



# From science to practice: genetic estimate of brown bear population size in Slovenia and how it influenced bear management

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## Abstract

Rapid development of molecular genetics has provided ecologists and wildlife managers with a powerful set of tools for studying and monitoring wildlife. We applied these tools to estimate the size of the brown bear population in Slovenia in 2007. In the years after the estimate was made public, we followed how this estimate affected policy and management actions in Slovenian bear management. We designed and executed a large-scale noninvasive genetic sampling across the range of this species in the country with a network of volunteers and estimated the size of the brown bear population in Slovenia using mark-recapture modeling. In a highly intensive 3-month sampling in autumn 2007, we collected 1057 samples. A total of 931 samples were successfully genotyped, yielding 354 different genotypes. Using mark-recapture and correcting for the edge effect caused by bears moving in and out of the sampling area across the Slovenian-Croatian border, and accounting for detected mortality, we estimated “winter” population size (after annual mortality, before reproduction) at 424 (95% confidence interval 383–458). We also observed an uneven male and female ratio of 0.405 and 0.595, respectively. Using “citizen science,” we managed to conduct a highly intensive large-scale sampling with modest financial resources, something that would be impossible to do otherwise. We produced the first robust, scientifically defensible estimate of the brown bear population size in Slovenia. Although at first reluctantly considered by managers as equivalent to other “traditional” population monitoring data, awareness of the importance of the estimate grew with time. It became the first reference point for understanding population dynamics, a basis to which current and future development of the population is being compared to. As such, we can expect it will profoundly affect Slovenian bear management in the years to come.

**Keywords** Noninvasive genetics · Mark-recapture · Brown bear · *Ursus arctos* · Wildlife management · Population size · Science and policy · Citizen science

## Introduction

Rapid development of molecular genetics has provided ecologists and wildlife managers with a powerful set of tools for studying and monitoring wildlife populations (Schwartz et al. 2007). This is especially true for noninvasive genetic sampling (Waits and Paetkau 2005), which is increasingly

becoming the method of choice for the estimation of census population size in many species (e.g., Waits 2004; Schwartz et al. 2007; Poole et al. 2011; Guertin et al. 2012; Scriven et al. 2013; Wultsch et al. 2014; Karamanlidis et al. 2015; Morin et al. 2016; Rehnus and Bollmann 2016; Wilton et al. 2016; Humm et al. 2017; Moqanaki et al. 2018). However, there is rarely a follow-up describing the actual application of the results to conservation and management, and the impact this has had on the population in the wild.

One of the flagship species for the application of noninvasive genetic sampling for population size estimation has been the brown bear (*Ursus arctos*). A large, powerful animal, the bear tickles the imagination and holds an important place in the lore of many cultures (Lescureux et al. 2011). On the other hand, bears can cause considerable damage to property and can, under certain circumstances, be dangerous to people (Herrero 2018; Støen et al. 2018). Even though a part of the

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public literally worships this charismatic large carnivore, it is often met with considerable opposition from other interest groups, and management for bear-human coexistence is frequently a very fine line to be walked (Huber et al. 2008; Majić et al. 2011).

Centuries of persecution have exterminated brown bears from most of Western Europe where only a handful of bears still remains in the wild (Zedrosser et al. 2001). Large populations remain in Northern, Eastern, and Southern Europe. One of these remaining populations is the Alps-Dinara-Pindos population that stretches along the Adriatic coast from the borders of Italy and Austria in the north and all the way to Greece in the south. Bears in Slovenia represent the northwestern part of this large population. While the total area of the bear range in Slovenia is relatively small, the population density seems very high (Jerina et al. 2013). The importance of these bears is disproportionate to their numbers as they form the only “bridge” for the much-coveted natural recolonization of the Alps by this species and have been the source of animals for bear reintroductions to Austria, Italy, and France (Clark et al. 2002). However, bears have been a source of controversy in Slovenia for some time now. Increasing numbers of registered conflicts with humans and high official estimates of this species’ abundance have nearly doubled the cull quotas in the early 2000s from what they used to be in the 1990s (Kryštufek et al. 2003). Sustainability of these quotas has been questioned by experts (Reynolds 2002), and a need for a credible, science-based estimate was recognized.

In this work, we report on the first genetic survey of brown bear population size in Slovenia, which should serve as the foundation for rigorous long-term monitoring of the population. We also follow up on how the results were used in subsequent years and evaluate how they contributed to generating new policies and management actions in Slovenia in the decade following the survey. We (1) designed and executed a large-scale, cost-effective noninvasive sampling of brown bears across the range of this species in Slovenia with a network of volunteers, (2) genetically tagged a large number of bears, and (3) estimated the size of the brown bear population in Slovenia using mark-recapture modeling. Finally, we (4) examined how this first science-based estimate was received and applied by the managers. With this, we are providing an account of how a well-designed population-monitoring scheme using noninvasive genetics can be implemented with relatively low costs and used for the conservation and management of a difficult-to-manage species. We also explore how scientific results have translated to management practice, and touch on the opportunities and challenges that the higher precision and reliability of thus obtained estimates present for bear management.

## Methods

### Study area

We sampled the entire area of permanent bear presence in Slovenia, covering approximately 6000 km<sup>2</sup> (Fig. 2). The main part of the study area is in the Dinaric Mountains, which span the length of the eastern Adriatic coast to form one of the largest continuous forest complexes in Europe. Density of human population is relatively low for European standards, with on average of about 100 people per square kilometer (<http://www.luminocity3d.org>). Human residence is in most cases limited to valleys, leaving large, continuous patches of dense forests that expand across the border with Croatia. The most common forest plant community is the Dinaric beech-fir forest, *Abieti-Fagetum*. A small part of the study area to the south belongs to the Mediterranean biogeographic region, and the western part assumes pre-Alpine characteristics. While there are bears present in the Julian Alps at the border with Italy (NW Slovenia), these are just few individuals and sampling these areas would not affect the total estimate. However, we did sample in these areas opportunistically.

### Study design and power analysis

In a pilot study using noninvasive genetic sampling, which we performed in two relatively small study areas in Slovenia in years 2003–2006, we obtained the highest amplification success rate from scat samples in autumn and early winter (Skrbinšek et al. 2007a; Skrbinešek et al. 2010). In the same study, we also found that the population behaved as an approximately closed population even in small study areas (175 or 240 km<sup>2</sup>, respectively) if samples were collected within a short, 3-month timeframe (Skrbinšek et al. 2007a). This was the basis for the decision to plan for an intensive, 3-month-long noninvasive sampling session in autumn 2007, from 7 September until 30 November.

To understand the sampling effort required to obtain a reasonable confidence interval of the mark-recapture estimate, we performed a simple power analysis using a simulation study in the program MARK (White and Burnham 1999). We used 600 animals as the best-guess upper limit population size, a pessimistic 70% expected genotyping success rate (based on a pilot study, see Skrbinešek et al. 2010), and a simple Huggins’ model where rate of capture and recapture was assumed to be identical (Huggins 1989) to both the simulation and the estimation model. We simulated sampling and successfully genotyping 1000, 800, and 600 samples (1429, 1143, and 857 samples taking the expected genotyping success rate into account) to understand the width of the confidence interval that would be obtained in the ideal circumstances. We simulated six sampling sessions and used 1000 iterations in each simulation run. Although the simulation was

not entirely realistic, it provided a reasonable estimate of the minimum effort we would need to obtain an acceptable result, and we used its results to scale the sampling effort.

