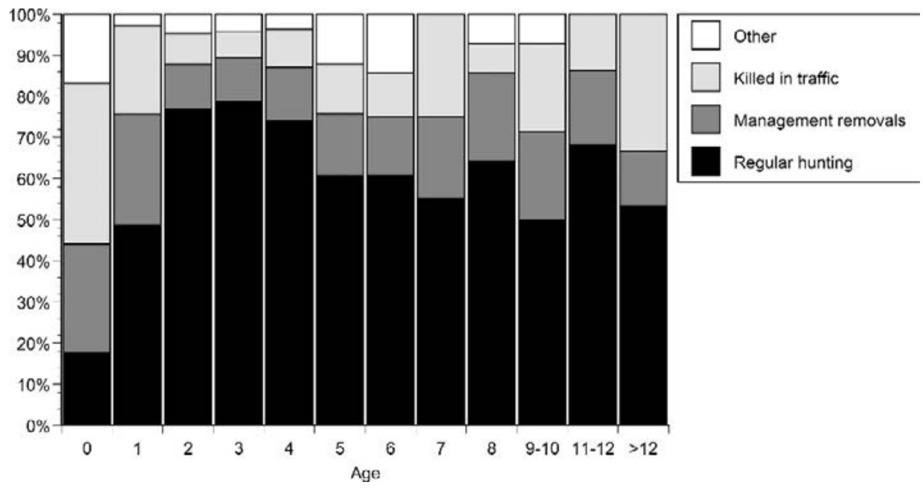

Fig. 3. Relative importance of causes of removal for different ages of removed brown bears in Slovenia (n = 927). Age refers to the bears removed in that year of life, e.g., age 0 represent bears <1 year old.

hunters, we suggest there are few unrecorded illegal killings and their effects on our conclusions are negligible (we note that most recorded mortalities attributed to illegal killings refer to mistakes in estimates of weights, most often discovered only after official weighing). About 3% of the recorded removed bears died from natural causes and most were young animals. Our data do not allow estimating unrecorded natural mortality, but its proportion among subadult (1–3 years) and adult (≥3 years) bears can be inferred from recent telemetry studies. Fifty-nine subadult and adult bears were monitored with VHF or GPS telemetry in Slovenia for 38 bear-monitoring years during 1993–2010 (Kaczensky et al. 2002; Krofel et al. 2010a,b; P. Kaczensky, Research Institute of Wildlife Ecology, University of Veterinary Medicine, Vienna, Austria, unpublished data). Twelve of these bears died, of which 8 were legally shot during hunting, 2 died in vehicle collisions, 1 was poached in Austria (Kaczensky et al. 2011), and 1 was presumably poached in Slovenia; none died from natural causes. Here it must also be noted that hunters were asked (although not ordered) not to shoot collared bears, and for many hunters collared bears are less interesting to shoot, so the proportion of legally shot bears (and thus human-caused mortality) in proportion to natural mortality is likely underestimated. These data suggest that undetected natural mortality was low compared with other causes of mortality and likely did not influence our results. Because the density of hunters and foresters, as well as mountaineers, hikers, amateur speleologists, mushroom-pickers, berry-pickers, and others afield is high in Slovenia, and because reporting any bear found dead is compulsory, we believe that most bears that died from natural causes were found and recorded. Additional indirect evidence for good ground coverage and consequently support for a high probability of finding bears dead from natural causes comes from the high number (10 of 12) of non-functioning, dropped radiocollars found by the general public and returned to the authors.

Natural mortality among cubs was likely to be more underestimated than other age classes because proportion of mortality from natural causes was probably largest for this class. We know of 15 cubs that probably died of natural causes. Several dead cubs were evidently killed by other bears, but because of small size and because infanticidal males often consume killed cubs, their carcasses were less likely to be found in the field than those of other bears. Although we lack telemetry data to document the natural mortality rate for cubs, we do have some indications of low natural mortality of cubs from 14 years of systematic counts of bears observed at feeding places (done 3 times annually, during different seasons), in which litter sizes were recorded (>6,700 bears observed at 352 locations during 1994–2008). Data on change in average litter size when the same cohorts of cubs were followed through different seasons and years suggested that infanticide or other causes of natural mortality among cubs was uncommon.

In Slovenia, demographic structure of harvested bears differed considerably from that in Scandinavia, where low selection in hunting was observed due to the low bear encounter rates for individual hunters (Bischof et al. 2008a). The situation in Slovenia is more similar to North America and Eastern Europe, where removal is more selective by sex or age classes (Bunnell and Tait 1980, Adamič 1997, Derocher et al. 1997, McLellan et al. 1999, Czetwertynski et al. 2007). Most bears in Slovenia are removed by hunting, which has prescribed structure that favors removal of smaller and therefore younger animals. Among sexually mature bears, the ban on hunting of females with cubs favors removal of males. Other studies have shown that even without such rules, males are more vulnerable to removal due to their greater mobility (Bunnell and Tait 1980, Noyce and Garshelis 1997, McLellan et al. 1999), shorter denning period (Derocher et al. 1997), higher tolerance to human proximity, and more frequent visits to bait stations (Bunnell and Tait 1980, Noyce and Garshelis 1997). It is therefore not unexpected that hunting in Slovenia is considerably male-biased.

