Estimating abundance of a recovering transboundary brown bear population with capture-recapture models

Cécile Vanpé[1], Blaise Piédallu[2], Pierre-Yves Quenette[1], Jérôme Sentilles[1], Guillaume Queney[3], Santiago Palazón[4], Ivan Afonso Jordana[5], Ramón Jato[6], Miguel Mari Elósegui Irurtia[7], Jordi Solà de la Torre[8], Olivier Gimenez[2]

1 Equipe Ours, Office Français de la Biodiversité, Impasse de la Chapelle, 31800 Villeneuve-de-Rivière, France

2 CEFE, Univ. Montpellier, CNRS, Univ. Paul Valéry Montpellier 3, EPHE, IRD, Montpellier, France

3 ANTAGENE, 6 allée du Levant, 69890 La Tour de Salvagny, France

4 Fauna and Flora Service, Department of Territory and Sustainability, Dr. Roux, 80. 08017 Barcelona, Spain

5 Medi Ambient, Conselh Generau d'Aran, Plaça dera Libertat, 16, 25530 Vielha, Spain

6 Departamento de Producción y Asistencias Técnicas, Sociedad Aragonesa de Getión Agroambiental, S. L. U., Ctra HUV-Fornillos, 22195 Fornillos de Apiés, Huesca, Spain

7 Servicio de Biodiversidad, Sección de Espacios Naturales y Especies Amenazadas, Gobierno de Navarra-Nafarroako Gobernua, Pamplona-Iruñea, Spain

8 Unitat de Fauna, Departament de Medi Ambient, C/ Prat de la Creu 62-64, AD500 Andorra la Vella, Principality of Andorra

Correspondence: Cécile Vanpé, Equipe Ours - Office Français de la Biodiversité, Impasse de la Chapelle, 31800 Villeneuve-de-Rivière, France. Email : cecile.vanpe@ofb.gouv.fr

Short title: Abundance of the Pyrenean brown bear population

Abstract

Abundance of small populations of large mammals may be assessed using complete counts of the different individuals detected over a time period, so-called minimum detected size (MDS). However, as population is growing larger and its distribution is expanding wider, the risk of under-estimating population size using MDS is increasing sharply due to the rarely fulfilled assumption of perfect detection of all individuals of the population, and as a result, the need to report uncertainty in population size estimates becomes crucial. We addressed these issues within the framework of the monitoring of the critically endangered Pyrenean brown bear population that was on the edge of extinction in the mid-1990s with only five individuals remaining, but was reinforced by 11 bears originated from Slovenia since then. We used Pollock's closed robust design (PCRD) capture-recapture models applied to the cross-border non-invasive sampling data from France, Spain and Andorra to provide the first published annual abundance estimates of the Pyrenean brown bear population and its trends over time. Annual population size increased and displayed a fivefold rise between 2008 and 2020, reaching > 60 individuals in 2020. Detection heterogeneity among individuals may stem from intraspecific home range size disparities making it more likely to find signs of individuals who move more. We found a lower survival rate in cubs than in adults and subadults, since the formers suffer from more mortality risks (such as infanticides, predations, mother death or abandonments) than the latters. Our study provides evidence that the PCRD capture-recapture modelling approach can provide reliable estimates of the size of and trend in large mammal populations, while minimizing bias due to inter-individual heterogeneity in detection probabilities and allowing the quantification of sampling uncertainty surrounding these estimates. Such information is vital for informing management decision-making and assessing population conservation status.

Keywords: abundance estimation, capture-recapture models, non-invasive monitoring, Pyrenees, *Ursus arctos*

Introduction

Estimating accurately and precisely animal population size and its trend over time is essential to monitor conservation status and to inform management decision-making (Nichols & Williams 2006). However, when animals are rare, elusive, solitary, largely nocturnal, highly mobile, and/or inhabiting wide home range in remote and/or rugged habitats (such as most large carnivores), population monitoring can be particularly challenging (Thompson 2013). Invasive physical tagging-based methods are almost impossible and population monitoring thus often relies on non-invasive sampling methods such as molecular tools or camera trapping (Long et al. 2008; Thompson 2013). For species lacking unique natural individual patterns, non-invasive genotyping of DNA extracted from animal hair or scat often remains the sole practical solution (Waits & Paetkau 2005).