### Motivating and managing a network of volunteers, and providing feedback

Initial estimates showed that our budget would not support organizing field crews to search for scat samples, and the only viable option was in recruiting a large number of volunteers. We organized such a network of volunteers with the help of Slovenian Hunters Association and Slovenia Forest Service. We prepared sampling equipment (three sampling tubes and an instruction booklet for each participant) and distributed it through hunting clubs (*sensu* Bellemain et al. 2004), regional forest service offices, and special purpose hunting reserves (state-owned hunting areas managed by Slovenia Forest Service). In an attempt to maintain approximately the same sampling effort throughout the study area, we used GIS (ArcGIS, ESRI, Redlands, CA, USA) and CORINE land cover data to calculate the amount of forest in the area covered by each hunting club or hunting reserve. In an attempt to obtain an equal sampling effort throughout the study area, we stratified sampling by hunting area. Most hunting areas are small (average area  $\sim 50 \text{ km}^2$ ), which allowed us fine scaling of the sampling effort. To decrease the heterogeneity that could occur because of different individual motivation of the participants, participants were not expected to go out of their way to find samples, but were rather to collect samples they encounter during their usual activities. We also used relative local bear population densities estimated from annual bear counting from high hunting hides (Jerina et al. 2013) and the best-guess upper limit of the bear population size (600) to estimate the highest expected population density. We used this estimated highest population density as the baseline for the amount of sampling material required per area unit for every bear to have a fair chance of being included in sampling even at the highest population density. We then distributed the material proportionally to the area of forest cover in a hunting ground regardless of the presumed population density of bears in each area to obtain approximately equal sampling effort. Sampling material was organized in “personal sampling kits” (2–6 50 mL vials and an instruction booklet). Since the number of people sampling (not the amount of vials in the field) is the measure of sampling effort, we distributed the number of sampling kits per hunting area with regard to the available bear habitat in the hunting area. In the absence of a reliable habitat suitability model, the forest cover was used as a proxy for available bear habitat.

We put considerable effort in the preparation of the sampling materials. From the start, we considered that we need to make all the materials we would hand out look and feel as professional as possible if we wanted to be taken seriously. We tested various sampling vials to make sure they were as leak-proof

as possible. Leakage of collected bear scats over personal belongings and/or clothes could be strongly demotivating for the participants and could endanger the entire sampling if it happened frequently. We designed and printed an illustrated instruction booklet with an introduction of the project and detailed sampling instructions, and our direct contact data if they had any additional questions. We packed everything in neat “personal sampling kits” in a vibrant color (signal orange) that would make them harder to lose or overlook.

We made an effort to make participating in the study as simple as possible and require minimum additional work from the participants besides collecting a sample. We distributed the sampling material to locations in the field (a hunting club headquarters, a Slovenia Forest Service local office, etc.) where the participants could collect it, often while engaging in other activities. We also organized sample pickup at regular intervals at the same locations.

To motivate the people to participate, we published three comprehensive articles in the main Slovenian hunting magazine “Lovec” (which all of Slovenia’s 22,000 registered hunters are subscribed to as a part of their mandatory annual Hunting Association membership fee) prior to sampling, describing the project and asking people to participate (Skrbinšek et al. 2007b; Skrbinešek et al. 2007c; Skrbinešek et al. 2007d). We gave ten lectures at different locations around the bear range presenting the project to employees of hunting reserves and representatives of all participating hunting clubs. During the sampling, we made telephone calls to the leaders of hunting clubs, asking about possible problems and suggestions, and we made rounds around hunting clubs to collect samples and provide additional sampling material if needed. We also made sure that during the sampling, we were always available either by email or on our personal mobile phones. When results became available, we provided feedback to participants by publishing two articles in the “Lovec” hunting magazine, by publishing all results and project reports at the project webpage (<http://www.medvedi.si>), and by producing personalized tables and maps for each hunting club detailing where each sample was collected, who collected it, and what specific results were associated with it (e.g., the sex of the bear, a map of other places where its samples were found).

### Sample collection, storage, tracking, genotyping, and quality assurance

While most of the samples were bear scats, we also collected tissue samples of all detected bear mortality. Bear mortality sampling is done routinely since 2003, and non-detected mortality is generally considered to be low (Skrbinšek et al. 2012a).

Both scat and tissue samples were collected in 96% non-denatured ethanol. Volunteers were asked to keep the samples

in a cool, dark place. Upon arrival in the laboratory, they were stored at  $-20\text{ }^{\circ}\text{C}$  until analysis.

Each sample tube was fitted with a printed label that contained a form for field data entry to keep the data with the sample. At the time of collection, the location of the sample was recorded either by GPS or in a  $1 \times 1$  km grid the hunters routinely use for monitoring of hunting species' harvest (Jerina K., personal communication). Subjectively, the estimated age of each scat was also recorded, and the participants were instructed not to collect samples they subjectively considered older than 5 days (Skrbinšek et al. 2010). We used a dedicated laboratory for DNA extraction from noninvasive samples where we enforced strict rules regarding the movement of personnel, equipment, and material to prevent contamination and used negative controls throughout the process. Upon entry in the laboratory, the data about a sample was entered into a relational database, and barcodes were used to track samples through the genotyping process and eliminate manual data entry. We used a single reaction 13-plex PCR protocol to amplify 12 polymorphic microsatellite loci and a sex determination locus in a single reaction and a single sequencer run. We used a modified multi-tube approach (Taberlet et al. 1996; Adams and Waits 2007) with up to eight re-amplifications of each sample according to the sample's quality and matching with other samples. We used the maximum likelihood approach for estimating genotype reliability, and set reliability thresholds for accepting a genotype to 0.95 for samples that were genotype-matched to other samples and 0.99 for samples that did not match any other sample. The full analysis and genotype quality assurance protocols for noninvasive samples are detailed in Skrbinšek et al. (2010). Analysis protocols for tissue samples are detailed in Skrbinšek et al. (2012b).

