

# Reconstruction of brown bear population dynamics in Slovenia and Croatia for the period 1998-2018

Action C5: Establishment and optimization of an integrated, population-level surveillance of brown bear conservation status

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Suggested Citation:

Jerina, K., Polaina, E., Huber, Đ., Reljić, S., Bartol, M., Skrbinšek, T. Jonozovič, M. (2018)

Reconstruction of brown bear population dynamics in Slovenia and Croatia for the period 1998-2018, prepared within C5 action of LIFE DINALP BEAR Project (LIFE13 NAT/SI/0005): 46 pp.

February 2018

Univerza v Ljubljani



ZAVOD za GOZDOVE  
SLOVENIJE  
Slovenia Forest Service

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## Izvleček

Populacijska dinamika oz. spreminjanje številčnosti populacije v času je eden glavnih parametrov pri upravljanju in raziskavah prostoživečih živalskih vrst. V pričujoči ekspertizi smo za obdobje 1998-2018 rekonstruirali populacijsko dinamiko rjavega medveda v Sloveniji in na Hrvaškem, ocenili relativno rodnost populacije, njeno dejansko preteklo in trajnostno antropogeno in lovno smrtnost ter obseg nezabeležene smrtnosti. Za rekonstrukcije smo uporabili metodo starostno-spolnih strukturiranih matrik in napovedno modeliranje »age-at-harvest & predictive modelling«, ki se diametralno razlikujeta po predpostavkah; poleg tega smo dinamiko enkrat rekonstruirali ob predpostavki, da so medvedi v Sloveniji demografsko zaprti, drugič pa, da so popolno povezani s »hrvaškimi« medvedi. S primerjavami rezultatov smo lahko ocenili vplive kršenja predpostavk uporabljenih metod na ugotovljene populacijske dinamike in končno pripravili sintezni model, ki odpravlja hibe posameznih pristopov. Vsa modeliranja temeljijo na časovni seriji podatkov o spolu in starosti evidentirane smrtnosti medvedov v obeh državah; za kalibracijo modelov smo uporabili točkovne ocene številčnosti in spolne sestave medveda v Sloveniji leta 2007 in 2015 ter na Hrvaškem leta 2015, ugotovljene z neivazivnim genetskim vzorčenjem.

Rezultati različnih pristopov so zelo podobni, kar nakazuje, da so ocene kakovostne. Po napovedih modelov se je številčnost dinarske populacije medveda v zadnjih 20-ih letih naglo, in bolj ali manj stalno povečevala. Povprečna geometrijska letna stopnja rasti populacije je v Sloveniji znašala 4.5 % (CI: 3.9-5.2 %) in na Hrvaškem 5.0 % (CI: 4.3-5.7 %). Ocene za Hrvaško (in torej tudi ca skupno populacijo) so verjetno manj zanesljive, saj je bila kakovost vhodnih podatkov v začetnem obdobju tam slabša, za kalibracijo modelov ni bilo na voljo druge zanesljive ocene številčnosti, predvsem pa več rezultatov/podatkov nakazuje, da se je smrtnost samic in nasploh mlajših medvedov na Hrvaškem slabše evidentira/lo – je podcenjena (možen obstoj krivolova). Spomladi leta 1998 je po oceni v Sloveniji živelo 405 (330-460) medvedov, za leto (leto 2018) pa znaša ocena pomladanske številčnosti že 975 osebkov (CI 875-1130). Populacija v obeh državah skupaj je za pomlad leta 2008 ocenjena na 850 osebkov (675-1015), leto (2018) pa že na 2145 (1875-2450) osebkov. Pri tem pa je treba opozoriti, da se je za Slovenijo doslej praviloma poročalo ocene za pozno jesensko obdobje, ko so številčnosti medveda na najnižji letni ravni. Naše poročane vrednosti pa so »pomladanske«, ko je številčnost v letnem ciklu - po kotitvi mladičev - najvišja (»jesenske« ocene so za 24 % - kolikor pri nas znaša relativna rodnost - nižje od »pomladanskih«).

Zabeležena antropogena relativna smrtnost medveda je v Sloveniji v povprečju letno obsegala 15 % številčnosti populacije in na Hrvaškem 13 %; v Sloveniji se je antropogena relativna smrtnost v analiziranem obdobju postopno zmanjševala, na Hrvaškem pa hitro povečevala, kar je posledica diametralnih sprememb intenzivnosti lova na medveda med državama. Le-ta je v zadnjih letih na Hrvaškem večji, kot v Sloveniji. Z lovom se je v Sloveniji povprečno letno odvzelo 12 % in na Hrvaškem 11 % populacije. V Sloveniji je lov usmerjen predvsem na lažje (mlajše) medvede obeh spolov (kar skuša slediti naravnim vzorcem smrtnosti) na

Hrvaškem pa med odrasle samce (ekonomika trofejnega lova). Iz rekonstruiranih starostnih struktur je razvidno, da je delež odraslih samcev v primerjavi z deležem odraslih samic v populaciji (zelo) nizek.

Neevidentirana smrtnost je po zelo grobi oceni za obe države skupaj znašala okoli  $\frac{1}{4}$  celotne smrtnosti, kar pomeni, da se okoli  $\frac{3}{4}$  vse smrtnosti beleži. Vendar je ocena neevidentirane smrtnosti lahko podcenjena, zlasti v primeru obstoja krivolova.

Več različnih ocen/podatkov potrjuje, da je relativna rodnost dinarske populacije zelo visoka; njena najbolj verjetna vrednost znaša 24 %. Ob predpostavki, da bo delež evidentirane smrtnosti v prihodnje ostal podoben dosedanjemu, znaša -z demografskih vidikov - trajnostna antropogena smrtnost dinarske populacije 18 - 20 %, trajnostna (ki populacijo natanko stabilizira) lovna smrtnost pa 14-17 % (odvisno od deleža samic med ustreljenimi medvedi, v katerem se Hrvaška in Slovenija močno razlikujeta), kar je znatno več od dosedanje povprečne relativne lovne smrtnosti.

Dela populacije medveda v Sloveniji in na Hrvaškem sta demografsko tesno povezana, kar je delno nevtraliziralo razlike v upravljanju (odstrelu) medvedov med državama (delež samic in starost uplenjenih medvedov) in blažilo vplive trofejnega lova na zastopanost odraslih samcev v populaciji. Poleg tega se je številčnost populacije v obravnavanem obdobju naglo povečevala. Zato povečana lovna smrtnost samcev ni mogla močneje spremeniti spolne sestave populacije v prid samic. Če pa se bo intenzitete odstrela s ciljem regulacije številčnosti populacije (upočasnitve/zaustavitve rasti) v prihodnje povečevala, k čemur so močne pobude, bo treba prilagoditi pravila/izvedbo lova (npr. težnostne kategorije, jesenski vs. pomladanski lov), da bo lovna smrtnost med spoloma bolj izenačena, kar zlasti velja za Hrvaško. Sicer bo lov (lahko) drastično spremenil spolno razmerje populacije v prid samic, z vsemi negativnimi stranskimi učinki.

Pristop modeliranja populacijske dinamike, ki smo ga razvili, je izredno racionalen, podaja številne pomembne informacije/podatke za upravljanje in raziskave, in je zato vreden premisleka za vključitev v shemo rednega monitoringa medveda. Pristop bo mogoče enostavno uporabiti tudi za napovedovanje dinamike številčnosti ob različnih prihodnjih scenarijih upravljanja v eni ali drugi državi. Za kakovostne napovedi pa so potrebne zanesljive evidence smrtnosti medvedov. Evidence pa so lahko zanesljive le ob urejenem lovstvu/upravljanju prostoživečih živali, kjer ni motivov za krivolov, kar je treba z ustrezno prilagoditvijo zakonodaje in njeno vpeljavo v prakso še spodbujati.

## Abstract

Population dynamics – i.e. change in population size over time – is one of the key parameters in management and research of wildlife species. In the present study, we reconstructed the population dynamics of brown bear in Slovenia and Croatia, and estimated its relative natality, its actual past and sustainable present anthropogenic and hunting mortality, and the extent of unrecorded (background) mortality for the period 1998-2018. The reconstructions were elaborated using age-at-harvest and predictive population modelling, which are based on contrastingly different assumptions; additionally, dynamics were alternatively modelled under the assumption that bears in Slovenia are demographically isolated, and assuming they form, together with Croatian bears, a completely panmictic population. The comparison of results allowed us to evaluate the strength of violations of assumptions on estimated population dynamics and finally produce a robust synthetic model. All modelling was based on an extensive long-term dataset on sex and age of recorded dead bears from both countries. The models were calibrated with “point” estimates of size and sex structure of the bear population in Slovenia in fall 2007 and 2015, and Croatia in fall 2015, which were determined based on non-invasive genetic sampling.

The results of the different modelling approaches were strikingly similar, indicating that our estimates are probably accurate. The final model predicted that the brown bear population in Slovenia and Croatia was increasing more or less constantly - and rather rapidly- over the studied 20-year period. Mean geometric annual population growth rate was 4.5% in Slovenia (3.9-5.2%) and 5.0% in Croatia (4.3-5.7%). However, the estimates for Croatia (and thus also for joint population) were probably less reliable because the quality of input data was poorer at the start of the study period and several independent results indicated that the mortality of females and subadult bears was underreported there. These evidences suggest that poaching might be taking place unnoticed. In spring 1998, estimated population size of bears in Slovenia was 405 (CI: 330-460) and “spring” estimate of population size for the current year (2018) was 975 individuals (CI: 875-1130). The mean population size in both countries combined was around 850 individuals (675-1015) in spring 2008, and 2145 (1875-2450) in the current year (2018). However, it should be noticed that previously reported population size in Slovenia corresponded to late autumn, when size is at the annual minima. Instead, we reported here “spring” estimates, when the population size – after new reproduction - is at annual maxima (“autumn” estimates are 24% - i.e. by value of relative natality of our bear population – lower than “spring” estimates).

Recorded relative anthropogenic brown bear mortality averaged 15% annually in Slovenia and 13% in Croatia; in Slovenia relative anthropogenic mortality was slowly decreasing and in Croatia rapidly increasing during the study period, which is a consequence of divergent changes in hunting intensity: in recent years relative hunting mortality of bears in Croatia exceeded the mortality in Slovenia. On average, hunting removed 12% of the population annually in Slovenia, and 11% in Croatia. In Slovenia, hunting mostly targets lighter

(younger) bears of both sexes, aiming to mimic natural mortality patterns; whereas in Croatia hunting is trophy-oriented and targets adult males. Reconstructed age-sex specific population structure indicates that proportion of mature males in population was very low compared to proportion of reproductive females.

Unrecorded mortality considering both countries together roughly summed up to about  $\frac{1}{4}$  of total bear mortality, which means that  $\frac{3}{4}$  of all mortality was recorded. However, unrecorded mortality may be underestimated, in particular if poaching is taking place.

Multiple independent analyses confirmed that relative natality of the Dinaric population is high (24%). Assuming that the rate of recorded mortality would remain similar in the future, demographically sustainable anthropogenic relative mortality of the Dinaric population would be around 18-20%, and sustainable hunting mortality around 14-17% (depending on share of females among hunted bears, which is much lower in Croatia than in Slovenia). These figures are considerably higher than the relative past and present hunting mortality.

The Slovenian and Croatian parts of the brown bear population are strongly connected from a demographic point of view, which partly buffered the differences in management (harvest) between countries (share of females and age of hunted bears) and mitigated the impacts of male-biased hunting on population sex structure. Because population size increased in the study period, elevated male hunting mortality could not significantly skew the population sex structure in favor of females. However, if hunting intensity will increase in the future in order to regulate the population (to slow or stop population growth), hunting would need to be adjusted to better balance the sex structure of hunted bears (e.g. body weight regulations, autumn vs. spring hunting), particularly in Croatia. Otherwise, hunting might result in extreme female-skewed population structures, with numerous possible negative side effects.

The population dynamics modelling approach that we developed is a rational option and provides valuable information for both management and research, therefore it is worth considering it to be included in future repertoire of regular brown bear monitoring scheme. Moreover, it is ready to use for predicting the future evolution of population size under different management scenarios. To carry out quality analyses as the one presented here, reliable monitoring of bear mortality is a must. Reliable monitoring directly depends on well-functioning of hunting and wildlife management, which would desirably eliminate any motivation for poaching. This should be further encouraged by enforcement of legislation in practice.



# 1. Introduction and aims

Knowing the population dynamics of a species (i.e. changes of population size over time) is an essential precondition for many aspects of wild-animal management and research. Data on absolute and/or relative population size and their dynamics over time form the basis for management planning, studying species impacts on habitat and other animal and plant species (and vice versa, the impact of other species on the study species), and also to further assess the influence of population size on damages and other interactions with humans. It is therefore unsurprising that population dynamics is often one of the first parameters to be determined or monitored by researchers and wildlife managers.

Population size and dynamics are in the focus for various stakeholders in particular when it comes to protected, conflict-prone and charismatic species such as large carnivores, including brown bear. Because brown bear is severely endangered in several parts of the world, it is important to know its population size in order to evaluate its conservation status and design effective conservation measures. Human-bear conflicts may occur under many circumstances: as a consequence of bear damages to agriculture, livestock and/or apiculture, or because of their predation on other wild animals (e.g. moose calves) and even derived from their behaviour of bark stripping. Furthermore, conflict situations may also arise when bears wander into settlements, catalysing people's fears. The public typically demands increased culling as the first solution. Hunting is an important management measure in many viable populations, but it is only permissible in protected species if it does not endanger the favourable state of the population, which requires previous evaluation of population size and dynamics. For charismatic species such as brown bear, knowing the population size and its dynamics is also important when communicating with stakeholders.

Many methods have been developed to determine population size and infer population dynamics. They vary in precision, accuracy, purpose, costs, technical complexity, requirement of human resources, and depend on the size of study area and the biological characteristics of the target species (e.g. seasonal migrations, size of individual and population ranges, population density, habitat of the species in relation with detectability of individuals). When selecting the method to use, it is necessary to specify the overall aim of the monitoring (i.e. the desired accuracy and frequency of population estimates), taking into account the economic costs and trying to get the most of available data.

Across the bulk of the project area, mostly in Slovenia and to a lesser extent in Croatia, several studies and monitoring activities have been conducted throughout the years, which provide an excellent basis for reconstruction of the population dynamics of the target population. Namely, the best sources of data are (i) long-term records of bear mortality and (ii) "point" estimates of brown bear population size conducted by non-invasive genetic methods in Slovenia in 2007, and in both Slovenia and Croatia in 2015.

Slovenia and Croatia present a relatively high density of human settlements. In terms of hunting management, their territories are divided into small hunting grounds (few thousand

hectares each) and besides, in Slovenia, there are larger special-purpose hunting grounds where full-time employed district hunters are permanently present. Reporting of hunting and all other mortality events (traffic accidents, fallen animals) is mandatory for all game species and large carnivores, including brown bear. Additionally, hunting of brown bear is intensive in both countries compared to other countries. Brown bear is still interesting for a variety of stakeholders, including hunters, who have therefore provided systematic reporting on those species. Consequently, legal harvesting and other human-related mortality events account for a large portion of total brown bear mortality.