Sex ratio is less male-biased in other causes of removal (management removals, traffic accidents, bears found dead). We assume this is primarily because the protection of females with offspring does not occur in these removals. For sex ratio of bears killed in traffic accidents, the proportion of females is lower in Slovenia (44%) than the neighboring part of the population in Croatia (56%; Huber et al. 1998). This might indicate an edge effect due to male-biased dispersal, which causes that area closer to the periphery of the population (i.e., Slovenia) to have a higher proportion of males than areas with large part in the population core area (Croatia; e.g., Jerina and Adamič 2008a). The proportion of females was especially high among live captures for export, a consequence of the preferences of the importing country. Nevertheless, males still accounted for most removals (59%) due to the high proportion of hunting in total removals. Because of this and because of equal sex ratio among cubs (Fig. 2; Mace and Waller 1998, Chapron et al. 2009), we would expect a considerable female-biased sex ratio in the living population. However, the genetic survey of bear scats in 2007 showed that the proportion of females in the wild was 55% (Skrbinšek et al. 2008). Such a sex ratio is less biased than expected according to removal data and may be explained by immigration of dispersing males from Croatia, where legal harvest rates are considerably lower than in Slovenia and have different demographic structure. This indicates that different harvesting regimes in different parts of the same population may buffer the demographic effects of selective hunting.

The proportion of females among removed bears increased with annual removal. This is similar to harvests of red grouse (*Lagopus lagopus scoticus*) where the sex ratio was unintentionally altered with a change in harvest intensity (Bunnefeld et al. 2009). Changes in sex ratio may have important consequences for population dynamics (Milner et al. 2007). Population trends among ursids are most sensitive to female survival rate (Taylor et al. 1987, McLellan et al. 1999) and the impact of harvest is reduced when more males than females are removed (Derocher et al. 1997). However, effects of male-biased removal should also be considered, including increased risk of infanticide (Swenson et al. 1997), lower female reproduction due to avoidance of food-rich habitats occupied by infanticidal males (Wielgus and Bunnell 2000), and decreased natality rate due to lower age of males caused by harvest (Milner et al. 2007).

About 80% of bears removed in Slovenia were removed when <4 years old. Such removal rate is high compared to other brown bear populations in Europe and North America (McLellan et al. 1999, Wakkinen and Kasworm 2004, Bischof et al. 2008a, Chapron et al. 2009, Groff et al. 2010). For females, survival increases considerably after their first litter (typically at 3 or 4 years) and for males when their body mass exceeds 150 kg (on average after 6 years; Jerina and Adamič 2008b). However, the overall proportion of older bears among removals in Slovenia was small. This is probably a consequence of the high harvest rates of this group in Croatia (Budor et al. 2009), where unlike Slovenia, there are no body mass limitations for hunting and sport-trophy hunting (i.e., hunting with more pronounced economic benefits where the main goal is to obtain or sell the trophy) is more prevalent. Adult males in Slovenia have large home ranges and many extend into Croatia (e.g., 9 of 19 males radiocollared in Slovenia had transboundary home ranges; Krofel et al. 2010b), where some may be removed.

Conflict bears killed in management removals were younger than bears removed by hunting (Table 1), even though management removals were not subject to limitations favoring removal of young bears. This indicates that subadult bears came into conflict with humans more frequently than older bears, similar to observations in North America (McLellan et al. 1999). We attribute the lower age of bears that died in traffic accidents to increased vulnerability due to inexperience (Huber et al. 1998). We note, however, that differences in bear ages were relatively small and therefore the explanatory power of our models was low. Nevertheless, the biological importance of these results is still high, because even small changes in demographic structure of removed bears could cause strong effects in population dynamics and sex structure because differences accumulate over time.

Evolutionary and genetic consequences of hunting should also be considered, especially when the population is heavily exploited, as is the case with brown bears in Slovenia. Evolutionary changes caused by selective hunting have been documented in several harvested large mammal species (e.g., bighorn sheep [*Ovis canadensis*], Coltman et al. 2003; mouflon [*Ovis gmelini musimon*], Garel et al. 2007; red deer [*Cervus elaphus*], Proaktor et al. 2007). Consequently, some authors have proposed that managers should strive to mimic natural mortality patterns (Harris et al. 2002, Milner et al. 2007). For brown bear, natural mortality is lower in adults and higher among cubs and subadults (Miller et al. 2003). Such structure was observed in this study, suggesting the removal structure in Slovenia is similar to natural mortality structure even though it is largely human-caused. Bischof et al. (2008b) suggested caution in application of natural mortality structure to prescribed removals because of possible amplification of traits selected by natural mortality, which can occur if harvest mortality is additive.

One of the major evolutionary hunting-induced changes, which may be expected in Slovenia, is selection for females with lower age of primiparity.

Females that have cubs earlier will on average produce more offspring (and have higher fitness) and should thus be positively selected, as has been suggested for the Scandinavian population (Bischof et al. 2009) and also indicated by the comparison of European bear populations with North American, where human persecution has a shorter history (Zedrosser et al. 2011). Impacts of harvest on age of primiparity may be even greater in Slovenia because of considerably higher harvest rates among young age classes and complete protection of females from hunting once they have cubs. This may be indicated by high proportion of females living in Slovenia or originating from this population that have cubs at age 3 or 4 years (Zedrosser et al. 2004, Groff et al. 2010, K. Jerina et al. unpublished data), whereas in other populations age of primiparity is considerably higher (Hensel et al. 1969, Knight and Eberhardt 1985, Craighead et al. 1995, Mace and Waller 1998, Støen et al. 2006). However, additional research would be needed to rule out other effects (i.e., habitat factors). Future studies should also emphasize the effects hunting rules have on bear behavior. For example, because bear hunting in Slovenia can be carried out only under good visibility, hunting pressure could favor nocturnal behavior in bears.

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