### Matching of samples with the same genotype and assigning individuals to samples

Although discovering samples that have the same genotype (and should, in principle, belong to the same individual) seems straightforward, this is not necessarily the case. Incorrect matching either “merges” the actual individuals if the information in analyzed loci is too low or creates “new” virtual individuals if the samples are erroneously considered to have different genotypes because of genotyping errors. The first problem decreases with increasing the number of loci used; however, this exacerbates the second problem. Genotyping errors, even with the most strict quality assurance protocols, are unavoidable in noninvasive samples (Taberlet et al. 1999; Waits and Paetkau 2005). Incorrect matching can cause considerable biases in mark-recapture estimates (Roon et al. 2005). A solution has been proposed to analyze the minimum number of loci that still provide enough resolution to reliably identify individual animals, minimizing the error (Paetkau

2004). While this does make intuitive sense, the problem is that in noninvasive samples, an odd locus will not amplify reliably in a sample, and even with low number of loci analyzed, the errors caused by allelic dropout remain a significant issue. In such case, a large number of samples will be discarded, losing data and limiting the number of recaptures, while much of the problem of incorrectly assigning individuals to samples will still remain. Also, some samples will not reach the genotype reliability criteria with any sensible amount of repeats, but may provide a reliable multi-locus genotype match with another, reliably genotyped sample. Another problem that we have not yet seen mentioned in the literature, but becomes very real when a large number of animals are included in the study, is the multiple-testing problem. Some measure of probability of identity (PID) between two randomly selected animals or siblings ( $\text{PID}_{\text{sib}}$ ) is typically considered to determine the number of loci required to obtain enough resolution to discern between animals (Waits et al. 2001); however, the directly calculated PID or  $\text{PID}_{\text{sib}}$  is valid only for a single comparison between two individuals. In a study, there are  $N \cdot \frac{N-1}{2}$  comparisons (where  $N$  is the number of individuals included in the study), so an appropriate multiple-testing correction should be used to correct the PID and  $\text{PID}_{\text{sib}}$  values for the study. When  $N$  gets large, the resolution of a modest set of loci quickly becomes inadequate.

We took another approach of analyzing a large number of loci and allowing for mismatches resembling allelic dropout (a non-amplifying allele, which is the most common genotyping error in noninvasive samples—see Broquet and Petit (2004)). We used a large dataset of brown bears from the same population genotyped using tissue samples with a very low error rate (Skrbinšek et al. 2012b) to explore the distribution of mismatches, and used this mismatch distribution to set thresholds for allowable genotype mismatch. If the observed mismatches could not be caused by allelic dropout (e.g., three or four different alleles at the same locus in both samples), the samples were considered to belong to different animals or additional evidence was collected through further repetitions of the genotyping procedure.

### Mark-recapture analysis

We used several mark-recapture modeling approaches. We used the Capwire approach (Miller et al. 2005) with the R-package capwire (Pennell et al. 2013). We also used the generalized linear model approach with the information-theoretic model selection (Burnham and Anderson 2002), as applied in program MARK (White and Burnham 1999). To provide a robust validation of the final results, we used Chao's  $M_h$  model (Chao et al. 1992), which has a lower statistical power but should also be robust to capture heterogeneity and generally performs well in large datasets (Miller et al. 2005). Separate

models were done for males and females, and for both sexes combined.

The Capwire model assumes continuous sampling, which fits with how our data has been collected. An additional advantage of this model is that it is reasonably robust to capture heterogeneity. We used likelihood ratio test to select between the even capture rate model (ECM) and the two innate rates model (TIRM).

In order to meet the requirements of discrete sampling sessions in MARK, we considered the data collected within a certain time interval (sampling interval) as a single sampling session. All captures of an individual animal within an interval were aggregated into a single capture, lowering the capture heterogeneity and increasing robustness of the analysis. On the other hand, aggregation into sampling intervals invariably means loss of data (Petit and Valiere 2006). To find the ideal limits of each sampling interval, we programmed a recursive optimization routine in R programming language (R Core Team 2010) which iterated through all possible combinations of uneven interval durations for a given number of intervals and found a solution with the minimal data loss and the maximum number of animals captured in each interval. The duration of each sampling interval (in days) was included in the modeling as a linear covariate. To estimate the day when the scat was deposited by the animal, we corrected the sampling date by subtracting the estimated age of a scat.

We used the Huggins model (Huggins 1989), including the newer derivations that allow for heterogeneity and misidentification (Lukacs and Burnham 2005; Cooch and White 2007), to construct an a priori model set using the biological knowledge of the species and data/study characteristics (Burnham and Anderson 2002). Since these models use the same likelihood, they can be compared in the same model set using the information-theoretic approach. We used the median C-hat method to estimate goodness of fit of the most parameterized model (Cooch and White 2007). As there is no reason to expect behavioral response in the detection of scat samples, we equaled the probability of first captures with the probability of recaptures. In the maximum model, we grouped the animals by sex, included the variation in capture probability between sampling intervals, and included the number of samples collected in a sampling interval (not the same as the number of captures as multiple captures of the same individual during the same interval get aggregated, but an indicator of sampling intensity) as a covariate of capture probability. We used Akaike's second-order information criterion (AICc) (Akaike 1974; Sugiura 1978) for model selection, constructed a confidence set of models with  $\Delta\text{AICc} < 3$ , and considered model averaging using Akaike's weights for the final parameter estimation (Burnham and Anderson 2002).

All the models we used assume a demographically closed population. Since sampling was relatively short, and before reproduction, the majority of mortality is recorded and

included into the dataset (as mortality on capture), we assumed that the sampled population should behave as demographically closed. We tested this assumption using the Pradel model (Pradel 1996) with recruitment parameterization (Boullanger et al. 2002).

The population is geographically (and consequently demographically) completely open towards Croatia because the national border crosses bear habitat without providing any significant physical obstacles to bear movement. We therefore expected some edge effect in the form of inclusion of animals that had only part of their home range in our study area. This meant that our estimate would actually estimate a "superpopulation". We used the correction proposed by Wilson and Anderson (1985) to correct the edge effect and estimate the instantaneous population size for Slovenia (the number of bears expected to be present in a certain moment in our study area), which is the parameter required for management purposes. We used detected pairwise distances between locations of samples of the same animal to calculate  $W$ , which is the width of the strip of Croatian territory bordering our study area from where the animals would have a non-negligible probability of being included in our sampling. Because of expected differences in habitat use,  $W$  was calculated separately for each sex. To obtain the instantaneous population size estimate (the expected number of individuals inside the sampled area at a certain time point), we used the  $A_s/A_t$  as the correction factor for our superpopulation estimate, where  $A_s$  is the surface area being sampled, and  $A_t$  the total area including the edge strip in Croatia.

### Assessing the impact of the population size estimate on bear management

We were interested in how the final population size estimate was received by the managers and used in management decisions. The brown bear is listed in Annex IV of the EU Habitats Directive (Council Directive 92/43/EEC) as a strictly protected species. The Directive is legally binding for all EU member states, making the bear also a strictly protected species in Slovenia. However, applying derogations set out in Article 16 of the Habitats Directive, every year a cull quota is decided and permitted through a special decree of the competent ministry. Most of the culling is done through regular hunting, with the quota being strictly prescribed by weight classes and spatially distributed throughout the bear range. Some bears are culled as problem bears. The basis for setting the quota is an expert opinion by the Slovenia Forest Service, reviewed by the Institute of the Republic of Slovenia for Nature Conservation and discussed in an expert committee. Pending that, the proposal is open for comments by stakeholders and the interested general public and discussed in a stakeholder committee. The final decree is drafted by the

competent ministry and signed by the minister, providing the legal background for the yearly cull.

The key document in the process is the expert opinion by the Slovenia Forest Service, and we examined these documents from years 2000 to 2015 to see the reasoning behind the setting of the cull quota and how our estimate affected this reasoning. We also checked the ministerial decrees for the same period and the actual bear mortality to track the effect of the estimate.