Abundance of small populations of large mammals may be assessed using censuses or complete counts of the different individuals detected over a time period (Wilson & Delahay 2001; Keating et al. 2002) – so-called minimum detected size (MDS). In the case of genetic identification, MDS is then defined as the number of unique genotypes identified among the genetic samples inside the study area (e.g., Creel et al. 2003; Solberg et al. 2006). However, MDS are often expensive, time consuming, and logistically demanding (Blanc et al. 2013). In addition, as population is growing larger and distribution is expanding wider, the risk of under-estimating population size using MDS is increasing sharply due to the rarely fulfilled assumption of perfect detection of all individuals of the population (Solberg et al. 2006), and the need to report uncertainty in population estimates becomes crucial (e.g., Forney 2000; McGowan, Runge & Larson 2011). To address these issues, capture-recapture (CR) surveys are often used to estimate population abundance while accounting for the impossibility to detect exhaustively all individuals in a population (Otis et al. 1978). While originally limited to live-trapping studies, CR models have been specifically adapted for use with non-invasive DNA-based sampling, which implies individual identification errors due to genotyping errors, uncertainty in the date of individual detection, and possibility of collecting

multiple samples of the same individual across space within a single sampling occasion (Lukacs 2005; Lukacs & Burnham 2005).

In standard closed-population CR models, the population is assumed to be closed to changes in abundance both geographically (no immigration nor emigration) and demographically (no births nor deaths) and all individuals are supposed to have identical detection probabilities whatever their individual attributes (e.g., age, body mass, social status) and habitat features (home-range location and composition) (Otis et al. 1978). But these conditions are rarely fulfilled in real populations of wild mammals. For the last decades, considerable advances to these standard models have been developed to help alleviate issues linked to closure violation and detection-probability heterogeneity (see a review by Lukacs & Burnham 2005). In particular, the Pollock's closed robust design CR modelling (PCRD; Kendall, Nichols & Hines 1997) was developed in a maximum-likelihood framework to study survival, temporary emigration, and animal abundance while minimizing bias due to heterogeneity in detection probabilities among individuals. PCRD models were also formulated in a Bayesian framework (Schofield & Barker 2011; Rankin et al. 2016), offering several advantages over the Frequentist approach, including improved estimation under low sample sizes and use of prior information. However, this is only for the few last years that the Bayesian implementation of PCRD models has been made possible without ecologists having to code themselves custom-made complex sampling algorithms (Rankin et al. 2016; Riecke et al. 2018).

In the Pyrenees Mountains at the border of France, Spain and Andorra, the brown bear (*Ursus arctos*) population, after decades of persecution, was on the edge of extinction in the mid-90s with only five relict individuals remaining (Taberlet et al. 1997). Since then, the successful translocation of 11 bears originating from Slovenia (Quenette et al. 2019) has allowed the population to demographically recover slowly. However, the fate of this critically endangered population (UICN France et al. 2017), isolated from the nearest Cantabrian brown bear population by about 300 km, is still uncertain (Le Maho et al. 2013) with a MDS estimated at 64 individuals in 2020 (Sentilles et al. 2021a) and a high consanguinity rate (Beaumelle 2016; Bassi 2021). In this context, implementing

reliable methods to accurately estimate annual population abundance and its trend over time is crucial to monitor the conservation status of this brown bear population threatened with extinction and implement successful management plans.