Monitoring of harvested bears has a long tradition in Slovenia. For some regions, records of annual number and sex composition of hunted bears are available for the last 250 years with brief intermissions (e.g. for former Auersperg estates in Kočevje area). Since the Second World War all mortality of bears has been systematically recorded in the entire country. From 1991 onwards bears have been aged by measuring tooth sections. Until the establishment of the Slovenian Forest Service (SFS) the extraction of premolars (P1) for bear ageing was non-systematic since samples were mostly obtained from taxidermists. The SFS subsequently took on the task of extracting the sample tooth of all registered dead animals, thus after 1998 tooth samples of all dead bears are collected. In Croatia, systematic ageing of all culled bears started in 2005; although pre-2005 summary data on annual recorded mortality are also available for some regions.

Due to its large body mass and omnivore diet, brown bear has large individual home ranges and population distribution ranges. This species is also characterized by long seasonal and daily migrations, and is able to accomplish long movements during dispersal. In Europe, almost all brown bear populations span multiple countries, which is also the case of the Alps-Dinaric brown bear population. In particular, the population segments of Slovenia and Croatia present a tight demographic connection, with individuals from these areas continuously moving from one country to the other. Thus, previous telemetry studies showed that almost half of the bears in Slovenia present cross-border home ranges. Cross-border demographic characteristics require additional efforts for coordinated population management, and they must also be considered when estimating population size and reconstructing population dynamics.

For this study, we count on long-term continuous data on bear mortality from Slovenia and Croatia derived from systematic records; in addition, we have reliable population size estimates for both countries derived from non-invasive genetic methods (2007 for Slovenia, 2015 for both simultaneously). All this will allow us to conduct a solid reconstruction of brown bear population size dynamics, and to determine other relevant demographic parameters such as natality, background mortality, sex and age structure, and their change over time. Furthermore, we will be able to evaluate the effect of cross-border demographic interdependence of both parts of the population on its size and dynamics.

The study has four primary aims/purposes:

- (a.) To provide a reliable estimate of brown bear population dynamics in Slovenia and Croatia for the past 20 years, i.e. after 1998.
- (b.) To test conceptually contrasting methods of assessment of population dynamics, to estimate their robustness/reliability by comparing differences and similarities, and to produce the most reliable final estimate.
- (c.) As a “side result” of the population dynamics reconstructions, to estimate age-specific relative natural (background) bear mortality, relative fertility, age structure of the population –and their evolution over time– and other required parameters to forecast future population size under various management scenarios, which forms the basis for the action C.9 »*Brown bear population size and management scenario modelling system*«.
- (d.) To give recommendations for improvements in similar future studies and in management actions, particularly those involving cross-border populations.

## 2. Material and methods

### 2.1. BASELINE DATA

#### 2.1.1. Data on brown bear mortality in Slovenia and Croatia

Population dynamics predictions were based on temporal data series of removed individuals of brown bears from Slovenia and Croatia. In Slovenia, it is mandatory according to national legislation to report all dead bears, regardless of cause, to the competent organism, the SFS, which has maintained this record since 1994. This record includes individual level information on estimated sex and age, body measurements, date, location, and cause of removal. Reported sex and hunter-estimated age are included in the data, and additionally assessed by SFS experts. Age was determined by analysing first premolar (P1) tooth sections in Matson's lab whenever possible (Craighead et al., 1970), body measurements are carried out by SFS officials and, when cause of death cannot be determined by SFS personnel, carcasses are inspected by the National Veterinary Institute.

In Croatia, each bear hunted in quota has to be processed by local hunting organization, and in the case of any other cause of shot, responsibility of reporting is on the Bear Intervention Team. Obligatory samples include the P1 tooth for aging and a piece of muscle for genetics. In any case, it is strongly advised to contact the Veterinary Faculty in Zagreb to supervise the process. The written record includes information on sex and age (estimated by the collector and by tooth measurement), body mass, date, location and cause of removal. In any case, the report and the samples (when applicable) have to be reported to the Ministry of Agriculture of Croatia.

Removals data from Slovenia covered the period 1994-2017, and for Croatia 1999-2016. In Slovenia, complete data (total removed individuals, sex and age structure for each year) were only reliable from 1998 onwards (Jerina & Krofel, 2012), thus records older than that were excluded; for the year 2017, total mortality was available, but not sex and age structure, thus an average of the previous period was considered.

For Croatia, complete data were available for the period 2005-2016. As for 2001-2004, summary information on sex structure and total removed individuals was known and average age structure for the period 2005-2012 was considered. For the period 1998-2000, and for 2017, no information was available for Croatia, however we made some assumptions in order to obtain a time series covering the same period as for Slovenia, acknowledging that they may not be as realistic as desired but allowing us to jointly evaluate the brown bear population within both countries. Thus, from 1998 to 2000, total removed individuals were considered to be the same as on average during 2001-2005 period and have average age structure of the period 2001-2012. For 2017, we assumed that the number of individuals removed from the population was following the trend from previous 5 years, and the age structure was taken as the average of the period 2012-2016. This separation between data before and after 2012 in

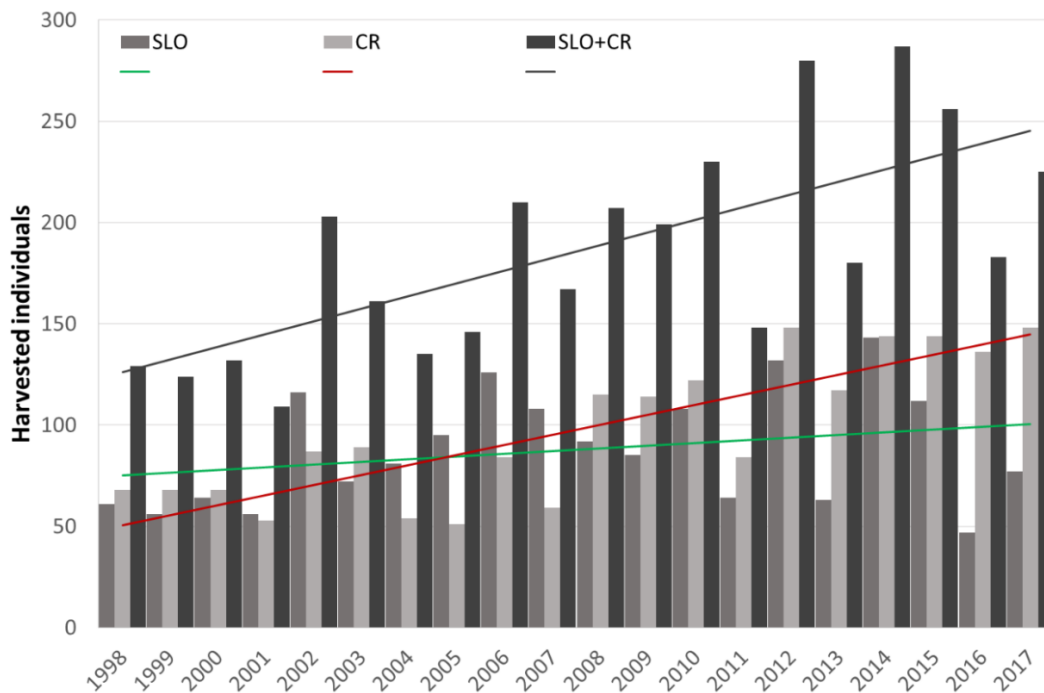
Croatia responds to a change in legislation that year which encouraged hunting of females.

For the purposes of the present study, our main concern was to have estimates of age and sex for each individual extracted from population. In Slovenia, by May 2017, around 19% of records lacked information on accurate estimate of age, and around 2% on sex assignment; in Croatia, as of November 2016, around 15% of records did not contain information on individuals' age, and about 3% the records miss sex assignment. Broadly, missing data were missing at random; although there was a slight trend towards smaller individuals presenting more missing data on age information in Slovenia and Croatia. In Croatia, age data tended to be more incomplete in older records; whereas there was not a clear pattern in Slovenia (Appendix 0).

To maximize the number of individuals considered for further analyses, we imputed missing data following a multivariate imputation by chained equations, implemented in package 'mice' within the R software (Buuren & Groothuis-Oudshoorn, 2011). This method generates several (as many as the user specifies, in our case 5) plausible values for a given variable, from which the mode was finally selected as the most likely imputed value. If the mode could not be computed (e.g. none imputation was repeatedly assigned), the average was calculated (in the case of continuous variables). For the imputation process, data from Slovenia and Croatia were analysed together.

Through the entire period, around 185 bears were annually removed from the population in both countries. The removal grew from around 135 individuals in 1998 to 225 in the final year. Total removal increased by 6.3 individuals on average annually (Figure 1). The dynamics were not parallel in both countries: in Slovenia total annual recorded mortality was 88 bears and increased slowly, by 1.3 individuals per year; in Croatia it averaged 98 individuals and rose by 4.9 individuals on average annually. Recorded mortality in Slovenia accounted for about 60% of total recorded mortality for both counties in 1998, and a third less, around 40%, in 2017.

The structure of causes of mortality is similar in both countries, but there are noteworthy differences in sex and age structure, in particular due to differences in hunting mortality. The share of females among recorded mortalities averaged 43% in Slovenia and 32% in Croatia, 36% considering both. The share of females among recorded mortalities gradually increased in Slovenia, from roughly 37% in 1998 to 46% in 2016; in Croatia is increased during 2005-2016 from roughly 28% to 33%. Even though Croatia changed management regulations in 2012 to increase the share of females among harvested bears, this hardly had any effect judging from available data. Among hunted bears, the share of females was 42% in Slovenia and 28% in Croatia, 36% considering both. Average age of hunted bears was 2.9 years in Slovenia and 4.5 years in Croatia, or a combined 3.6 years. Hunting (which includes derogations and intervention culls of conflict individuals) is targeted at both sexes and younger individuals in Slovenia; in Croatia it targets adult trophy males, the result of commercially-focused hunting.



**Figure 1.** Number of extracted brown bears per year for Slovenia, Croatia and in both countries together. Bars represent total numbers, lines show linear temporal trends.

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### 2.1.2. Point estimates of population size based on non-invasive genetics

One of the currently most established methods for determining population size is non-invasive genetic sampling based on the capture-mark-recapture principle. This method was used in autumn 2007 to estimate the size and sex structure of the entire bear population in Slovenia, and in autumn 2015 for the bear population in Slovenia and in Croatia. The estimate for 2007 was final (Skrbinšek et al., 2008), whereas estimates for 2015 were nearing completion as of

the writing of this report. For the purposes of the present study, we used the following values for size and sex structure of the population following the author's recommendations:

- Slovenia, 2007: size 424 (383-458); sex ratio M:F = 40.5:59.5 (Skrbinšek et al., 2008)
- Slovenia, 2015: size 599 (559-641); sex ratio M:F = 40.5:59.5 (Skrbinšek, *personal communication*)
- Slovenia and Croatia together, 2015: 1387 (1271-1547): sex ratio M:F = 40.5:59.5 (Skrbinšek, *personal communication*)

All figures of population size represent annual minima. Sampling (of bear faeces) was always conducted in autumn. The final estimate excluded all recorded mortality during the sampling period, i.e. until the end of the respective year, when bears start denning. Because we can assume mortality during the sampling period to be negligible (in autumn the cubs are larger; infanticide stops), these can therefore be considered unbiased estimates of minima for those years, pre-reproduction. To estimate size after reproduction (i.e. maximum size in year, early spring next year), natality need to be added to these estimates.

In Slovenia and Croatia brown bear has relatively high natality, the consequence of: (a) change in sex structure of the population in favour of females, caused by male-biased hunting, in particular in Croatia, (b) early primiparity and short inter-litter interval (2-year), which is the result of favourable habitat conditions (short winter, long vegetation period, southern latitudes), and perhaps, to a certain extent, elevated carrying capacity due to intensive artificial feeding in both countries.

We have yet to determine relative brown bear natality with robust direct methods in Slovenia or Croatia, but multiple datasets indicate it probably is high:

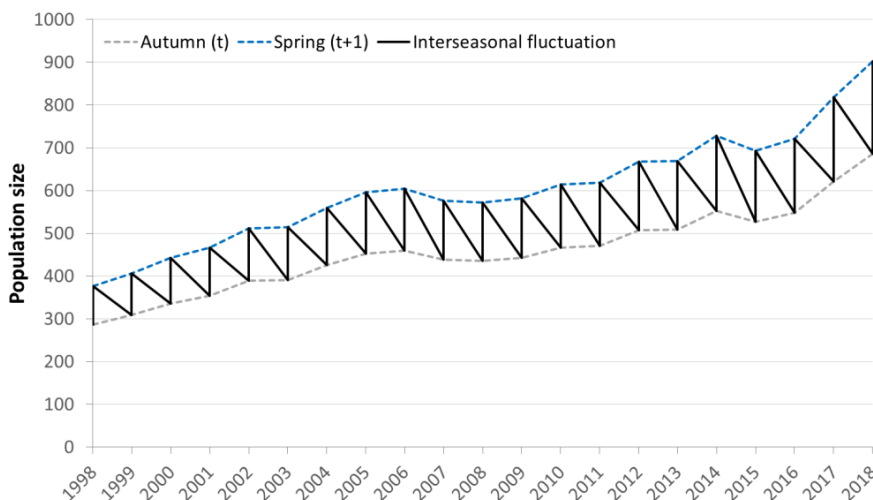
- In summer and autumn, the share of cubs (0+ year old) observed at feeding sites ranged from 23% to 27%, average 25% (Jerina & Krofel, 2012); in spring months this share is expected to be lower, given that females with cubs avoid sites with high likelihood of encountering other bears, in particular males, as a way to reduce infanticide.
- In autumn, the share of females with 0+ cubs at counting sites was estimated to be almost 15%. Assuming females have cubs every two years, the share of reproductive females would be 29% and, at average litter size of 1.9, the relative natality rate would be 28 % (SFS, 2017).
- In spring, the share of 1+ cubs at counting sites was estimated to be 21% (SFS, 2017); bearing in mind that a portion of cubs die during the first year, which decreases litter size, and that a certain proportion of females lose entire litters. On the other hand, females with 0+ cubs visited feeding sites less frequently in spring, which means the reported share is not a precise indicator of relative natality.
- Reconstructions based on age-at-harvest data showed a relative brown bear natality in Slovenia and Croatia of around 25% combined, including background mortality and a 24% based just on recorded mortality (this report, see section 4.1).

- Calibrated predictive models (this report, see section 3) accounting for sex and age structure and age-specific brown bear fecundity and mortality predicted 24% relative natality in Slovenia and Croatia.

Each of this data has shortcomings: females with cubs may visit feeding sites less often than other bears, in which case their share at feeding site may not necessarily be an unbiased representation of reality; population reconstructions from age-at-harvest data may produce biased results because of unrecorded mortality; population predictive models are underpinned by parameters from other population studies, even if calibration process excluded less likely values. On the other hand, these approaches are conceptually diverse and although they use completely different assumptions, their estimates are fairly comparable. We therefore believe they are very close to the real values.

For the purposes of the present study we always used relative natality estimate of 24% as the final value. Because this value represents the share of cubs in the population with cubs, the correction coefficient for the calculation of minimal annual size estimates (late autumn) into maxima post-littering (spring next year) was 1.32 (i.e. increase by 31.6%). Notably, this relative natality is not “fictitious”, it accounts for cubs who left their dens, used feeding sites, may be culled as part of conflict-prone families or died in traffic accidents and were included in mortality records; in short, they were managed.

It is important to mention that differences between pre-littering and post-littering size estimates are large and easily exceed differences in population size between years (Figure 2). We therefore propose that in subsequent communication with the public we should agree on a reporting figure (perhaps average annual values) to minimize misinterpretation and abuse. For research purposes, meanwhile, we should use the estimate that makes most sense to meet specific goals, e.g. for population dynamics, this would be the estimate which includes natality.