## Results

### Power analysis simulation study

The simulation study showed that in a population numbering 600 bears and with 70% genotyping success rate, we would, in ideal circumstances, need 1429 samples to obtain a population estimate with an expected 8% confidence interval and 857 samples to obtain an expected 18% confidence interval (Table 1). Since we considered 20% to be the maximum acceptable confidence interval and understood that the actual data would be considerably noisier than the ideal simulated data, we scaled the study with the aim to collect at least 900–1000 samples.

### Sample collection and genotyping

Following the power analysis, we started an intensive field campaign that would allow us to obtain a sufficient number of samples within a period of time during which the population could still be treated as closed. Volunteers that participated in the sampling came from 105 hunting clubs, 4 special purpose hunting reserves, and 6 regional offices of the Slovenia Forest Service, plus additional volunteers that contacted us directly. We distributed 5613 sampling tubes to more than 1000 people. We received 1057 scat samples collected by 391 different people for analysis. All samples were relatively fresh, with the mean estimated scat age of 2.17 days (SD = 1.51). We also collected and genotyped tissue samples of 26 bears that were killed (legally shot or traffic mortality) during the sampling.

We managed to successfully genotype 931 samples (88% of all collected samples). We recorded an average allelic dropout of 10.05% and an average false allele rate of 0.38%. On average, we performed 3.61 PCR amplifications and genotyping analyses per sample—minimum two in high-quality samples that matched other samples and maximum eight in marginal samples.

Although we made an effort to keep the network of volunteers active through direct contact by telephone throughout the sampling period, we could see some variability in sampling intensity (Fig. 1). The sampling intensity was very high in the beginning but started decreasing until we revisited all participating hunting clubs after 8 weeks of sampling. After the visit, the intensity increased again and gradually dropped until the end of the sampling period. While there was, as expected, heterogeneity in the sampling effort between areas sampled by different hunting clubs or special purpose hunting reserves (managed by the Slovenia Forest Service), individual areas covered by these organizations are small enough that they typically do not cover even a single bear home range, meaning that even if for example a hunting club would completely boycott the project, any bears in its area would still have a considerable probability of being captured in the neighboring hunting clubs. This small-scale heterogeneity would be difficult to address explicitly and was handled through the use of mark-recapture models that relax the capture homogeneity assumption.

We found 354 different genotypes, 159 (45%) males and 195 (55%) females. This provided a mean recapture rate of 2.70 (Fig. 2).

### Mark-recapture modeling

The results of the Pradel model with recruitment parameterization were 0.994 and 0.006 for survival and immigration, respectively. These values are close to what we would expect for a closed population (survival = 1 and immigration = 0), supporting the assumption of population closure.

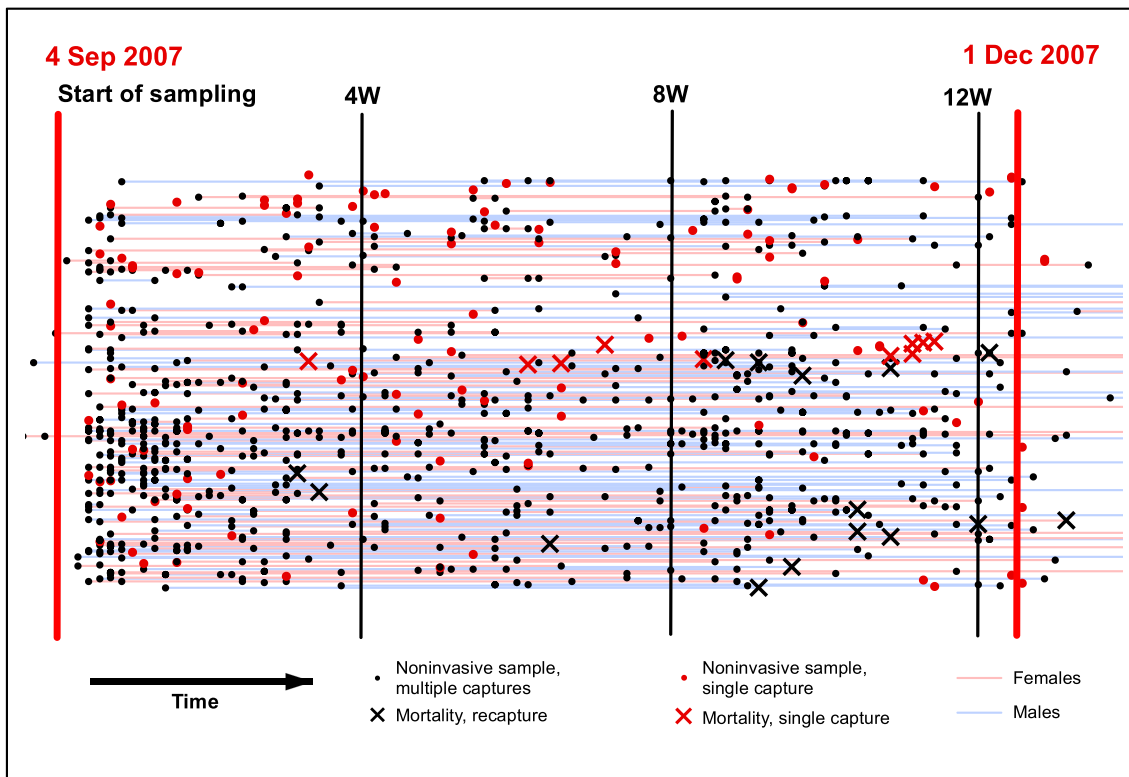
Using Capwire, the TIRM model seemed to provide a better fit to the data than the ECM, indicating some capture heterogeneity in the data.

In the Markov chain optimization routine designed to optimize the sampling intervals for MARK, we aimed for approximately 0.3 capture probability in each capture interval.

**Table 1** Power analysis of mark-recapture effort and expected confidence intervals in idealized circumstances.  $N_s$  number of genotyped samples,  $N_{sc}$  number of collected samples assuming 70% success rate,  $p$  simulated capture probability in each of 6 sampling

$N_s$	$N_{sc}$	$p$	$\hat{N}$	$SE(\hat{N})$	CI	CI (%)
1000	1429	0.28	600.46	12.7	576–625	8
800	1143	0.22	600.59	18.37	565–637	12
600	857	0.17	601.57	27.84	547–646	18

sessions,  $\hat{N}$  estimated number of individuals,  $SE(\hat{N})$  standard error of  $\hat{N}$ , CI breadth of 95% confidence interval, as absolute numbers and as percentage of  $\hat{N}$



**Fig. 1** Graph of the mark-recapture process. Time increases from left to right, each symbol is a sample, and lines connect samples of the same individual. We can see the peaks of sampling intensity in the first 2 weeks of sampling and in the 2 weeks following the re-visits of the hunting clubs in week 8

Following the optimization for minimal data loss, we obtained seven capture intervals covering the entire sampling period. Median C-hat goodness of fit test for the most parameterized model (Huggins  $c = p(\text{sex}, t)$ ) showed a very reasonable model fit ( $C\text{-hat} = 0.352$ ,  $s.e. = 0.022$ ).