Monitoring of the Pyrenean brown bear population relies on non-invasive sampling of all bear presence signs collected in the Pyrenees, either opportunistically (i.e. collection of bear data or samples by any mountain users with no specific sampling design) or using a systematic sampling approach (i.e. specific planned operations following a standardized procedure) (Sentilles et al. 2021a; Sentilles, Vanpé & Quenette 2021). Importantly, as many large carnivore populations in Europe (e.g., Bischof, Brøseth & Gimenez 2016), the Pyrenean brown bear population is transboundary and occupies a highly politically and administratively fragmented landscape, ranging across two administrative regions, divided in six different counties in France, and three autonomous regions and one county with specific autonomous status in Spain (Fig. 1). As such, cross-border multi-scale population monitoring cooperation is implemented to avoid population size overestimation, due to individuals with home range overlapping borders detected in several political jurisdictions (Bischof et al. 2016; Gervasi et al. 2016).

The aim of this study was to use cross-border non-invasive sampling data collected from 2008 to 2020 in France, Spain and Andorra and for which individual identification was possible through genetic analyses or visual evidence to provide the first published estimates of annual abundance of the Pyrenean brown bear population, based on a robust-design CR modelling approach.

Material and Methods

Brown bear biology

The brown bear is part of the few species among members of the Carnivora order with an omnivorous diet (Wroe & Milne 2007). In the Pyrenees, 70 to 80% of the diet are composed of plants (including bilberries, cranberries, nuts, acorns, beechnuts, raspberries, ferns, sorbs, apples

and rosehips), and 20 to 30% are of animal origin (mainly ant larvae, bee broods, carrion, small mammals, wild and domestic ungulates) (Couturier 1954). Mating occurs in May-June, births (with litter size ranging from 1 to 3 cubs and interbirth interval being most frequently 2 years) from January to March, and hibernation between November and March (Chapron et al. 2003). Cubs remain with their mother generally for 1.4 years, but in some rare cases for 2.4 years, before dispersing (Swenson et al. 2000). Brown bears are mostly solitary animals (except for females accompanied by their cubs and rutting period), with a promiscuous mating system (Schwartz et al. 2003). Males have larger home ranges than females, with possibilities of both intra- and inter-sexually overlap (Dahle & Swenson 2003). Dispersal is sex-biased towards males, with philopatric females establishing their home ranges in or adjacent to their mothers' home ranges (Støen et al. 2005). In Europe, female and male brown bears reach sexual maturity between 3.5 to 5 years old (Chapron et al. 2003).

Brown bear population monitoring and sign collection

This study was carried out in the Pyrenees Mountains in South-Western Europe, where the cross-border population of brown bears is present in the major part of the mountain range in France, Spain and Andorra and ranges over > 10,000 km² in 2020 (Sentilles et al. 2021a; Fig. 1).

Four different non-invasive methods were used to monitor the brown bear population in the Pyrenees over the study period from 2008 to 2020 (Table S1):

- Systematic by trails (ST) corresponded to walking transects (from 8 to 10 km long), spread homogeneously over the area of known, regular bear presence, which covers about 3,000 km² in France (Sentilles et al. 2021a; Vanpé et al. 2021). These transects were surveyed ten times (at least once per month) between May and November each year in search of bear signs. Trails were set in function of available bear habitats and passage areas detected using VHF and GPS collars or bear presence signs. Transect staff accompanied occasionally by a scat detection dog (Sentilles et al.

2021b) searched for bear hair and scats on trails and in their immediate surroundings. To improve the chances of getting hair samples, between five and seven hair traps were scattered along each itinerary. Each hair trap consisted in three small barbed wires fixed at three different heights onto the tree and where an attractive product (i.e. turpentine until 2016, smola since 2017) was applied to encourage bear rubbing behaviour. Some of these hair traps were associated with a facing camera trap (similar to the systematic by camera traps method) to help detecting females with cubs and assessing the age class and number of individuals that rubbed on the focused tree as well as the date of hair deposition.