**Figure 2.** Differences between population size for late autumn and spring period. Late autumn estimates were usually reported until now, but here we report the population size in the subsequent spring. Grey dashed line



shows the reconstruction based on the reported genetic abundances estimated for late autumn (minimal yearly values); black dashed line represent the reconstruction for next spring (maximum yearly values), once natality of new current cohort has been added; solid line illustrates the inter-seasonal fluctuations of the population.

During the reconstruction of population dynamics, the models were calibrated with non-invasive genetic “point” estimates of population size in late autumn 2007 (recalculated to spring estimates in 2008) and 2015 (spring 2016; Table 1). Size confidence intervals of all population size estimates were unified in advance, so upper and lower boundaries always represented the same proportion of the mean estimate. This removed the effect of wideness of confidence intervals on the result of population dynamics modelling (the models use multiplicative relations). An additional assessment was made for population size in both countries together in 2008 under the assumption that the Slovenian-Croatian population is completely panmictic, i.e. that the size dynamics in period between 2008 and 2016 was the same in both countries. This is the assumption underlying the second set of predictive population dynamic models (see section 2.2.1)

**Table 1.** Population estimates for bears in Slovenia and Croatia according to the two genetic estimates (2007 and 2015 field campaigns; results after adding next spring natality are presented).

|                                      | Slovenia         |                  | Slovenia & Croatia  |                     |
|--------------------------------------|------------------|------------------|---------------------|---------------------|
|                                      | 2008             | 2016             | 2008*               | 2016                |
| Number of bears; mean (min-max)      | 558<br>(512-607) | 788<br>(723-858) | 1292<br>(1186-1405) | 1825<br>(1675-1986) |
| Sex structure; proportion of females | 0.595            |                  |                     |                     |

\*Assuming equal growth in both countries during 2008-2016

## 2.2. METHODS OF MODELLING OF POPULATION SIZE DYNAMICS

Two contrasting approaches were used to reconstruct population size dynamics: (a) reconstruction using age of bears removed from the population (age-at-harvest method), and (b) predictive population demography models (predictive modelling). Because the assumptions underlying both approaches are very different, we believe that together they cover most of the range of realistic possibilities. Comparing and merging both sets of results will allow us to evaluate reliability and improve the final results.

The principal objective of this study is to determine the brown bear population dynamics in Slovenia. However, bears in Slovenia functionally represent only a part of a larger population and a great proportion of individuals presents cross-border home ranges. Both reconstruction methods are partially based on recorded mortality data. Bear management in Slovenia and Croatia differs in terms of intensity, and sex and age structure of the removal individuals, which could skew the predicted population size and size dynamics in each country, if analysed separately. Therefore, two sets of analysis were conducted for each of the mentioned reconstruction methods: (a) one assuming a completely demographically isolated bear population in Slovenia, and (b) a second assuming it is completely panmictic, i.e. that management (harvest) in Slovenia has an equal impact on its status than management

(harvest) in Croatia. By comparing and merging both sets of results, we will be able to determine the effects of demographic openness of parts of the population and remove them from the results for the individual country.

### 2.2.1. Predictive modelling

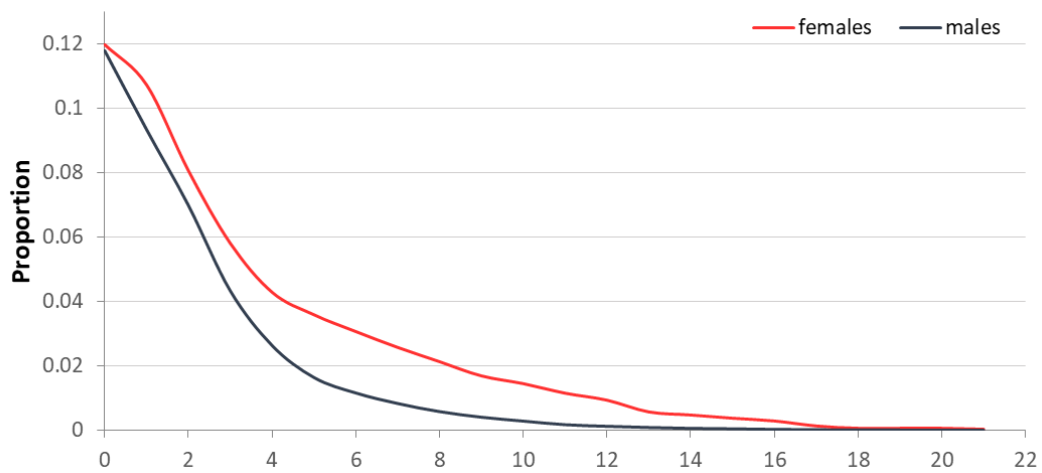
The population dynamics was reconstructed using the following parameters, based on estimates of previous studies:

- (a.) Initial age structure of the population in 1998 separately for both sexes (fixed; see below)
- (b.) Adults sex ratio of the initial population (ranging values; Table 2)
- (c.) Recorded bear mortality for each year for the period 1998-2017 (frequency, separated by sex and age, from 0 to 21 years),
- (d.) Age-specific female fertility, litter size and inter-litter intervals (ranging values; Table 2)
- (e.) Cubs-of-the-year sex ratio (ranging values; Table 2)
- (f.) Sex- and age-specific unrecorded mortality (mainly natural mortality, but may include poaching and other sources of unrecorded mortality; ranging values)
- (g.) Genetic estimates of size and sex structure of population in 2008 and 2016 (see Section 2.1.2 of this report).

Initial age structure was estimated from age-at-harvest data, separately for each sex, departing from combined data for both countries, assuming a cubs sex ratio of about 1:1 and correcting for age-specific natural mortality (further details in Jerina and Krofel, 2012). Data were additionally calibrated to match the sex ratio to non-invasive genetic estimates (F:M = 59.5:40.5; Figure 3).

**Table 2.** Description of parameters employed for predictive modelling of population dynamics of brown bears in Slovenia and Croatia. Allowed values (min-max) show the range of explored values of variables in models.

| Parameters                                 | Units  | Allowed values (min-max) | Data sources                 |
|--|--|--------------------------|------------------------------|
| Adults sex ratio                           | proportion of females                                | (0.555-0.645)            | Genetic survey (this report) |
| Cubs-of-the-year sex ratio                 | proportion of females                                | (0.45-0.55)              | Jerina and Krofel (2012)     |
| Primiparity                                | proportion of females of age 3 that are reproductive | (0-1)                    | Reljic et al (In prep.)      |
| Litter size                                | individuals  | (1.87-1.95)              | Bischof et al (2009)         |
| Interlitter interval                       | years  | (1.65-2)                 | Bischof et al (2009)         |
| Age- & sex-specific survival probabilities |  |                          |                              |
| Survival rate cubs                         | proportion   | (0.86-0.89)              | Reljic et al (In prep.)      |
| Survival rate female yearlings             | proportion   | (0.75-0.88)              | Bischof et al (2009)         |
| Survival rate female subadults             | proportion   | (0.9-0.96)               | Bischof et al (2009)         |
| Survival rate female adults                | proportion   | (0.91-0.95)              | Bischof et al (2009)         |
| Survival rate male yearlings               | proportion   | (0.82-0.96)              | Bischof et al (2009)         |
| Survival rate male subadults               | proportion   | (0.76-0.87)              | Bischof et al (2009)         |
| Survival rate male adults                  | proportion   | (0.85-0.92)              | Bischof et al (2009)         |

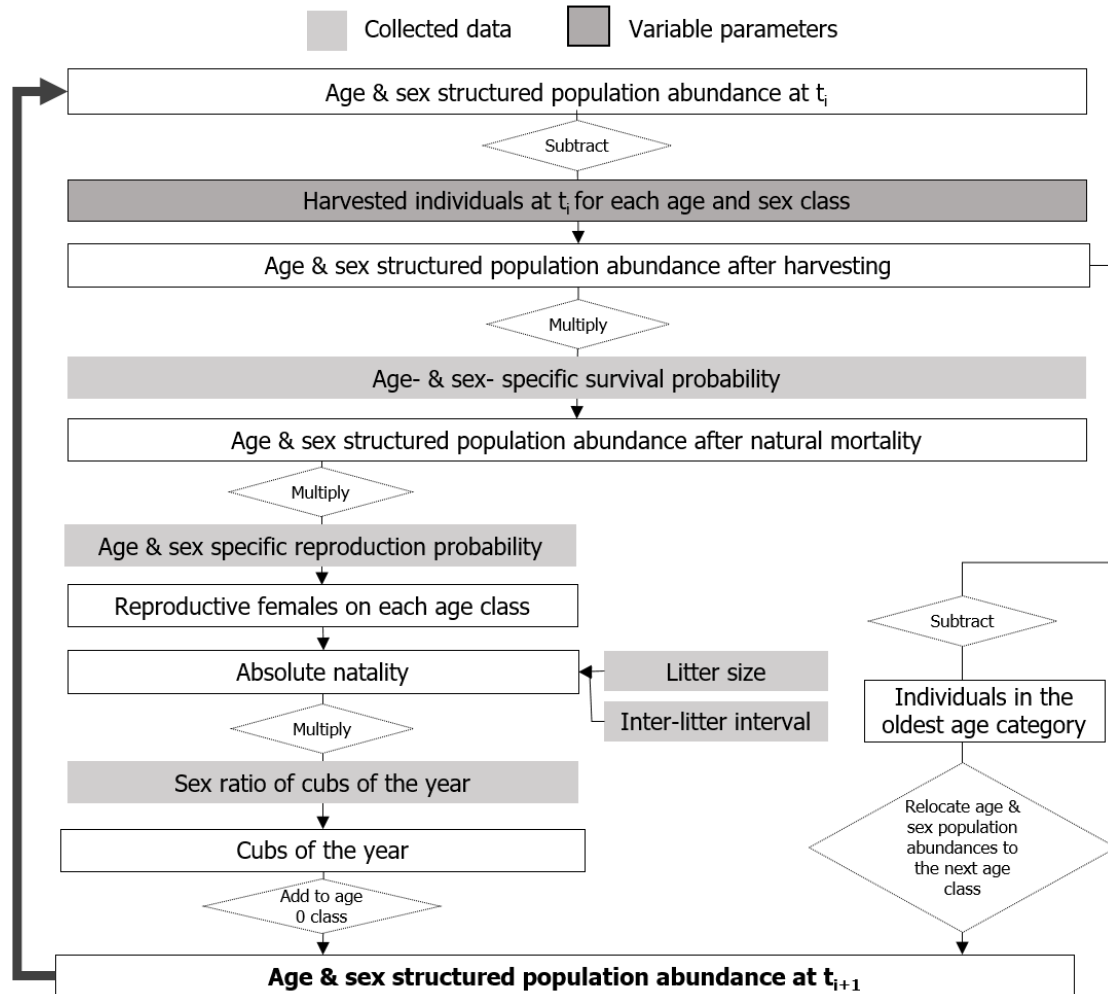


**Figure 3.** Initial age structure of population for brown bear males and females employed in the prediction modelling.

Population size was calculated for each year after 1998 separately by: (a) first subtracting recorded mortality for current year (sex- and age-specific); (b) then multiplying the matrix of surviving individuals with matrix of sex- and age-specific mortality to remove unrecorded mortality; (c) then calculating the number of reproductive females and number of born cubs; (d) and finally “ageing” all individuals by one year and adding the new born cubs, to transition our “population” into the next year (Figure 4).

Information on initial population size for 1998 was not available. Some of the used parameters were fixed (initial age structure separately for each sex; annual and sex- and age-specific recorded mortality), and others were varied along an interval of plausible values obtained from our own previous data or reviewed from literature (primiparity, litter size, unrecorded mortality; Table 2). The real value of these parameters is expected to lie within the provided interval. Using random sampling, we built 50,000 sets of experimental values of initial population size estimates for 1998 and values of all variable parameters. Each set of parameters was used to simulate the evolution of the population (total size, and sex- and age-structured) throughout the entire temporal interval, from 1998 to 2018.

From the whole ensemble of simulations, we finally selected those fulfilling the requirements of being comprised within the estimated intervals of population size and sex structure according to the genetic estimates of 2008 and 2016 (Table 1). From all simulations that accomplished these criteria, we calculated basic statistics of all parameters (size, sex- and age-specific mortality, etc.) to estimate most probable values for our population, narrowing the initial wider ranges considered from the existent literature.



**Figure 4.** Flowchart of the steps followed to carry out the predictive modelling of brown bear population within Slovenia and Croatia. It reads from top to bottom and each round (starting at the arrow point) results in a consecutive generation of age and sex structured population. The bold arrow indicates that the result of each round feeds the beginning of the next one. Rectangles show data results, rhombus show operations. Dark-grey boxes with black border represent directly collected data; light-grey boxes show parameters with uncertainty, varying among simulations (see Table 2).

The whole ensemble of simulations (N=50,000), with varying combinations of parameters on each, was run three times, one according to each of the following assumptions (3 scenarios):

Scenario 1: The assumption is that the Slovenian bear population is demographically isolated. Accordingly, only recorded bear mortality in Slovenia was used as input for all 50,000 simulations, out of which we selected those comprised within the genetic estimate of population size and sex structure for Slovenia (2008 and 2016).

Scenario 2: The assumption is that the parts of bear populations in Slovenia and Croatia are completely interconnected and that their size changed in parallel between 2008 and 2016. Accordingly, joint data on recorded mortality was used as input for all 50,000 simulations, out of which we selected those comprised within the genetic estimate of population size

and sex structure for Slovenia and Croatia. Population size in 2008 was estimated assuming that brown bear population size in Slovenia and Croatia increased proportionally (population shares in each country are the same for both years, see Table 1).

**Scenario 3:** The assumption is that relative unrecorded mortality and fertility parameters (primiparity, litter size) are the same in Slovenia and Croatia. The model used the combination of parameters selected in the modelling of the Slovenian demographically isolated population (Scenario 1) and joint data on recorded mortality from both countries. Simulations comprised within the genetic estimate of population size and sex structure for both countries together (2016) were selected.

For Scenarios 2 and 3, the temporal evolution of the population was predicted for both countries together. Then, population sizes were downscaled to Slovenia, considering that the share of this portion of the population according to genetic counts of 2015 –respect to the joint count– was around 43% (Table 1).

### 2.2.2 Age-at-harvest reconstruction

The age-at-harvest reconstruction method assumes that: (a) all mortality in the population is recorded and all individuals are sexed and aged without error; (b) the population is demographically closed, or, alternately, that the size and sex and age structure of immigrants and emigrants is equal; (c) all cohorts are closed, as a consequence, estimates are completely reliable only for the year in the past when all the then living individuals already died.

These assumptions were verified/approached in three ways. First, reconstruction was done once just using recorded mortality, and a second time assuming that a portion of mortality is not recorded. Calibrated sex- and age-specific mortality estimates from the predictive modelling were used for this purpose (Section 2.2.1). If, for example, five 10-year-old bears were registered as dead in a certain year and the probability of natural (unrecorded) mortality from age 9 to age 10 is 10%, the population likely had  $5/0.90 = 5.55$  bears, of which 0.55 died unrecorded. Secondly, to address the second assumption of the method, reconstructions were run once only with data on bear mortality in Slovenia and a second time using data from both countries (Croatia and Slovenia). Then, population size results were proportionally downscaled to Slovenia (43% from the joint population as for the genetic estimates; Table 1). Thirdly, beyond 2017 we added “expected” future mortality for the next 21 years (the age of the oldest bears in Slovenia). Future mortality scenarios attempt to cover the entire interval of likely outcomes and it was assumed that: (1) mortality will remain the same as the average for the last 5 years (AVER scenario); (2) mortality will increase linearly as per the trend for the past 5 years (TREND scenario); (3) mortality will be equal to the maximum in the past 5-year period (MAKS scenario); (4) mortality will be “sustainable”, i.e. maintaining a constant population size (SUST scenario; estimate in section 2.2.1); (5) mortality will increase linearly in parallel to the trend of increasing population size between 2008 and 2016 (GEN scenario; Appendix 1). In total, we created 2 (assumption a) x 2 (assumption b) x 5 (assumption c) = 20 scenarios – age-at-harvest predictions of population dynamics.