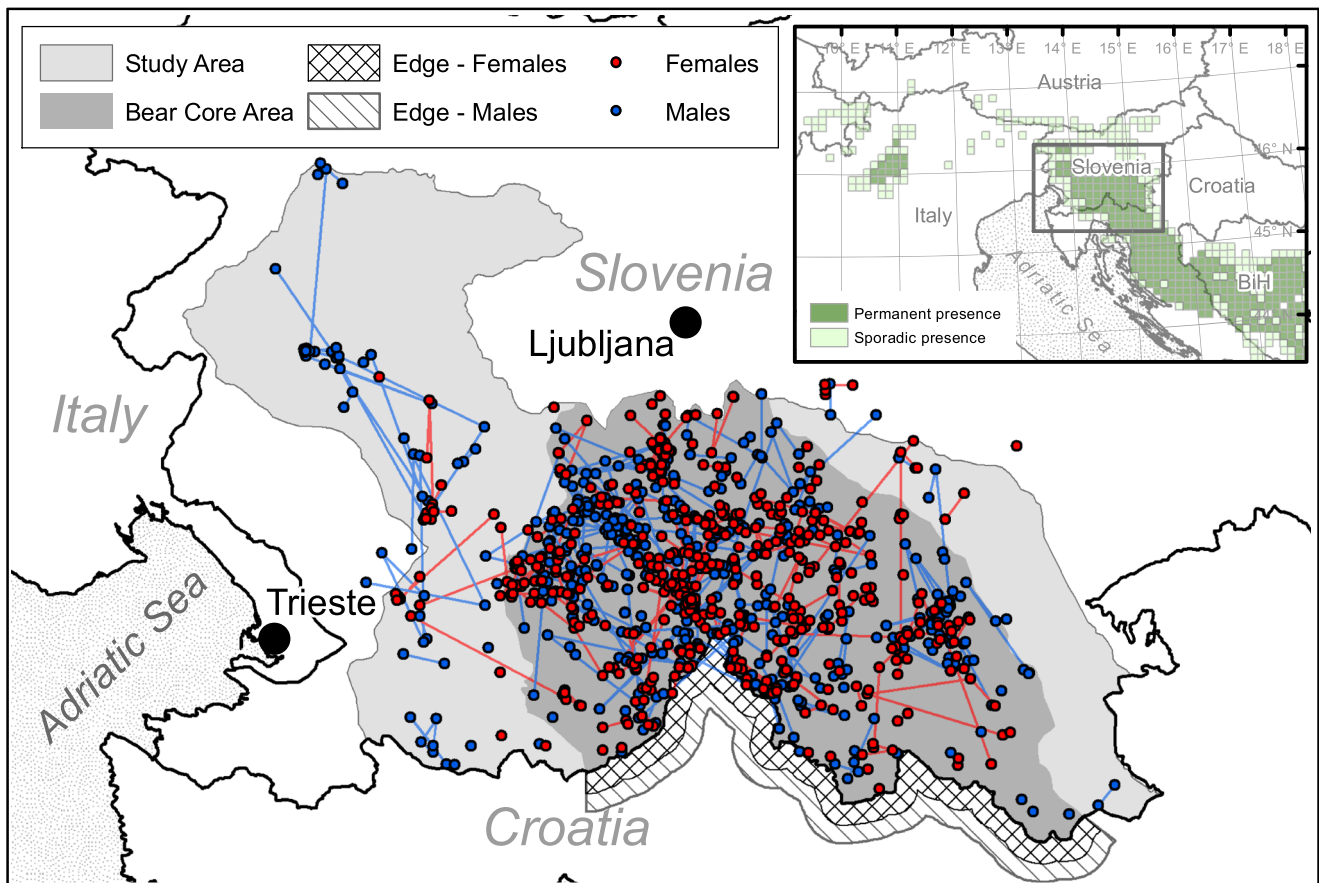
In Huggins’ models in MARK, the most parsimonious (best) model included the sex of the animals, heterogeneity modeled as two finite mixtures, and the number of samples collected per sampling interval as a linear covariate. A similar model that included misidentification had similar support in the data ( $\Delta AICc = 0.85$ ); however, as the misidentification coefficients for both groups were very close to 1, the model is more complex, and the abundance estimates were nearly identical to the best model, we decided not to include it in the confidence set. The only other model besides the best model that made it in the confidence set included the duration of each sampling interval instead of the number of samples as a linear covariate ( $\Delta AICc = 2.18$ ). The models that did not include either of the linear covariates of the sampling interval had low support in the data ( $\Delta AICc \geq 6.92$ ), and the models that did not account for heterogeneity had practically no support in the data ( $\Delta AICc \geq 35.05$ ). We did not use model averaging, but used the best model for the estimation of abundance since the only other model with a meaningful Akaike’s weight produced nearly the same estimate.

We obtained very similar results using all three modeling approaches (Fig. 3), and the estimates of models estimated

separately for males and females fit very well with the estimate where the data for both sexes was pooled. The Capwire provided the narrowest confidence intervals. This is not unexpected since the model conceptually fits better to our data (continuous sampling) and should therefore use the data more efficiently than the other two models, where some data loss occurs as the data is organized into sampling sessions. It should be reasonably robust to capture heterogeneity (Miller et al. 2005), so we used its estimate for the final result on (super) population size (Table 2).

### Edge effect correction

An implicit assumption in the edge effect correction we used is that of a homogenous population density. However, the number of different animals found was high in the “core” bear range in the Dinaric Mountains ( $N = 318$ ) and low in the border areas ( $N = 36$ , see Fig. 2), indicating considerable heterogeneity in population density. The low-density areas are separated from the core area by linear barriers (highways, main roads) and dense human settlements. It is reasonable to believe that this difference in densities was not caused by uneven sampling effort as (1) we took great care to keep this as uniform as possible and (2) the same population density pattern has been confirmed by independent data (Jerina et al. 2013). To account for this heterogeneity, we excluded the low-population-density areas from the calculation of the edge



**Fig. 2** Study area and locations of successfully genotyped samples, with the core bear range and the buffer zones in Croatia for edge effect correction. Lines chronologically connect samples from the same individual

effect correction factors (Fig. 2). The majority of excluded bears appeared in the area towards the Alps (northwestern part of the sampling area), separated from core area by the difficult-to-cross Ljubljana-Koper highway. These animals have a low chance of leaving the sampling area. By excluding them from the edge effect correction, we avoided the bias that including this large area with a very low population density would cause. We obtained the population size in the core area by multiplying the total mark-recapture estimates with the proportion of the directly detected individuals (each sex or both sexes together) within the core area (females = 0.933, males = 0.855, both sexes = 0.898). There was a considerable difference between males and females in the maximum observed pairwise distances between locations of samples of the same animal: 6167 m for females and 11,165 m for males. We calculated different edge effect correction factors for the core bear range for each sex separately and for both sexes together (females = 0.893, males = 0.828, both sexes weighted mean = 0.866).