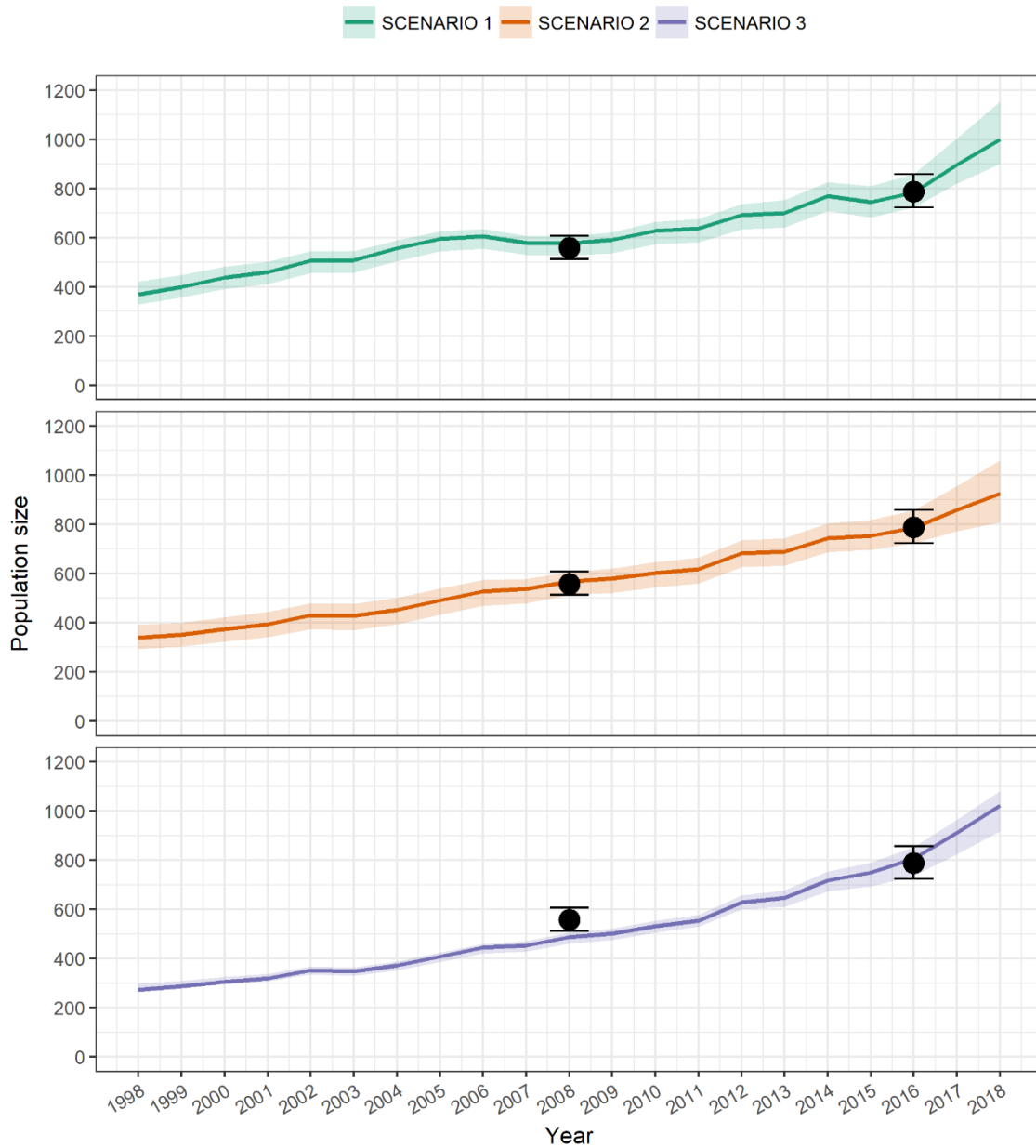
## 3. Results of reconstruction of brown bear population dynamics

### 3.1 RESULTS OF PREDICTIVE MODELLING

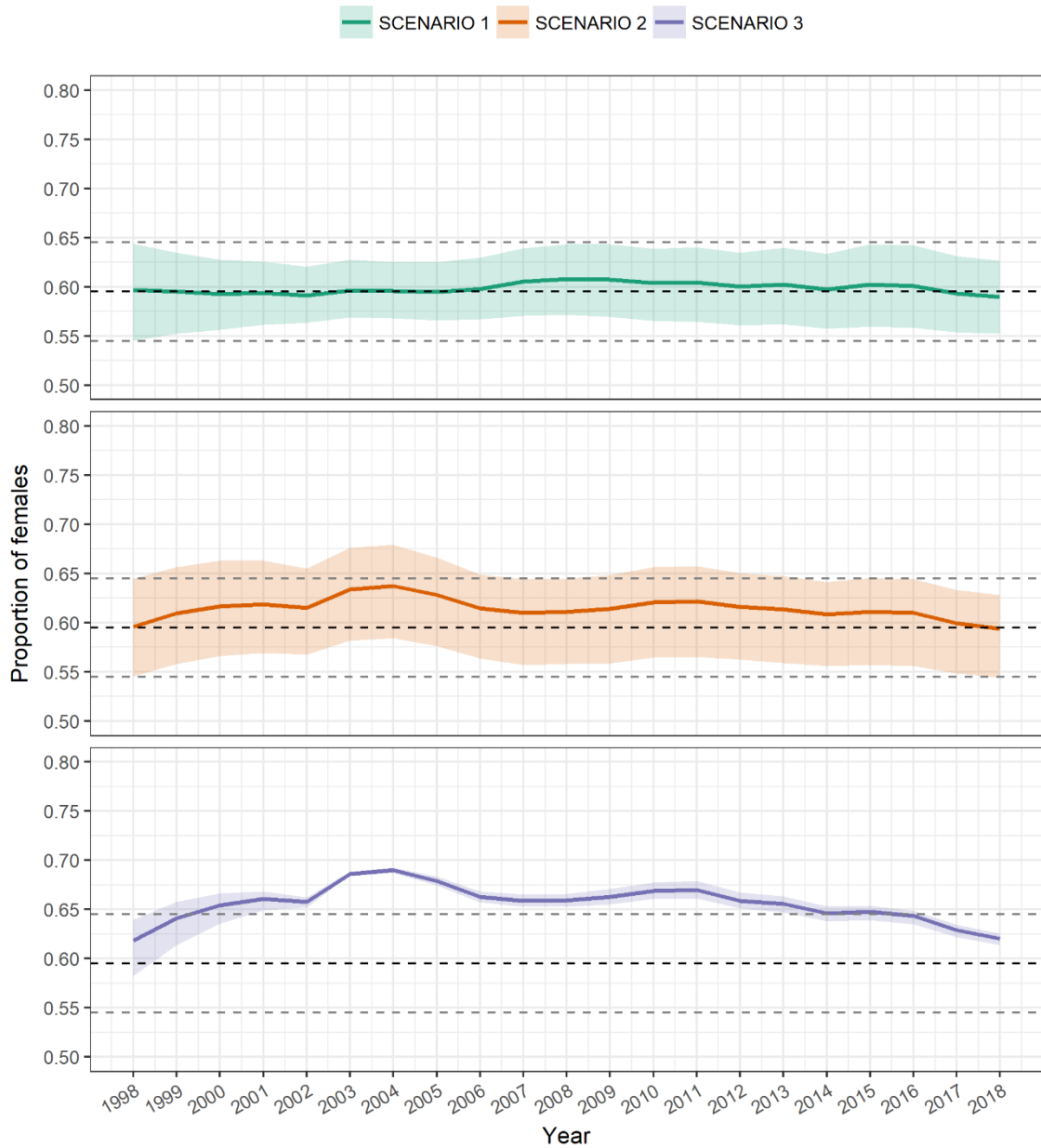
Three sets of brown bear dynamics models (Scenarios 1-3) were created with predictive modelling. Results of the first two sets were very similar, excepting that models assuming a panmictic population (Scenario 2) was less linear than models which assume demographic isolation (Scenario 1). This was expected, since inter-year differences in harvest intensity were smaller in both countries together than in each country separately. Predictions of the third set of models deviated considerably from the first two (Scenario 3), predicted past population sizes were unexpectedly low, and only few from the 50.000 tested models satisfied the interval estimates of size and sex structure in 2016; this scenario predicted exceptionally rapid future growth and rapid increase in the share of females (Figures 5 and 6). Given the large differences between this scenario and the rest, and considering that results are neither logical nor correspond to soft data, we discarded it for future analysis.

The first and second sets of models predicted that the brown bear population in Slovenia has increased during the period 1998-2018, with minor fluctuations. At the start, predicted population size was 370 (Scenario 1) and 340 (Scenario 2) individuals; at the end, 1000 and 925, respectively. The period in which the divergence between the two models was greatest was 1998-2007, when model 1 predicted a bigger size, a consequence of greater removal from the population at that time (compared to Croatia), which, according to the logic of the models, can only be supported by a larger population.

For each of the 3 scenarios we assessed which values of variable parameters across the entire interval of possibilities the models satisfy the conditions of size and sex structure in 2008 and 2016 (Table 2). The selected values may be considered as refined estimates from the initial interval. For each set of models, we therefore calculated the average of each parameter and compared it with the initial interval (average and relative rank; Table 3). Average age-specific mortalities were used as background mortalities in age-at-harvest models with added mortality.



**Figure 5.** Annual population size as calculated from prediction modelling, according to three different scenarios. Scenario 1 assumes that the Slovenian bear population is demographically isolated: scenario 2 assumes that the parts of bear populations in Slovenia and Croatia are demographically interconnected and that their size changed in lockstep between 2008 and 2016; scenario 3 assumes that relative unrecorded mortality and fertility parameters are equal in Slovenia and Croatia. Results for scenarios 2 and 3 are downscaled to only Slovenia.



**Figure 6.** Proportion of females in each year as calculated from prediction modelling, according to three different scenarios. Scenario 1 assumes that the Slovenian bear population is demographically isolated: scenario 2 assumes that the parts of bear populations in Slovenia and Croatia are demographically interconnected and that their size changed in lockstep between 2008 and 2016; scenario 3 assumes that relative unrecorded mortality and fertility parameters are equal in Slovenia and Croatia. Results for scenarios 2 and 3 are downscaled to only Slovenia.



**Table 3.** Selected values for the parameters varied during predictive modelling for Slovenia, according to the 3 scenarios considered. Allowed values are described in Table 2. Selected values show the average from the simulations that agreed with the genetic estimates of population abundance and sex ratio estimated for 2008 and 2016. The highest selected values comparing the 3 scenarios are marked with an asterisk (\*).

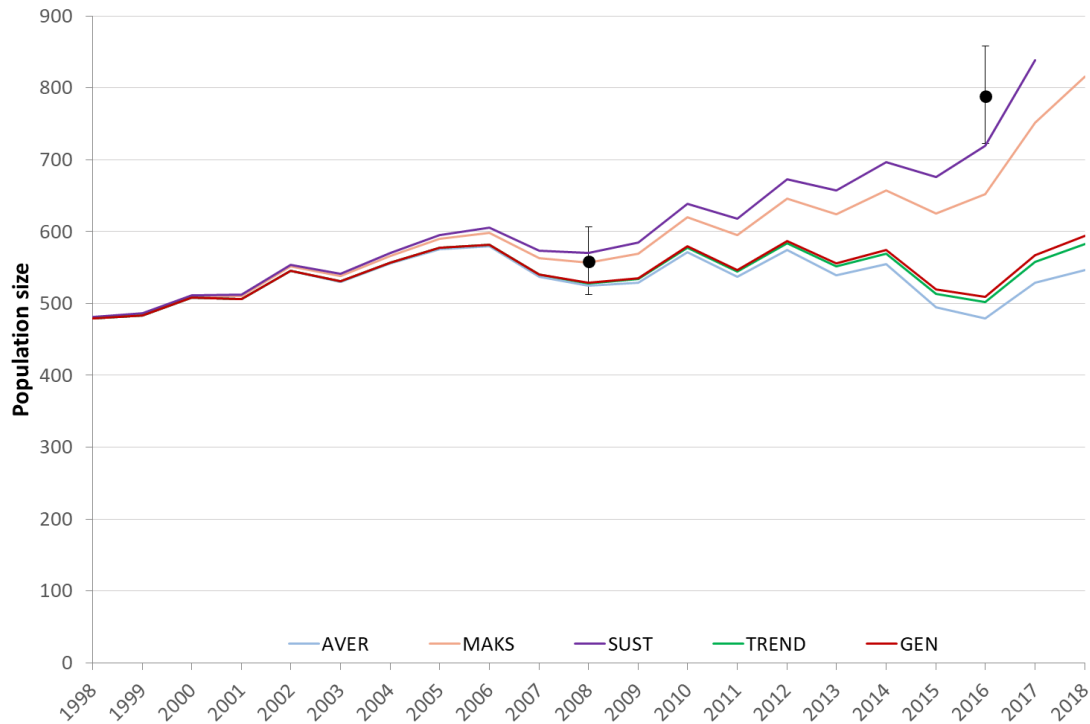
| Parameters                                 | Allowed values (min-max) | Selected values (mean & relative rank) |        |            |        |            |        |
|--|--------------------------|--|--------|------------|--------|------------|--------|
|  |                          | Scenario 1                             |        | Scenario 2 |        | Scenario 3 |        |
| Adults sex structure                       | (0.555-0.645)            | 0.597                                  | 0.461  | 0.596      | 0.455  | 0.618      | 0.705* |
| Cubs of the year sex structure             | (0.45-0.55)              | 0.531                                  | 0.809  | 0.482      | 0.323  | 0.514      | 0.639* |
| Primiparity                                | (0-1)                    | 0.599                                  | 0.599  | 0.534      | 0.534  | 0.907      | 0.907* |
| Litter size                                | (1.87-1.95)              | 1.912                                  | 0.520  | 1.910      | 0.506  | 1.917      | 0.585* |
| Interlitter interval                       | (1.65-2)                 | 1.781                                  | 0.373  | 1.805      | 0.443* | 1.722      | 0.207  |
| Age- & sex-specific survival probabilities |                          |  |        |            |        |            |        |
| Survival rate cubs                         | (0.86-0.89)              | 0.875                                  | 0.516* | 0.875      | 0.508  | 0.872      | 0.413  |
| Survival rate female yearlings             | (0.75-0.88)              | 0.831                                  | 0.626* | 0.818      | 0.525  | 0.797      | 0.359  |
| Survival rate female subadults             | (0.9-0.96)               | 0.935                                  | 0.577* | 0.931      | 0.509  | 0.926      | 0.434  |
| Survival rate female adults                | (0.91-0.95)              | 0.932                                  | 0.555  | 0.931      | 0.528  | 0.937      | 0.669* |
| Survival rate male yearlings               | (0.82-0.96)              | 0.885                                  | 0.461  | 0.892      | 0.513  | 0.915      | 0.679* |
| Survival rate male subadults               | (0.76-0.87)              | 0.811                                  | 0.468  | 0.817      | 0.521* | 0.794      | 0.312  |
| Survival rate male adults                  | (0.85-0.92)              | 0.886                                  | 0.517* | 0.885      | 0.497  | 0.873      | 0.328  |