The datasets generated during and analyzed during the current study are available from the corresponding author on reasonable request.

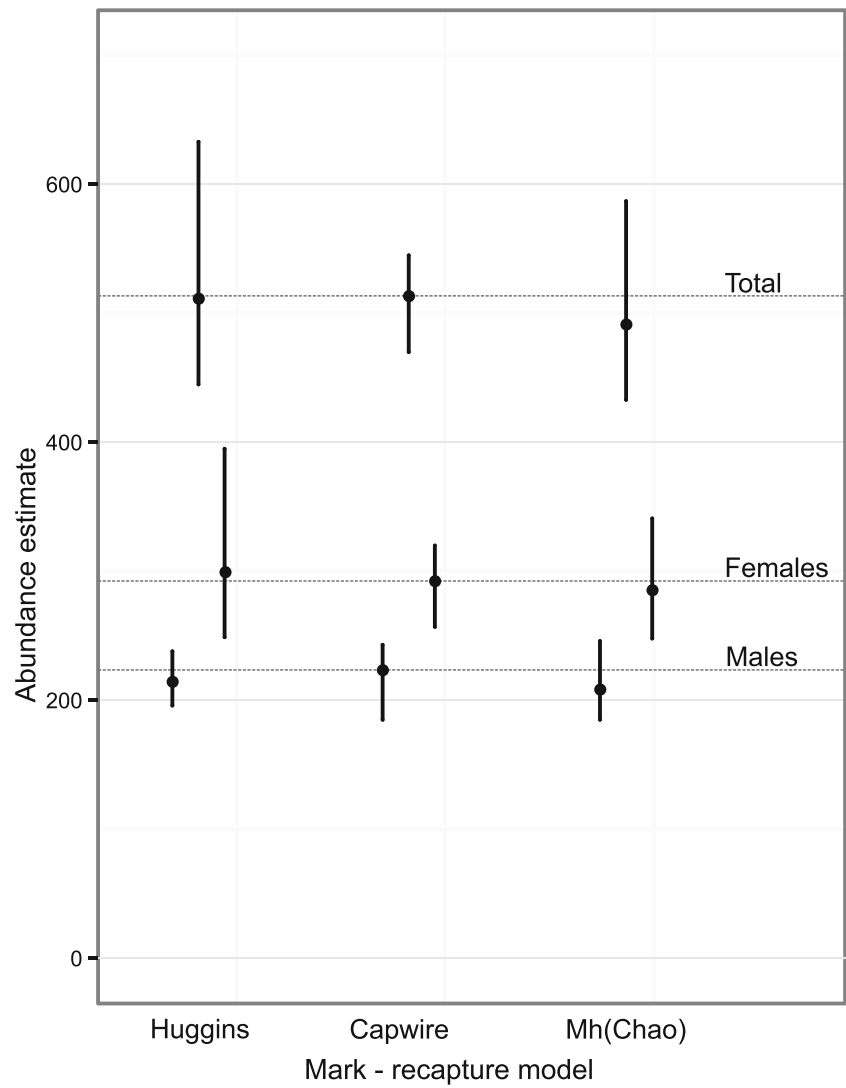
### The impact of new population monitoring data on bear management

The final result for the minimum yearly population size in Slovenia (subtracting all recorded mortality, immediately before reproduction) was 424 bears (383–458 95% CI). We made the results public in 2008 and received considerable media attention. Following a press conference, we gave a number of interviews to various media outlets and provided final report of the entire project to stakeholders and decisionmakers who are involved in the bear management in Slovenia. Since the data analysis methods we used for the estimate were improved from what was originally reported in the project report, there is a minimal difference (2.4%) between the estimate we provided for management purposes in 2008 and the estimate published here. The difference is well within the confidence interval and insignificant for any practical purposes.

Prior to the estimate presented here (report published in November 2008), the stated basis for management decisions was the estimated population size of 450–550 up until 2005 and 500–700 bears from 2006 onwards. Population was reported to be “stable and growing,” with the exception of 2008



**Fig. 3** Superpopulation size estimate (and 95% confidence intervals) of bears in Slovenia (no correction for edge effect) using three different modeling approaches. While the Capwire model provided the narrowest confidence intervals, the results obtained by different models are nearly identical



**Table 2** Sex-specific and total population size estimates of Slovenian brown bears by the end of 2007 obtained by Capwire, corrected for edge effect (Ncorr). In the brackets is the 95% confidence interval. After excluding mortality during sampling, the final (winter) estimate (Nf) represents the annual minimum population size, after finished cull and before reproduction. Sex structure was calculated for the winter estimate, and the spring estimate should produce less skew since mortality is greater in males

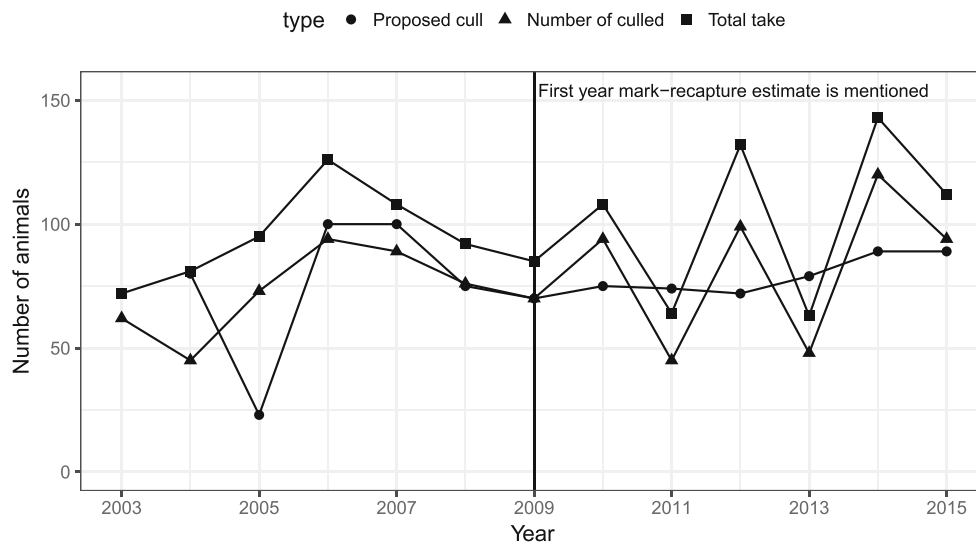
	Ncorr	Mortality in sampling period <sup>1</sup>	Nf	Sex structure (%)
Males	188(152–210)	17	171(135–193)	40.5
Females	261(228–291)	9	252(219–282)	59.5
Total	450(409–484)	26	424(383–458)	100

<sup>1</sup> Since an overall annual mortality of 108 brown bears was detected in 2007, the maximum (spring) estimate should include these animals. However, doing this might produce an overestimate if the high cull rates created a source-sink dynamics with the bears in Croatia

when it was reported as “somewhat decreasing” based on results from the counting of bears from high hunting hides, and as “growing” on the basis of recorded signs of bear presence in special purpose hunting reserves managed by the Slovenia Forest Service.

The genetic estimate was first mentioned in the expert opinion of the Slovenia Forest Service in 2009, but it was not clear how it was used in the final cull quota decision. Instead, in their justification, the managers leaned heavily on the traditionally collected data of recorded signs of bear presence in special purpose hunting reserves and deduced that the population is “stable and has favorable conservation status.” From 2010 to 2015, the expert opinion relied on the genetic estimate and other monitored parameters to assert that the population has “favorable conservation status.” Similar statements appeared in expert opinions up until 2015.

The proposed cull quotas have crept up during the first decade of the 2000s (shown only since 2003 in Fig. 4) up to 100 bears in 2006 and 2007, but dropped 25% to 75 in 2008.



**Fig. 4** Proposed cull, number of culled animals, and total mortality (including other mortality) in Slovenia for the period 2003–2015. The year when our mark-recapture estimate was first mentioned in the management documents is marked with a black vertical line. The “proposed cull” numbers were compiled from the Official Gazette of the Republic of Slovenia (<https://www.uradni-list.si>). Source for the “total mortality” (cull + other mortality) was the Slovenia Forest Service’s expert opinion on the culling of large carnivores in Slovenia

2016/2017 (Slovenia Forest Service 2016). Data for “number of culled” were gathered from quarterly reports by the Slovenia Forest Service, except for 2003, which was estimated from the document’s Fig. 5 (page 14) from the said report for season 2016/2017. This created considerable variance in yearly take and seeming discrepancy from the proposed cull since the quotas decided in one calendar year were partially realized in the next calendar year

They remained at approximately the same level until 2012 when they again started slowly increasing.

## Discussion

Population size is always presented as a critical parameter in management and conservation efforts, especially if a species is managed by hunting. On the other hand, estimating the size of a wildlife population is demanding and has been difficult to implement robustly in a species like the brown bear prior to the development of noninvasive genetic sampling (Bellemain et al. 2004; DeYoung and Honeycutt 2005). Until recently, managers of bear populations had to rely on indirect trends or value estimates that can be severely incorrect (e.g., Moqanaki et al. 2018). With the increasing availability of molecular genetics monitoring methods, it is interesting to observe how the management practices adapt to the new level of precision and robustness in the abundance data.

Brown bear management in Slovenia provides an example. Although the species is protected, the main management focus is the population control through culling. Culling is strictly regulated at the level of the competent ministry according to the Strategy for the management of brown bear (*Ursus arctos*) in Slovenia (adopted by the Government of the Republic of Slovenia at the 59th regular session on 24 Jan 2002). Population size is considered as the foundation for the setting of the cull quota, with the total mortality between 5 and 10% when the “population is balanced with

the environment,” or up to 15% in “exceptional circumstances” when it is not. The Strategy provides no explanation what the terms “balanced with the environment” or “exceptional circumstances” mean. Over the years, several population size estimates had been produced. While the official estimate for the territory of Slovenia (based on an expert opinion) was 450–550 from 2000 to 2005 and 500–700 bears in 2006 and 2007, as evident from official correspondence between the Slovenia Forest Service and the Institute of the Republic of Slovenia for Nature Conservation (Slovenia Forest Service 2006), other estimates based on different methodologies (counting sites from high hunting hides, monitoring of signs of presence in special hunting reserves) provided different results. Neither of the methodologies used could be defended as reliable, which provided considerable room for speculation. The problem was exacerbated by the media (Kokalj 2016) and some NGOs through different interpretations of various estimates that either inflated the population size to unreasonable numbers or presented the population as being threatened, seemingly depending on the personal position or agenda of the author. This produced a volatile atmosphere for brown bear conservation with vocal supporters of both positions. The number of bears killed, mainly through hunting, has more than doubled since 2002 from what it was in the 1990s (mean annual mortality 1990–2001 = 41.2 individuals; 2002–2007 = 99.5 individuals), causing concern among experts (Reynolds 2002), especially since it was based on the official population size estimates that many experts regarded as excessive.

One of our goals was to stop the speculations and provide a defendable, scientifically sound population size estimate of the number of bears in Slovenia, and we feel that we succeeded.

The “winter” population size estimate obtained in this study and made public in November 2008—424 bears (383–458 95% CI) minimum yearly size, after mortality and before reproduction—has been included in the official bear management documents as one of the management parameters since 2009. In addition, one of the most crucial stakeholder groups, the hunters, was directly involved in the study. The Hunters’ Association of Slovenia (membership is required for all hunters in Slovenia) fully supported the project, embraced our size estimate, and participated in its dissemination (e.g., organized a press conference where the estimate was first presented to the public). We took special care to provide feedback to each participating hunting club and published two comprehensive articles in the national hunting magazine “Lovec” which is distributed to all hunters in Slovenia as a part of their membership fee. The credibility of the estimate was never questioned even by the most vocal proponents of bear population size reduction even when it was lower than the official estimates (which have been questioned before as being too low).

It is difficult to compare the population size estimate presented here with the pre-2008 official estimates of approximately 500–700 bears since the methodology behind them or the point in annual population dynamics they apply to is not clear. If we consider the spring (maximum) population size as the critical point in annual population dynamics for cull quota setting and add to our winter (minimum) estimate all bear mortality detected in 2007 (108 animals), we can estimate the population size at 532 animals (491–566 95% CI). Comparing upper and lower limits of both intervals, the pre-2008 estimates overestimated the population size by 2–24%. Prior to the publication of our estimate, proposed cull quotas were lowered by 25% in 2009 compared to 2006 and 2007, and only slowly increased afterwards. The average annual brown bear mortality for years 2008–2015 (99.9 bears/year), after the population size had been robustly estimated, remained nearly the same as in the 2003–2007 period (96.4 bears/year), and the upward trends we had observed in the period before 2008 did not continue. Using the yearly maximum population size estimate, this is still 18.8% of the population size, and even using the upper limit of the (wider) confidence interval made available to the managers through the 2008 report (475) and the spring estimate (adding 108 animals killed in 2007), the mean mortality is 17.6%, which is higher than the maximum 15% allowed by the brown bear management strategy. These mortality rates were justified by the high number of bear-human conflicts and bear-caused damages to property, with the aim to increase the tolerance of brown bears by local residents (Slovenia Forest Service 2010; Brown bear (*Ursus arctos*) management strategy in Slovenia (2002)). Since there was no indication from other monitoring data that

the population was declining, the cull quota (and with it, the total mortality) started slowly increasing again in 2013. Despite seeming high, all monitoring data suggest that this cull rate and structure of removed animals appears to have been sustainable, although it is possible that immigration from Croatia may have been contributing to this perceived sustainability (a high contribution would still be unlikely as bears were being hunted all this time also in that neighboring country). The cull quota decision is complex and needs to encompass a range of direct and indirect effects for bear conservation. In addition to the obvious direct effect of controlling the population, strictly regulated bear culling has a range of other effects like reduction of damages and the direct benefits for the local community that come from bear hunting—maintenance of tradition, bear meat for human consumption, and direct revenue from hunting tourism. A less tangible yet just as important effect is also a feeling of “control” that bear population is being managed and maintained at an acceptable size (Kellert 1997). This complexity is overlooked in the current bear management strategy, which has been recognized as outdated and is currently under revision.