### 3.2 RESULTS OF AGE-AT-HARVEST RECONSTRUCTION

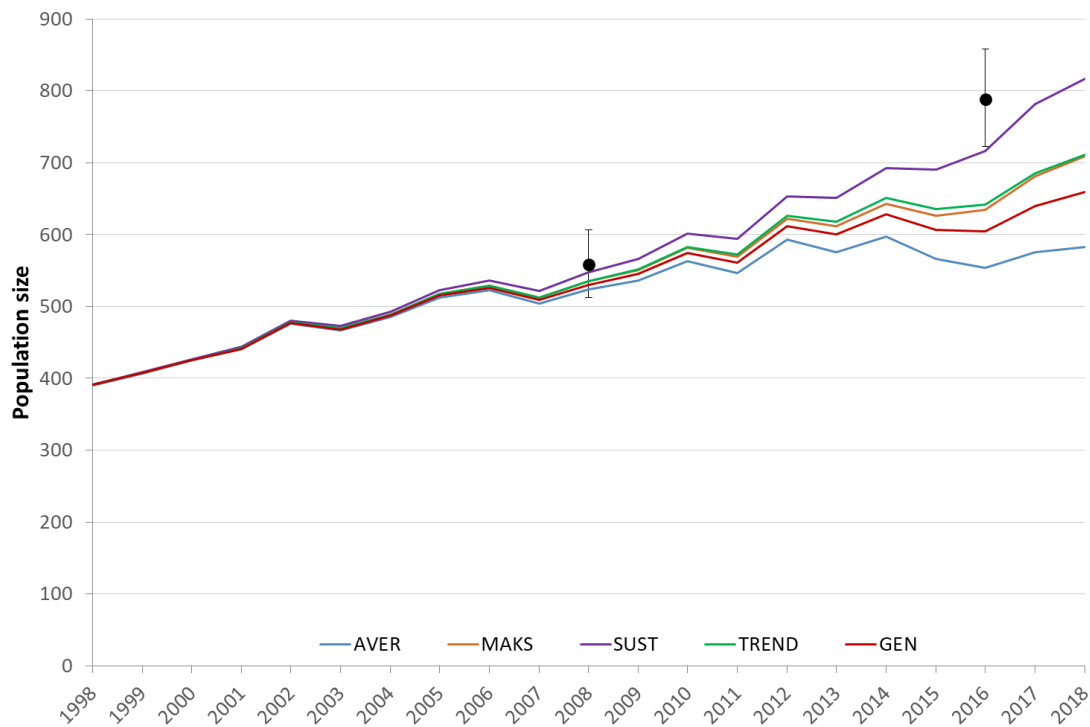
Age-at-harvest data were used to create 20 population dynamics reconstructions, with and without added non detected mortality (2 combinations), for Slovenia and both countries together (2 combinations), and five scenarios accounting for future potential removal from the population. The results without added unrecorded mortality are only show in the appendix because we know in advance that some mortality was unrecorded (Appendix 1). The models using data for both countries were proportionally reduced to the relative size of the brown bear population in Slovenia compared to both countries together (~43%).

Models that assumed demographic isolation of the Slovenian population uniformly predicted that the initial population was 480 individuals in 1998; for 2008 the sizes predicted by all models lie within the interval estimate of known size, whereupon the predictions diverged. In 2016 the empirically known size was achieved only by the model that assumed sustainable harvest (the highest mortality among all scenarios). Only this scenario was therefore retained for subsequent analysis. The mismatch of other models with the criterion of genetic-estimated population size can be explained because removals from the population were lower than natality, therefore mortality records do not produce sufficiently high population estimates (Figure 7).

Models that assumed a panmictic Slovenian-Croatian population predicted that the initial size was 400 individuals in 1998; aside from this divergence, the results were substantively identical to the models for an isolated population (Figure 8). Only the scenario which assumed a sustainable rate of removal from the population was therefore used for subsequent analysis.



**Figure 7.** Annual population abundance in Slovenia, as calculated from age-at-harvest modelling, according to five different scenarios, including age-specific natural mortality. AVER, mortality will remain the same as the average for the last 5 years; TREND, mortality will increase linearly as per the trend for the past 5 years; MAKS, mortality will be equal to the maximum in the past 5-year period; SUST, mortality will be “sustainable”, i.e. maintaining a constant population size (as estimated in section 2.2.1); GEN, mortality will increase linearly in lockstep with the trend of increasing population size between 2008 and 2016 as for the genetic count.



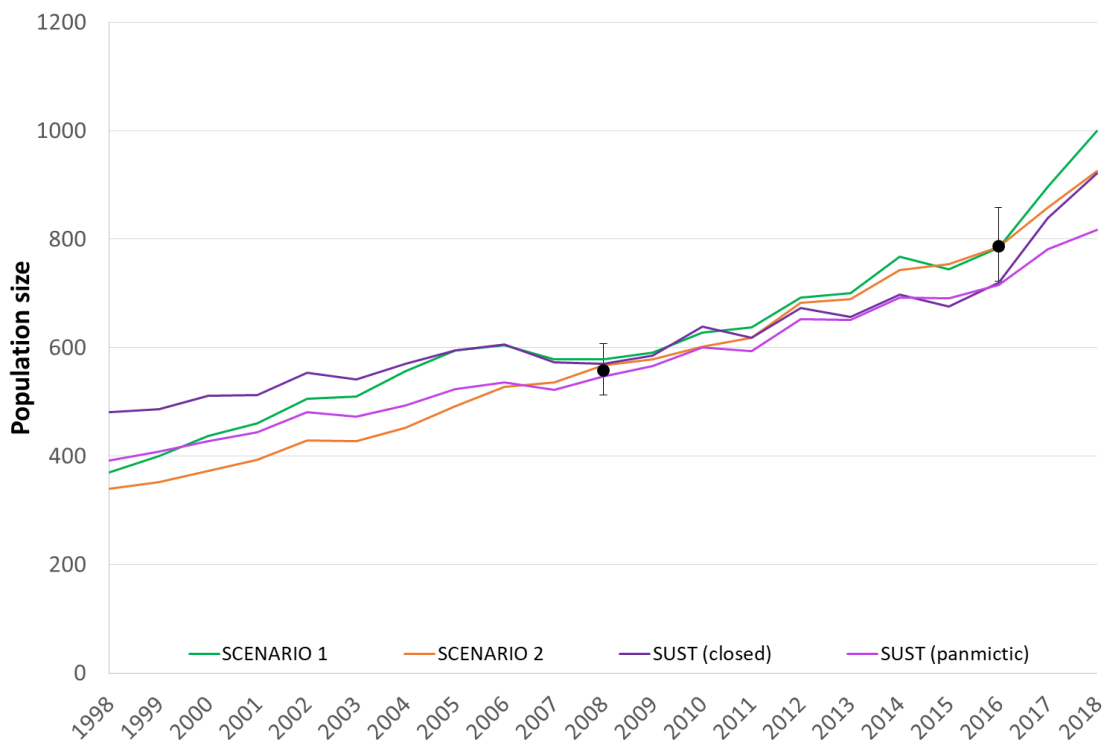
**Figure 8.** Annual population abundance in Slovenia, as calculated from age-at-harvest modelling, according to five different scenarios, including age-specific natural mortality and downscaled from the model fitted jointly for Slovenia and Croatia. AVER, mortality will remain the same as the average for the last 5 years; TREND, mortality will increase linearly as per the trend for the past 5 years; MAKS, mortality will be equal to the maximum in the past 5-year period; SUST, mortality will be “sustainable”, i.e. maintaining a constant population size (as estimated in section 2.2.1); GEN, mortality will increase linearly in lockstep with the trend of increasing population size between 2008 and 2016 as for the genetic count.

### 3.3. SYNTHESIS OF POPULATION SIZE MODELLING RESULTS

Each of the applied approaches (results) present advantages and shortcomings. Models assuming that Slovenia is demographically closed may overestimate actual population size in years in which bear mortality was disproportionately high compared to Croatia (initial period): bears with cross-border home ranges were more likely harvested in Slovenia than in Croatia, and vice-versa during last years. To mitigate this potential source of error at least partially, we estimated what share of the population functionally crosses the border, using an analysis of the distance of bear harvest locations from the border for Slovenia and Croatia, and data on diameter of average brown bear home range (Reljic et al., ; Jerina et al., 2012). We calculated the share of individuals which theoretically spend half the time in Slovenia and half in Croatia. In Croatia the share of such individuals is approx. 20% among females and 40% among males, about 1/3 total. Accordingly, the final estimate of the population size dynamics always factored in the weighted average of the model which assumes an isolated population (ponder 2/3) and the model that assumes panmictic population (ponder 1/3).

The models which use age-at-harvest data produce stable predictions for the past, but closer to the present their estimates increasingly diverge. This is understandable because the estimates depend on future harvest, which is unknown and subject to different scenarios. Accuracy of the predictive models is probably best in years in which they were calibrated (2008 and 2016), reliability drops with distance from this period. Estimates of initial size in particular are probably less robust (period after 1998), which is why both kinds of models (age-at-harvest and predictive) were merged into the final model to produce the most reliable estimates. In the period soon after 1998 the models using age-at-harvest data (which have fewer assumptions in general) produced higher estimates. The final model for the period from 1998 to first calibration (2008) was therefore calculated as the average of predictive and age-at-harvest models. We wanted to be conservative in the confidence interval and always used the widest intervals (union of estimates).

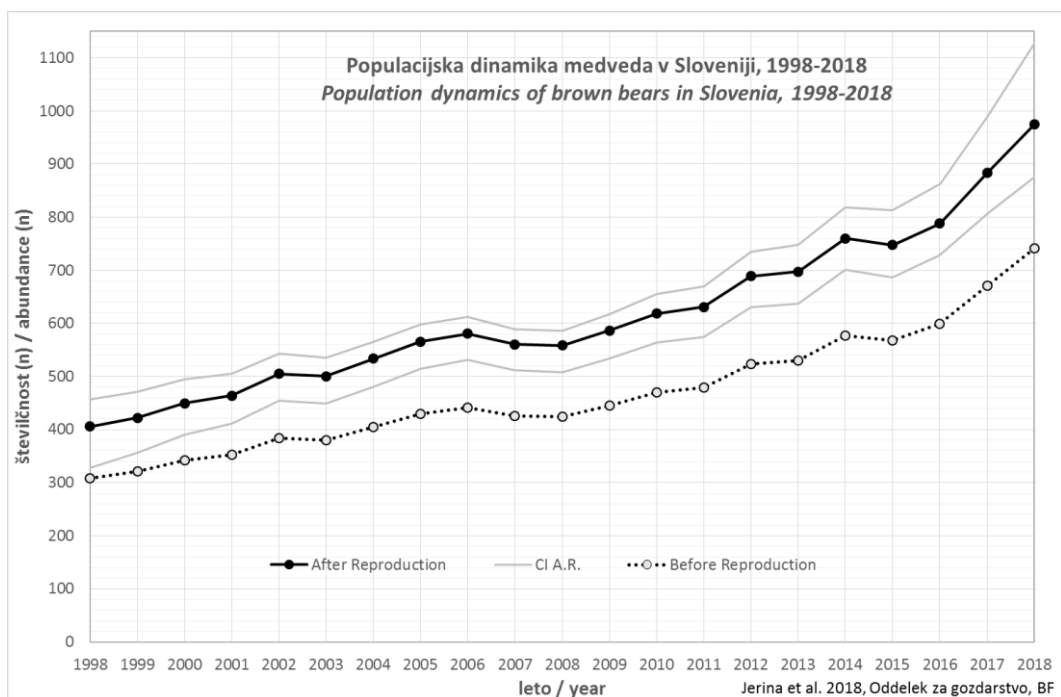
Both model synthesis procedures (spatially open/closed, and age-at-harvest/predictive models) are arbitrary to a certain extent. However, we believe that the final results are better than the baseline results because the merging mitigates the aberrations of various assumptions. Nevertheless, the differences between models are not wide (Figure 9).



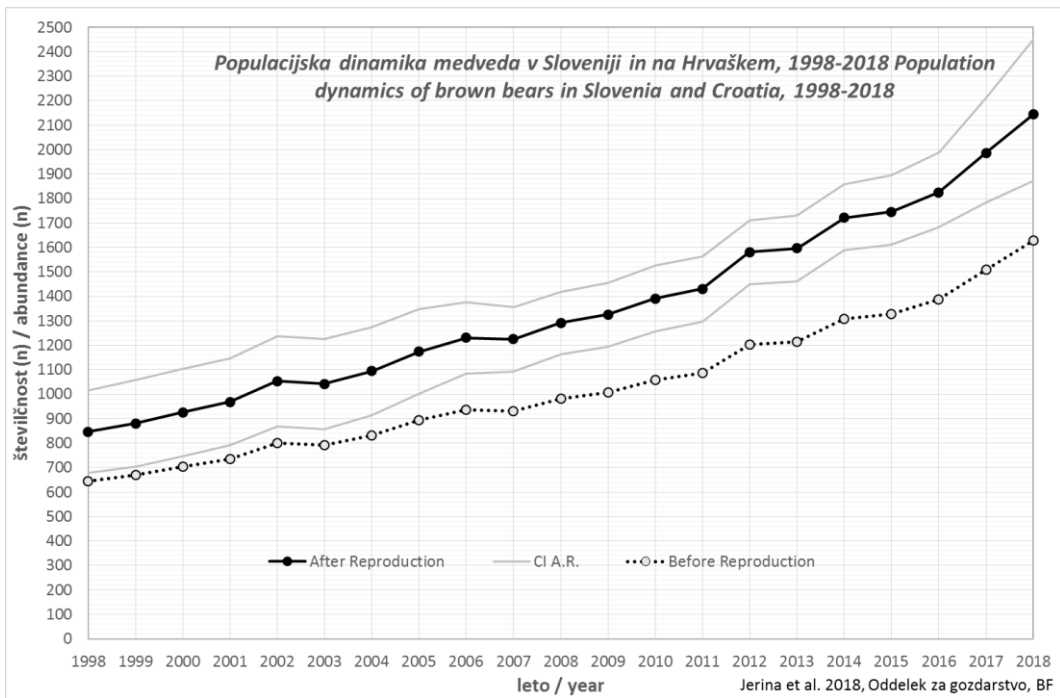
**Figure 9.** Summary of the best population reconstructions for Slovenia. Scenarios 1 and 3 correspond to the results of the projection modelling (Fig. 5), and SUST shows the sustainable scenario for either considering only Slovenia (closed; Fig. 7) or Slovenia and Croatia together, and downscaled to only Slovenia (panmictic, Fig. 8).