At a first glance, it would seem that the management had not taken the science into account, similar to what has been reported by Swenson et al. (2017). This may have been true to a degree in the first year following the publication of the results, but we did not have that perception in the years that followed. As scientists, we were also involved in a consultative role in the decisionmaking process, albeit in the final stages, but still with considerable possibilities to modify the decisions. While the cull quotas did not meet the management goals set in the bear management strategy, there was a long-time consensus that the strategy needed updating, but no efforts towards this have not been made until recently. Despite this, it is difficult to criticize the past management decisions here since a new study that is currently being finished (Skrbinšek et al. 2017) indicates that the brown bear populations grew considerably in the years following the estimate we are presenting here, despite the cull.

For decades, lethal control was almost the only tool applied to managing the population and solving conflicts, and many underlying problems (access to garbage and other anthropogenic food sources, urbanization of forest space) were not being addressed adequately. We hypothesize that one of the main reasons for this was the lack of robust understanding of the population size since conflicts with bears were by default attributed to there being too many bears. Indeed, a media content analysis done in 2016 shows that after we had published the results of our project, the topic of brown bear population size practically disappeared from the media space, while other sources of human-bear conflicts started appearing as an issue more and more often (Kokalj 2016).

As we moved away from 2007, and especially in the face of the increasing human-caused mortality, our estimate was

becoming less and less relevant, but was still considered as such. There is a need to expand the single-shot estimate into a long-term monitoring, as has already been done elsewhere (e.g., Karamanlidis et al. 2010; Kindberg et al. 2011). Although a new population size estimate is currently being done within the LIFE DINALP BEAR project (2014–2019, LIFE13 NAT/SI/000550), a comprehensive long-term national brown bear monitoring program that would include periodic population size estimates using genetics still remains elusive.

An important issue confirmed by our study is that by combining noninvasive genetic sampling and citizen science, it is possible to provide robust, reliable population size estimates of a difficult-to-monitor species in a rapid, cost-effective manner. The net cost of our study was 90,000€, which is very reasonable for the monitoring of a large carnivore species at a national level. A sampling of this scale and intensity for a reasonable cost would be completely impossible without the help of volunteers, but motivating and managing a large network of volunteers turned out to be a much more difficult feat than we first envisioned. We had two people working full-time for 5 months before the sampling even started, designing and preparing the sampling material, organizing the network of volunteers, and promoting the study, with a number of other researchers and students helping out at different stages of the process. This was essential, and we feel that without that effort the sampling would most likely not be nearly as successful as it was. During the study, it was also critical to stay in touch and keep the motivation high, and we could see a drop in motivation as sampling progressed despite all efforts.

We learned several valuable lessons in this study regarding the use of “citizen science”. First, volunteers do not work for free. Their payment is recognition, experience, and being a part of “something bigger”—the motivation will vary from person to person, but all participants have a reason why they would want to participate. A researcher should think hard about these motivations very early in the study and organize all activities leading to sampling around that. Second, to be taken seriously, one must look and act in a serious and professional manner. This means designing all project materials to look good and work well in the field. While we designed everything ourselves in this project, in later projects, we started engaging professional graphic designers to help establish the visual identity of a project. The same goes for communication—in the preparatory stage, the project should make sure to produce consistent, clear messages that would attract media attention and participants. Although we did not do that, it may, in some situations in large studies, even be a good idea to employ the help of a public relations professional or even a marketing agency. And last but not least, researchers should treat the volunteers with respect, provide as much direct feedback as possible, and go out of their way to acknowledge their contribution. Besides being a decent thing to do, such an approach increases the long-term potential for citizen science since people are more likely to participate

again if they have been treated fairly and have had an overall pleasant experience.

In general, the study and the results were received very well by the participants, particularly hunters and employees of the Slovenia Forest Service who also provided the majority of samples. We received positive feedback on the popular articles where we presented the results and several reports that were published by different national media, and were invited to present the results at several events organized by the Slovenian Hunters’ Association, regional hunters’ associations, and the Slovenia Forest Service. The study marks a start of collaboration with these organizations in the monitoring of large carnivores which still continues today.

We provided results in 1 year since the beginning of sampling, but with currently available methodological improvements (e.g., De Barba et al. 2016), some laboratory upgrades, and the gained experience, the results could be provided in half of this time—in time to support the next management decision. There are additional benefits of molecular genetics approaches, e.g., monitoring of effective population size (Skrbinšek et al. 2012a), genetic diversity, and population dynamics, to name but a few can be achieved with some careful planning and minimal additional costs. The better the monitoring, the more likely it is to ensure a favorable conservation status of the species. According to the Carnivore Guidelines (Linnell et al. 2008), the latter condition is really only fulfilled when “a detailed conservation/management plan” guarantees that the removal of animals, in combination with other derogations, does not adversely affect conservation status.

Although the potential of molecular tools for wildlife management and conservation has been frequently pointed out (e.g., DeYoung and Brennan 2005; Waits and Paetkau 2005; Schwartz et al. 2007; Swenson et al. 2011; Mueller et al. 2016), the managers still need time to adjust to this situation and utilize these tools to their full potential. Scientists may need to invest more effort in conveying how reliable these population size estimates are compared to other methods. With advances in genotyping and data processing, the cost of surveys will further decrease, making it even more appealing for long-term monitoring of critical species and/or populations. Reliable estimates, affordability, and speed with which samples and data can be processed will likely play an important role in negotiating complex quota systems in the future.

Our study was from its inception designed to inform management, as such studies often are. However, we tried to take it a step further and explore how our results contributed to policies and management actions in subsequent years. We have not seen this “follow-up” by scientists done often, but we argue that scientists should consider including it in their work whenever possible and practical. We feel that applied science should have direct impact on the real world, and scientists should see it as their responsibility that their results are interpreted and used correctly by the relevant actors.

An important effect of robust, scientifically defensible population size estimates is that they provide reference points. Particularly important is the first reference point, or the first reliable population size estimate, since it moves the understanding of the population from the realms of speculation and (informed) guesses to the world of hard facts. This is the case with our estimate, and there is a little doubt that it will profoundly affect the brown bear management in Slovenia for the years to come. A robust population size estimate provides much stronger support for management decisions, but may also rectify the idea that a specific population size is “correct,” with lower population sizes being considered as threatening the population or higher population sizes considered as the population being “out of control.” Neither is necessarily correct—animal populations should be recognized as dynamic entities that change through time, and the population size at the time of the first reliable estimate may not be ideal. In fact, especially with large carnivores, the “ideal” population size will change through time with changes in environment and human attitudes towards these species. The ability to track these changes with a degree of certainty provides us with tools to possibly reach that elusive ideal—to preserve a certain biodiversity component while addressing the needs and concerns of the people that share its landscape.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Genetic material from bear mortality was obtained according to the annual decree by the Ministry of the Environment of the Republic of Slovenia through the official institution in charge of brown bear monitoring, Slovenia Forest Service. No live animals were handled or harmed for the purpose of this research.

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