Using this procedure, the synthetic (final) model of population dynamics was first produced

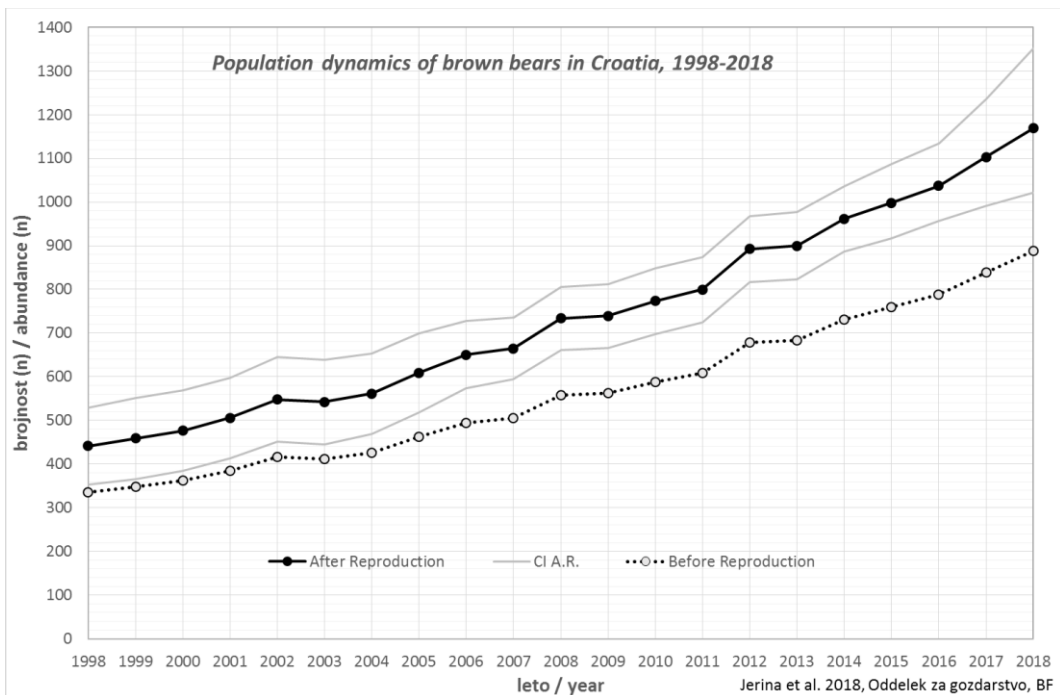
for Slovenia. In the combined model for both countries, corrections for spatial openness are not necessary, so we used the age-at-harvest model and the predictive model using actual values, not values corrected for Slovenia. The final model for Croatia was created by subtracting values for Slovenia from the data for both countries. All three final models provide the mean estimates of population size dynamics as well as conservative confidence intervals for these estimates. Estimates of dynamics of minimum annual size, i.e. size before reproduction, are shown in the same figures. In the past usually just pre-reproduction estimates were reported and we want to preserve comparability of our results with previously reported values.



**Figure 10.** Final (synthetic) model of brown bear population dynamics in Slovenia, 1998-2018.



**Figure 11.** Final (synthetic) model of brown bear population dynamics in Slovenia and Croatia, 1998-2018.



**Figure 12.** Final (synthetic) model of brown bear population dynamics in Croatia, 1998-2018.

## 4. Reconstruction of other population parameters relevant to management and research

As a “side” result, the models produce estimates of some other parameters relevant to management and research of brown bear in the study area during study period: age structure of the population, relative natality, relative unrecorded mortality, and relative sustainable hunting/anthropogenic mortality. Reliability of some of these parameters may be questionable because they are based on assumptions and models, probably even circular references in some cases, but since other estimates of these parameters are currently unavailable these may be considered the best available.

### 4.1 ESTIMATE OF RELATIVE NATALITY OF POPULATION

Relative natality was estimated from reconstructed sex and age structures of the population resulting from both principal approaches used (predictive and age-at-harvest modelling). In both cases, relative natality is expressed as share of cubs (individuals of age 0+) in total reconstructed population. Because the cohorts are not completed yet, age-at-harvest modelling used only reconstructions for first 5 years of available data; most of the individuals alive then have already died (the cohorts are almost completed).

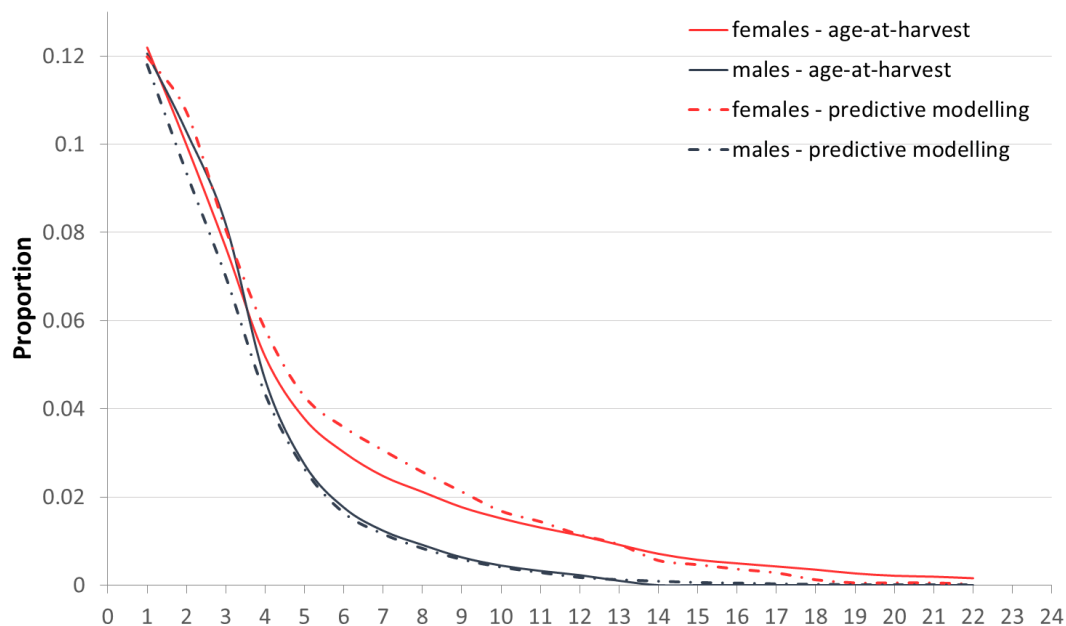
**Table 4.** Relative natality of brown bear estimated based on reconstructions of population age and sex structure using different modeling approaches, once just for Slovenian and once for combined Slovenian-Croatian data.

|  | Slovenia | Slovenia and Croatia |
|--|----------|----------------------|
| Predictive modeling  | 26.4%    | 23.8%                |
| Age-at harvest modeling with added non recorded mortality    | 26.9%    | 24.9%                |
| Age-at harvest modeling without added non recorded mortality | 25.8%    | 23.7%                |
| <b>Average</b>   | 26.4%    | <b>24.1%</b>         |

In prediction models, relative natality in the study period averaged 24% (for both countries together) and 26% for Slovenia only (table 4). Age-at-harvest reconstructions produce estimates of relative natality of 24-26% (with and without added mortality, for both countries and for Slovenia only). In both methods natality estimates are higher in scenarios taking into account just Slovenian data, and lower for combined data of both countries. Natality rates estimated only from data for Slovenia may be underestimated: lighter (= younger) bears must account for a large proportion of total harvested bears (share of bears under 100 kg must be 65% minimum), which means that hunting inherently increases the relative mortality of subadults. In Croatia, on the other hand, there are no such limitations and hunting is trophy-oriented (older males). We can therefore assume that estimates of relative natality based solely on Slovenian or Croatian data are biased. The estimates of the combined data from both countries, which are less likely biased, are the best: they lie in the 23.7-24.9% range. For the final estimate we therefore propose 24%, which we already used in previous parts of this study.

#### 4.2 ESTIMATE OF AGE STRUCTURE OF POPULATION

Due to previously described potential impacts of hunting regulations on natality estimates, age structure was analysed only for both countries combined using the same procedure as for natality. The procedure for calculating age structure from age-at-harvest data is described in the introductory sections of the present report (Figure 3). For comparison, data from both modelling approaches are presented together (Figure 13; data in table form are also presented in Appendix 2).



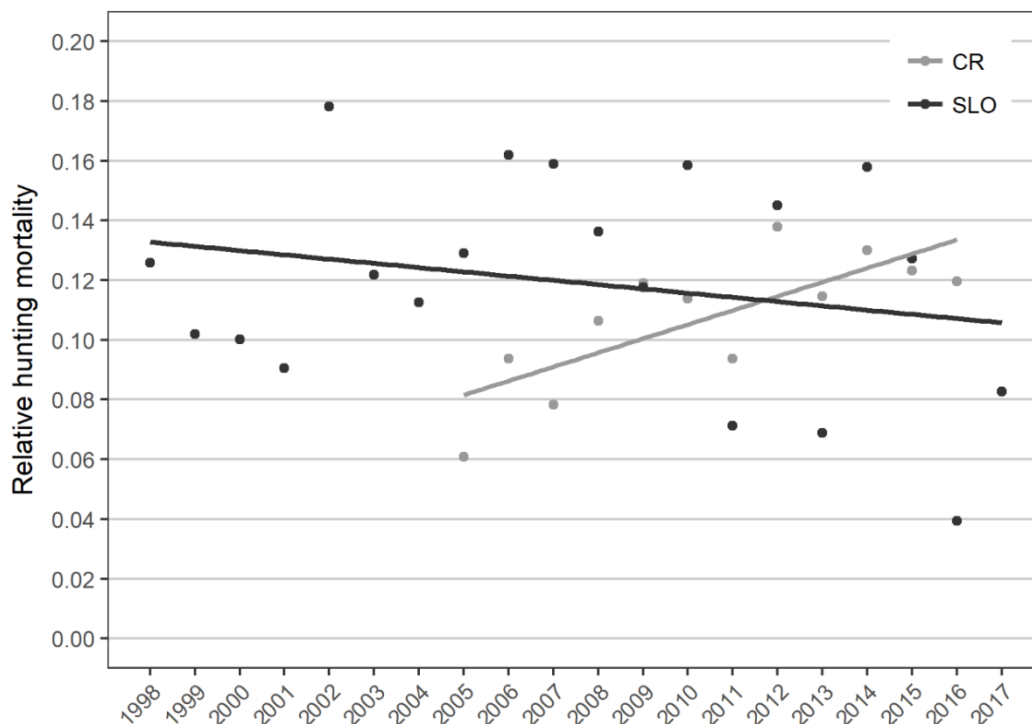
**Figure 13.** Estimated age structure of Dinaric brown bear population according to the age-at-harvest reconstructions and predictive modelling (Table A2.1).



### 4.3 POPULATION MORTALITY

In this section we estimated relative recorded, unrecorded and total mortality of the population, sustainable anthropogenic mortality, and sustainable hunting mortality. Relative recorded and anthropogenic mortality was estimated from size estimates in individual years (synthetic population dynamics models) and “unrecorded” mortality from predictive models, which were also used to calculate sustainable anthropogenic and hunting mortality.

Recorded mortality rates averaged 15% in Slovenia and 13% in Croatia, 14% combined; in Slovenia, it presented a decreasing trend and, in Croatia, it increased to the point where it already exceeded Slovenia’s in the last several years, almost exclusively due to more intensive hunting. In Croatia relative annual hunting mortality rose from 7% to 13% of the population in the period 2005-2016. In Slovenia, on the other hand, it declined from around 13% to 10% of annual population size (Figure 14). For the entire period with available data, hunting mortality averaged 11% in Croatia (2005-2016) and 12% in Slovenia (1998-2017).

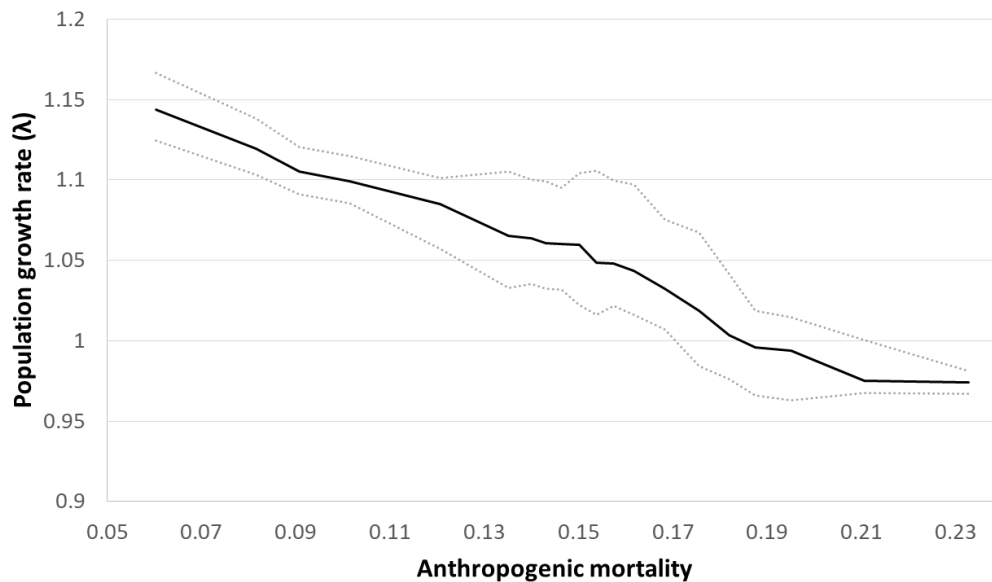


**Figure 14.** Comparison of temporal dynamic of relative hunting mortality between Croatia and Slovenia. Lines show linear regression trends.

In predictive models assuming that Slovenia was demographically isolated, unrecorded mortality was 28% of total mortality; in panmictic population models it was 23%. In practice, this means that for every three harvested bears recorded, one died unrecorded (due to natural or anthropogenic causes).

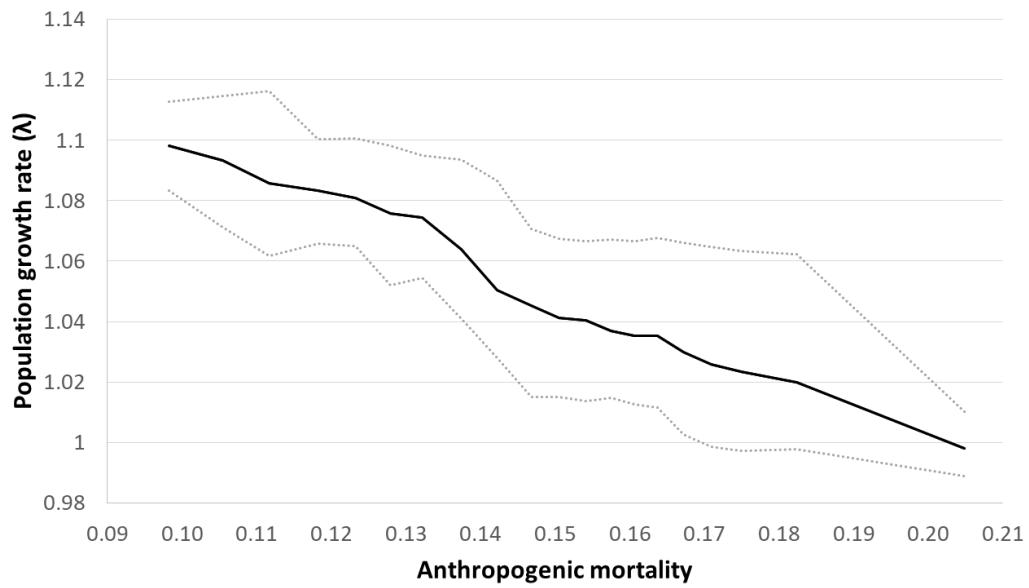
Relations between anthropogenic mortality and population growth rate were also estimated,

using the results of predictive models (Figure 15 and 16). Relations between relative anthropogenic mortality and growth rate were somewhat nonlinear, probably a consequence of increased harvesting of females in years when harvest was more intensive. The demographically isolated model predicted that anthropogenic mortality was sustainable (it stabilises the population) when it reached around 18% (CI 17-21%). In the panmictic model, sustainable anthropogenic mortality was 20% of total population (CI 17-21%). Total population's greater tolerance to harvest may be explained by the fact that in Croatia hunting focuses on males, whose mortality has a lower impact on population dynamics. Notably, these models assumed that male numbers did not represent a limitation to reproduction even if the populations were extremely female-biased, which is not realistic. These values therefore need to be interpreted cautiously.



**Figure 15.** Effects of anthropogenic mortality (expressed as proportion of population size; i.e. relative anthropogenic mortality) on population growth ( $\lambda$ ) of brown bear in Slovenia. Solid line shows the average; dashed lines represent 95% C.I.

Various types of hunting (regular, intervention) represent the bulk of total recorded mortality. In the last five years, direct hunting mortality as a share of total recorded mortality was 78% in Slovenia, and 83% in both countries combined. If this share were constant in the future, and independent of hunting intensity, sustainable hunting mortality (which exactly stabilises the population) in Slovenia would be 14% of the spring population size estimates (13.3-16.4%). For both countries together, the share would be slightly higher, averaging 16.6% (14.1-17.4%).



**Figure 16.** Effects of anthropogenic mortality (expressed as proportion of population size; i.e. relative anthropogenic mortality) on population growth ( $\lambda$ ) estimated for Slovenia and Croatia. Solid line shows the average; dashed lines represent 95% C.I.

## 5. Assessment of reliability of population dynamics models and discussion

The results of our modelling are inherently dependent on the quality of baseline data and suitability of used assumption and models. To verify the latter and remove potential weaknesses, we intentionally selected conceptually contrasting approaches basing on different assumptions. The results still match fairly well, which is a good sign. Nevertheless, our analyses were unable to remove potential weaknesses of baseline data, in particular quality of mortality records. If the records are not good, especially in the event of poaching or negligent or insufficient recording of legal harvest, the forecast estimates of size and dynamics are accordingly wrong, most likely underestimated. We believe such errors may have affected our estimates at the beginning of the study period and less so at the end, when we calibrated the results with genetic size estimates. The main assumption is that the genetic size estimates are completely reliable.

There are multiple evidences suggesting that female mortality in the available data is lower than real-world mortality. Reconstructions based on age-at-harvest data predict that sex ratio is strongly male-biased throughout the study period. This bias is partially present in Slovenia data (46% of females) and much more strongly in Croatia data (28%). When only data for Croatia were used, none of the predictive modelling scenarios satisfied the sex structure criterion. This could mean that actual parameters of sex-specific natural mortality in Croatia fall outside the applied interval estimates, but that is highly unlikely since broad intervals were used. The alternative –and more likely– explanation is that females in particular, but to some extent all younger individuals, are often disproportionately removed from the population without being recorded. One plausible explanation would be that non-reported hunting data of these categories is associated to poaching.

Even though it seems that our data underestimate actual anthropogenic mortality, we believe that, comparatively, this should not have significantly impacted the results in the case of Slovenia. However, it might have an impact on estimates of population size and sex ratio in the case of Croatia, both of which could be underestimated, especially in the initial period covered by the analyses, considering that the estimates towards the end of the study period are more accurately calibrated by genetic estimates of size.

One of the aims of this study was to prepare a conceptual framework and baseline data for predictions of future dynamics of brown bear population size in Slovenia and Croatia assuming different regimes of future management (different harvest scenarios; action C.9). Considering the possible mentioned weakness of baseline data used in the analysis (poorer recorded female mortality, possible poaching of females and subadult bears), the question is how these shortcomings could impact the quality of forecast of future population dynamics. However, it has to be pointed out that the presented models do not assume that mortality of all age categories is recorded to the same extend, the assumption is that the recording rate is

unchanged during the period for which models were calibrated (2008-2016) to the period when the models will be used (after 2018). If patterns of unrecorded mortality do not vary significantly in the future, our models should be accurate enough.

All presented models unequivocally show that the brown bear population in Slovenia and Croatia has significantly increased over the considered period. Average harmonic annual rate of growth is 4.5% for Slovenia (3.9-5.2%) and 5.0% for Croatia (4.3-5.7%). Our analyses also show that this population may withstand quite high anthropogenic mortality (around 17% of spring population size). To some extent, this is a consequence of high natality and low natural mortality, and partially due to selective hunting of males, which especially characterize Croatian section of the population. Bears are more sensitive to hunting in the category of reproductive females (Derocher et al., 1997; McLellan et al., 1999), which means that in general the effects of harvesting on population size are smaller if harvest is male-biased. But aside from impacting size, the skewed sex ratio of harvest may have various side effects. Such effects are stronger in the event of increased mortality of mature males, which is particularly prominent in Croatia, where large males with high trophy value represent the big portion of hunted bears. Intensive hunting of mature males may have unwanted side effects. In Scandinavia, for example, it has been recorded that in areas with strong intervention in the category of mature males, cub survival is reduced due to infanticide: after the dominant male is killed, its place is taken by another male unrelated to the cubs born in the area, which is why it tries, often successfully, to kill them.

The effect of selective hunting of dominant males in fast-growing populations (such as the Slovenian-Croatian population) is still comparatively unproblematic because the hunting-driven difference in sex structure is offset by reproduction (new animals), where the sex ratio is balanced. But it is completely different if hunting is targeted towards stopping population growth or even towards reducing population size. In that case, sex-biased hunting would strongly alter the sex ratio of the population, cumulatively, in favour of females.

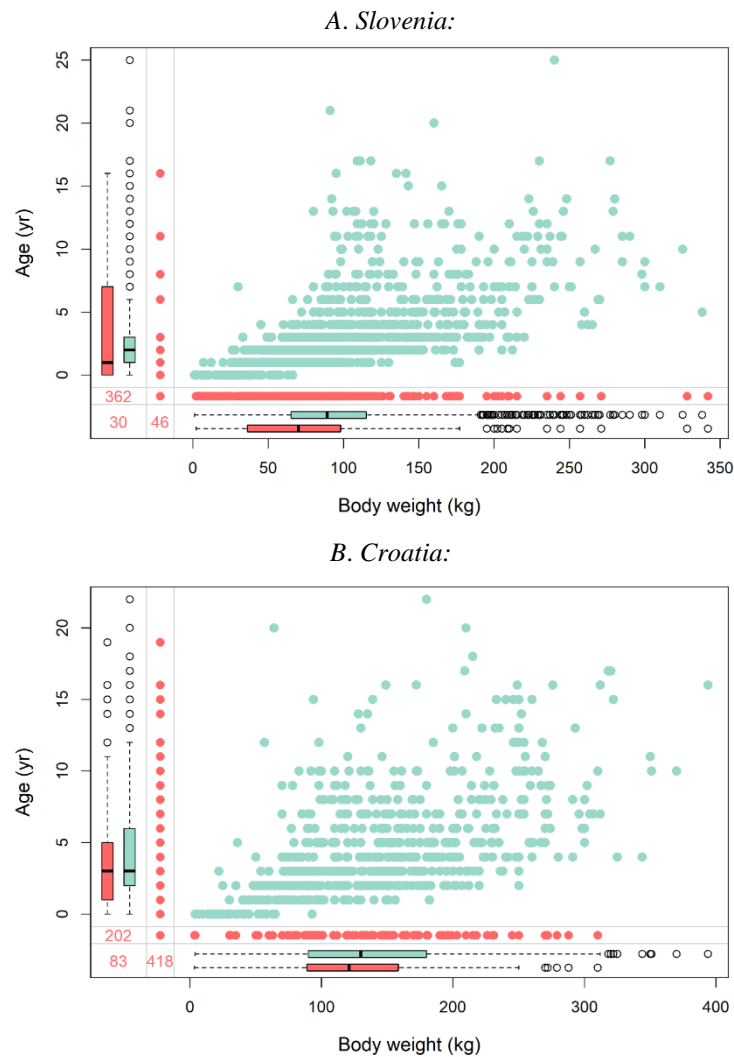
How to prevent these negative side effects of hunting may become one of the principal management challenges in the future. In both countries pressure by multiple stakeholders to restrict population growth is significant, but to stabilise population size, hunting mortality (cull rate) would have to be substantially increased. The share of females in removal from the population can be partially regulated by the body weight regulations applied in Slovenia, which attempts to imitate natural mortality patterns. The share of females also depends on the hunting season and is larger in autumn than in spring. Females stay with their cubs the entire first year of cub's life and until mating the following year (i.e. transition from spring to summer), but in autumn they are typically without cubs; which means that, in practice, autumns is the only period when adult females are not protected. During spring hunting season, there is an increased likelihood of hunting females with cubs by mistake, because they are not always accompanied by them, so hunters cannot recognize and avoid shooting them. While hunting bears is accepted as a necessary practice, delays in issuance of harvesting decrees, which is common in in Slovenia, do not have positive effects.

## 6. References

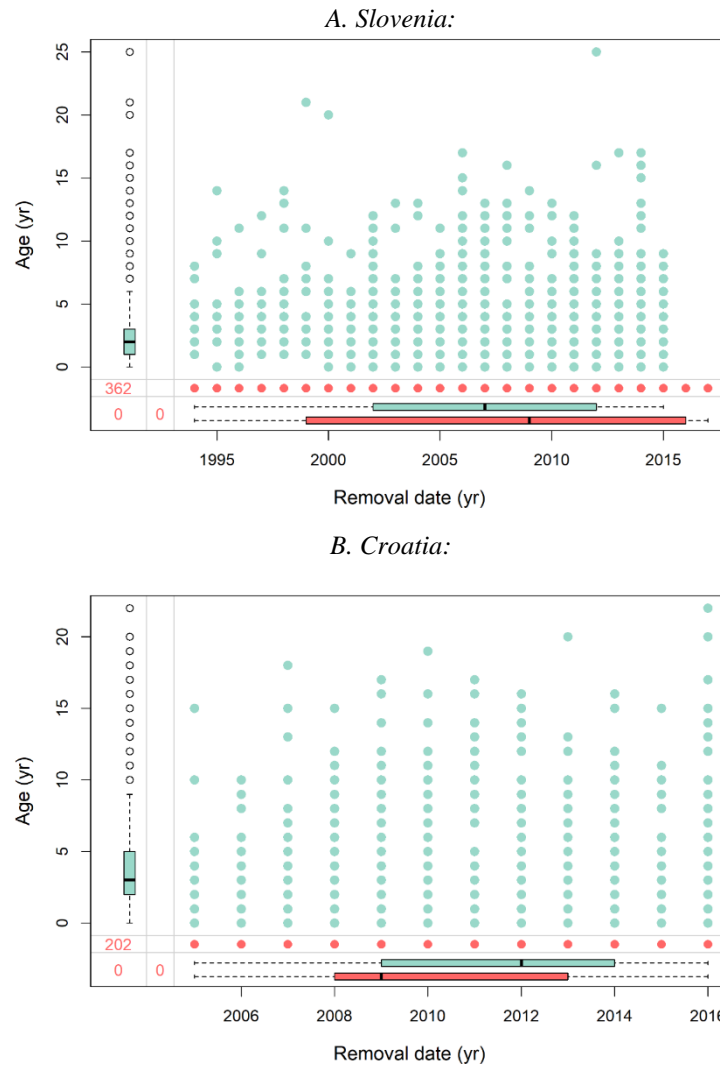
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## 7. Appendices

### Appendix 0. Complementary information regarding imputations of incomplete age data on brown bear records



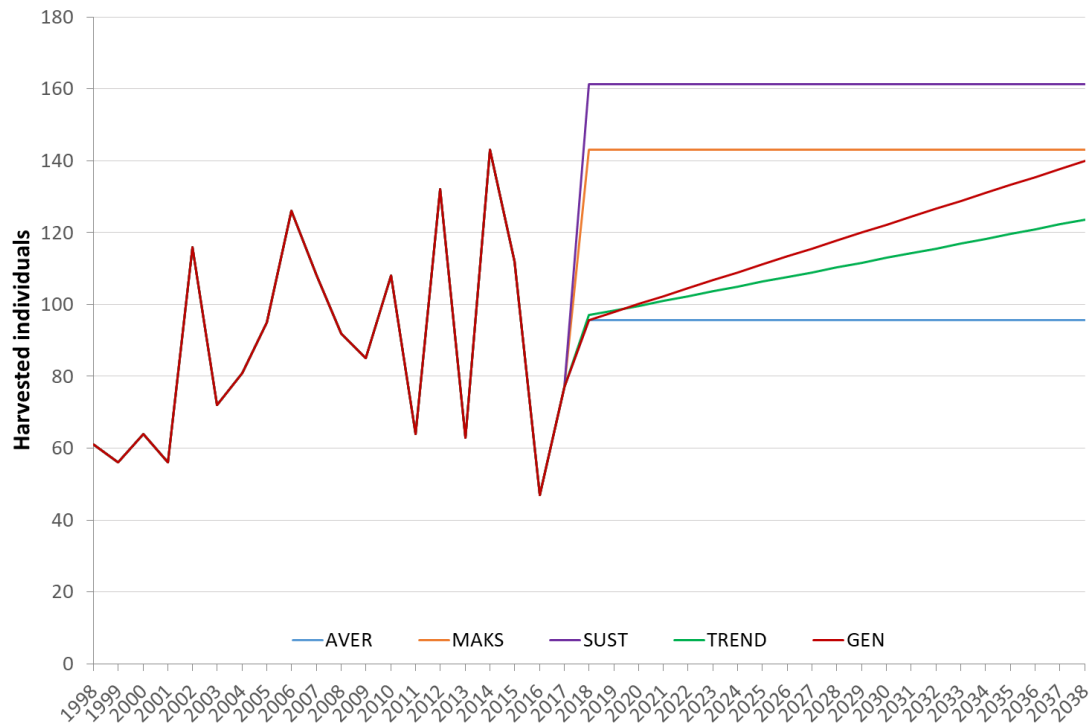
**Figure A0.1.** Margin plot of body weight versus individuals' age data (estimated by teeth section analysis) in databases from Slovenia (A) and Croatia (B). Green points represent individuals for which both body weight and age are available. Red points on left and bottom margins show records for which one of the variables are available, but not for the other. For Slovenia (A), there are 362 records missing information on individuals' age, 46 missing body weight and 30 missing both; for Croatia (B) 202 records do not include individual age, 418 miss body weight, and 83 miss both. Boxplots summarize the marginal distribution of missing (red) vs observed (green) data.



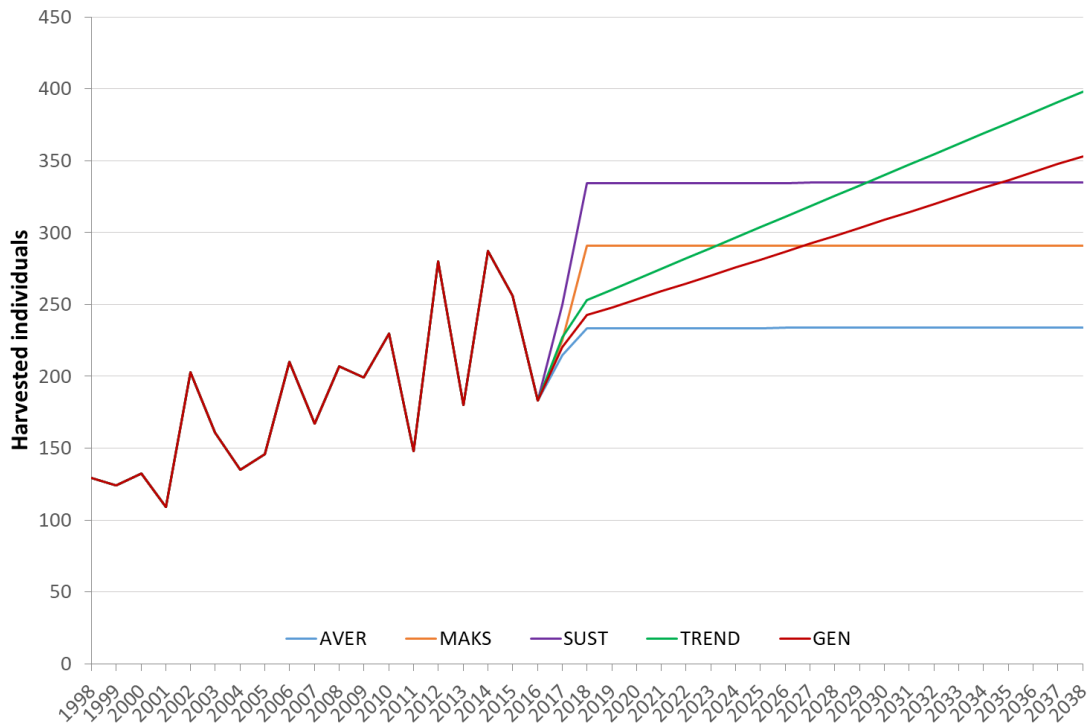
**Figure A0.2.** Margin plot of removal date (yr) versus individuals' age data (estimated by teeth section analysis) in databases from Slovenia (A) and Croatia (B). Green points represent individuals for which both body weight and age are available. Red points on left and bottom margins shows records for which one of the variables are available, but not for the other. For Slovenia (A), there are 362 records missing information on individuals' age; for Croatia (B) 202. Boxplots summarize the marginal distribution of missing (red) vs observed (green) data.



## Appendix 1. Complementary information of age-at-harvest reconstruction of the population

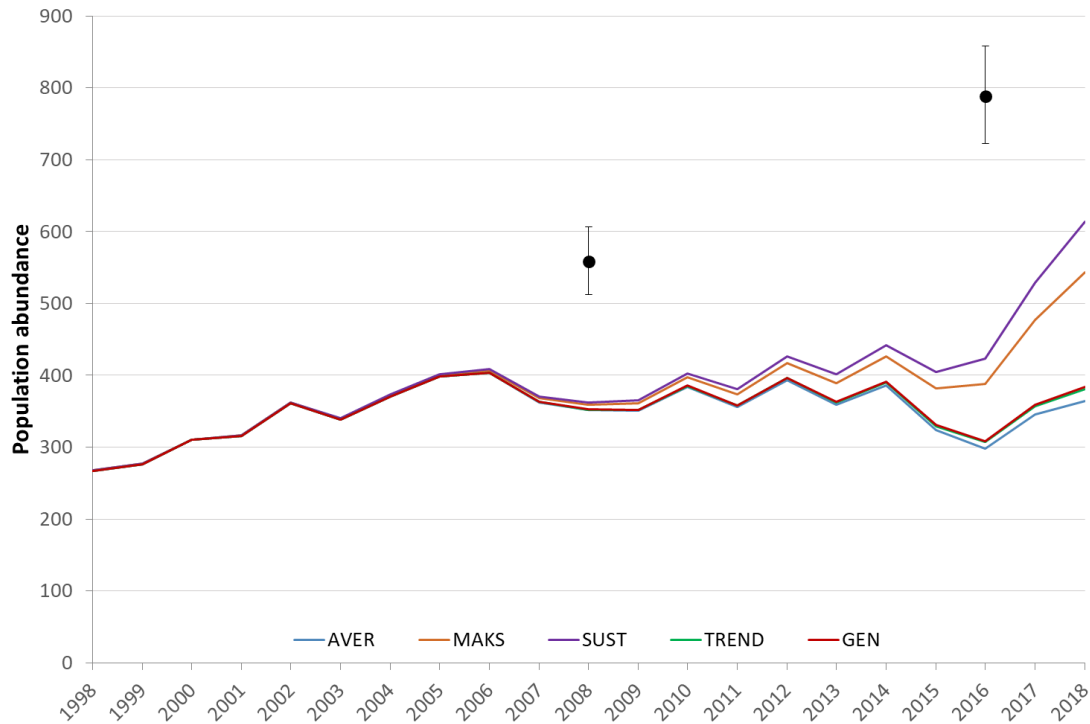


**Figure A1.1.** Different harvesting scenarios considered for the age-at-harvest reconstruction of the population of brown bear in Slovenia. For the period 1998-2017, record of removals were used, so they are the same for all scenarios. *AVER*, mortality will remain the same as the average for the last 5 years; *TREND*, mortality will increase linearly as per the trend for the past 5 years; *MAKS*, mortality will be equal to the maximum in the past 5-year period; *SUST*, mortality will be “sustainable”, i.e. maintaining a constant population size (as estimated in section 2.2.1); *GEN*, mortality will increase linearly in lockstep with the trend of increasing population size between 2008 and 2016 as for the genetic count.

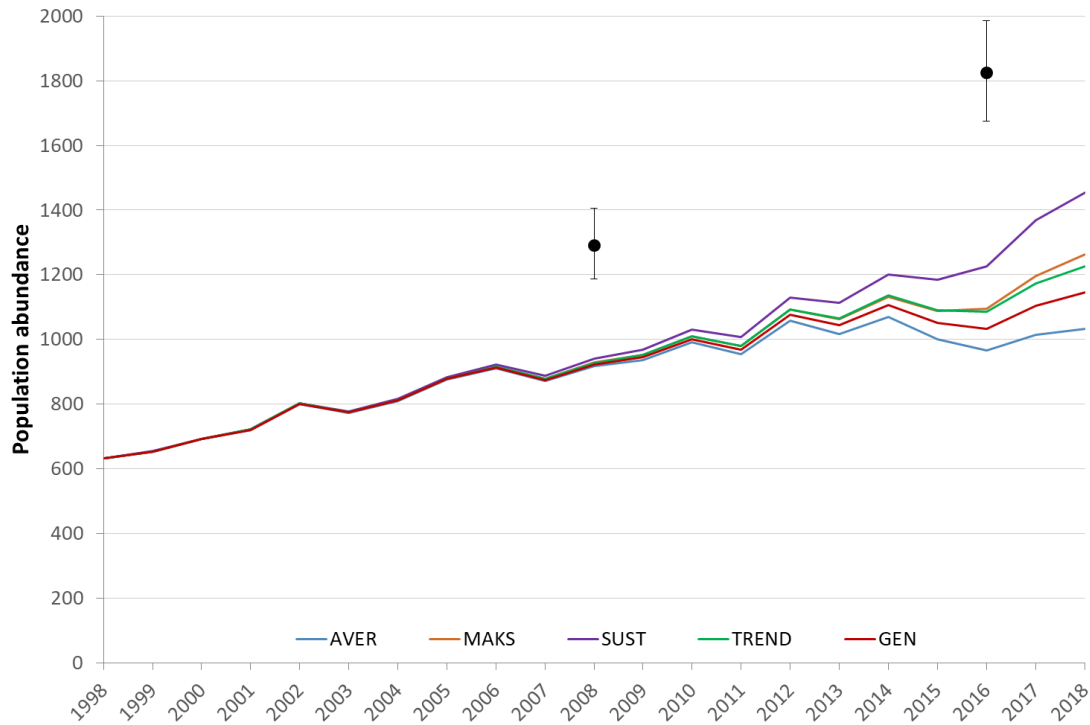


**Figure A1.2.** Different harvesting scenarios considered for the age-at-harvest reconstruction of the population of brown bear in Slovenia and Croatia. For the period 1998-2017, record of removals were used, so they are the same for all scenarios. *AVER*, mortality will remain the same as the average for the last 5 years; *TREND*, mortality will increase linearly as per the trend for the past 5 years; *MAKS*, mortality will be equal to the maximum in the past 5-year period; *SUST*, mortality will be “sustainable”, i.e. maintaining a constant population size (as estimated in section 2.2.1); *GEN*, mortality will increase linearly in lockstep with the trend of increasing population size between 2008 and 2016 as for the genetic count.

## Appendix 2. Results of age at harvest population reconstructions for scenarios without added non-recorded mortality



**Figure A2.1.** Annual population abundance in Slovenia, as calculated from age-at-harvest modelling, according to five different scenarios of future mortality, excluding age-specific natural mortality. *AVER*, mortality will remain the same as the average for the last 5 years; *TREND*, mortality will increase linearly as per the trend for the past 5 years; *MAKS*, mortality will be equal to the maximum in the past 5-year period; *SUST*, mortality will be “sustainable”, i.e. maintaining a constant population size (as estimated in section 2.2.1); *GEN*, mortality will increase linearly in lockstep with the trend of increasing population size between 2008 and 2016 as for the genetic count.



**Figure A2.2.** Annual population abundance in Slovenia and Croatia, as calculated from age-at-harvest modelling, according to five different scenarios, excluding age-specific natural mortality. *AVER*, mortality will remain the same as the average for the last 5 years; *TREND*, mortality will increase linearly as per the trend for the past 5 years; *MAKS*, mortality will be equal to the maximum in the past 5-year period; *SUST*, mortality will be “sustainable”, i.e. maintaining a constant population size (as estimated in section 2.2.1); *GEN*, mortality will increase linearly in lockstep with the trend of increasing population size between 2008 and 2016 as for the genetic count.

### Appendix 3 Complementary results of the reconstruction of the population of brown bear in Slovenia

**Table A3.1.** Age structure for males and females estimated from each the two applied methodologies: age-at-harvest reconstruction and predictive modelling. Averages of the two methodologies is also presented.

| Age-class | Age at harvest |       | Predictive modeling |       | Average |       |
|-----------|----------------|-------|---------------------|-------|---------|-------|
|           | females        | males | females             | males | females | males |
| 0         | 0.122          | 0.121 | 0.120               | 0.118 | 0.119   | 0.121 |
| 1         | 0.100          | 0.103 | 0.107               | 0.093 | 0.098   | 0.104 |
| 2         | 0.077          | 0.082 | 0.081               | 0.070 | 0.076   | 0.079 |
| 3         | 0.052          | 0.047 | 0.058               | 0.043 | 0.045   | 0.055 |
| 4         | 0.038          | 0.027 | 0.043               | 0.026 | 0.027   | 0.040 |
| 5         | 0.030          | 0.018 | 0.036               | 0.016 | 0.017   | 0.033 |
| 6         | 0.025          | 0.012 | 0.031               | 0.012 | 0.012   | 0.028 |
| 7         | 0.021          | 0.009 | 0.026               | 0.008 | 0.009   | 0.023 |
| 8         | 0.018          | 0.006 | 0.021               | 0.006 | 0.006   | 0.019 |
| 9         | 0.015          | 0.004 | 0.017               | 0.004 | 0.004   | 0.016 |
| 10        | 0.013          | 0.003 | 0.014               | 0.003 | 0.003   | 0.014 |
| 11        | 0.011          | 0.002 | 0.012               | 0.002 | 0.002   | 0.011 |
| 12        | 0.009          | 0.001 | 0.009               | 0.001 | 0.001   | 0.009 |
| 13        | 0.007          | 0.000 | 0.006               | 0.001 | 0.000   | 0.006 |
| 14        | 0.006          | 0.000 | 0.005               | 0.001 | 0.000   | 0.005 |
| 15        | 0.005          | 0.000 | 0.004               | 0.000 | 0.000   | 0.004 |
| 16        | 0.004          | 0.000 | 0.003               | 0.000 | 0.000   | 0.004 |
| 17        | 0.004          | 0.000 | 0.001               | 0.000 | 0.000   | 0.002 |
| 18        | 0.003          | 0.000 | 0.001               | 0.000 | 0.000   | 0.002 |
| 19        | 0.002          | 0.000 | 0.001               | 0.000 | 0.000   | 0.001 |
| 20        | 0.002          | 0.000 | 0.001               | 0.000 | 0.000   | 0.001 |
| 21        | 0.002          | 0.000 | 0.000               | 0.000 | 0.000   | 0.001 |

**Table A3.2.** Survival probability up to certain age for males and females in Dinaric brown bear population

| Age-class | males | females |
|-----------|-------|---------|
| 0         | 1.00  | 1.00    |
| 1         | 0.72  | 0.79    |
| 2         | 0.48  | 0.61    |
| 3         | 0.30  | 0.48    |
| 4         | 0.20  | 0.38    |
| 5         | 0.13  | 0.31    |
| 6         | 0.09  | 0.26    |
| 7         | 0.06  | 0.21    |
| 8         | 0.04  | 0.17    |
| 9         | 0.03  | 0.13    |
| 10        | 0.02  | 0.11    |
| 11        | 0.01  | 0.08    |
| 12        | 0.01  | 0.06    |
| 13        | 0.00  | 0.05    |
| 14        | 0.00  | 0.04    |
| 15        | 0.00  | 0.03    |
| 16        | 0.00  | 0.02    |
| 17        | 0.00  | 0.01    |
| 18        | 0.00  | 0.01    |
| 19        | 0.00  | 0.01    |
| 20        | 0.00  | 0.00    |
| 21        | 0.00  | 0.00    |

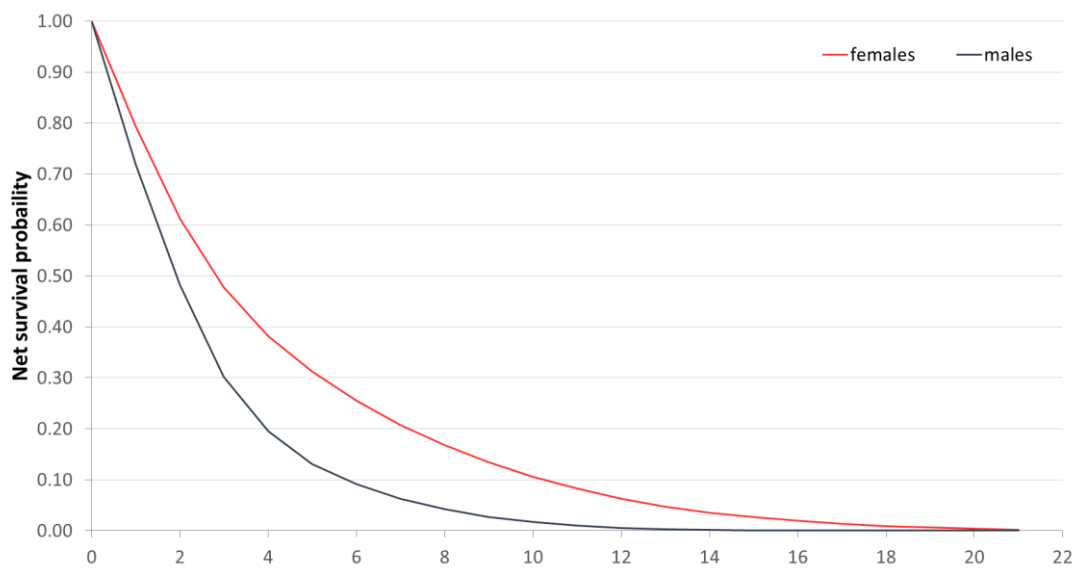


Figure A3.1. Net survival probability for brown bear males and females in Slovenia and Croatia