- Systematic by baited hair traps (SBHT) (only from 2008 to 2011) corresponded to enclosures of about 20-30 m² delimited by a strand of barbed wire fixed at a height of 50 cm and stretched around several trees. Bait consisting in about 1-L mixture of rotten blood and fish was poured into the center of the area with a reward consisting in corn grains to increase recapture probability (see Woods et al. 1999; Castro Arrellano et al. 2008; Gervasi et al. 2010). We used a 4 x 4 km grid cell size on the known female range area and a 8 x 8 km grid cell size on the remaining part of the study area and placed one baited station on each grid cell. The trapping grid was established following designs and guidelines outlined in previous DNA-based inventories in North America (Mowat & Strobeck 2000; Boulanger et al. 2002) and considering the average home ranges of bears in the Pyrenees. Hair traps were placed in the best predicted bear habitat, considering topography and accessibility by 4-wheel drive vehicles, a maximum of 10 min walk from vehicle and taking into account bear expert opinion. Sites were visited once every 15 days from May to September for sample collection and lure replacement.

- Systematic by camera traps (SCT) corresponded to automatic triggered cameras (essentially Leaf river Outdoor, HCO Soutguard SG 550 and Uway Nicht Trakker until 2013, and Bushnell Trophy Cam or NatureView HD and Reconyx HC600 or XR6 after 2013) equipped with movement detection that were fixed on trees in areas with frequent animal passages outside the walking transects and that were associated closed by with hair traps similar to the ones used for the

systematic by trails method. Each camera trap - hair trap station was visited once per month from April to November each year. We used a 4 x 4 km grid cell size on the known female range area and a 8 x 8 km grid cell size on the remaining part of the study area and placed one camera trap - hair trap station per cell. When hair samples could non-ambiguously be associated with photographs or videos, we analysed collected pictures in an attempt to individually identify bears based on natural (e.g., coat marks) or artificial (ear tags, radio-collars) marks, in order to avoid genetic analyses and decrease sampling costs.

- Opportunistic monitoring (OM) corresponded to the opportunistic collection (with no specific sampling design) throughout the bear potential range (covering > 10,000 km²) of all bear presence signs (such as hair, scats, tracks, scratches, eating clues, visual observations…) gathered by various mountain users, as well as all putative bear damages on livestock and beehives, after examination and approval of an expert agent (De Barba et al. 2010). Since 2014, verification of testimonies and damage reports have been occasionnaly carried out with the help of a scat-detection dog trained to search for brown bear scats (Sentilles et al. 2021b). Only hair and scat samples collected during the same period as the systematic monitoring were included in this study.

While all the four monitoring methods (ST, SBHT, SCT, OM) were used in France, brown bear monitoring consisted in the ST method combined with OM in Catalonia and Andorra, and in OM only in Aragon and Navarra. Although few individuals (mostly translocated animals and problematic bears) were temporally equipped with either VHF and/or GPS collars or ear tags over the study period, we focused here on the sole non-invasive sampling data. We paid a particular attention to evaluate the date when the signs were left by the bears and discarded any sign for which uncertainty in this date was too high to define precisely which month the bear was present (see Supplementary Materials).

Individual identification of bear signs

We used all validated non-invasive brown bear signs collected in the Pyrenees from 2008 to 2020 and for which individual identification was possible. Individual identification of bears was mainly based on genetic analyses of hair (stored dry in envelops) and scats (stored in microtubes filled with 96% ethanol) non-invasively collected in the field, as well as visual evidence (colouration, scars, GPS collars, or VHF ear tag transmitters) obtained by remote cameras (Sentilles et al. 2021b). This study complies with the standards, laws and procedures concerning animal research ethics of the countries, in which it was performed.

Genetic samples were analyzed at LECA-CNRS laboratory from 2008 to 2012 using a multiple-tubes Polymerase Chain Reaction (PCR) approach (Taberlet et al. 1997) and from 2013 to 2016 using high-throughput microsatellite genotyping on an Illumina platform (De Barba et al. 2017). From 2017 to 2020, samples were analyzed in our laboratory (see Supplementary information for method details). In all cases, a minimum of four repeats for each sample was carried out to avoid genotyping errors associated with low quantities of DNA (Miquel et al. 2006). A total of 13 microsatellites markers and one (for LECA-CNRS) to three (for our laboratory) sex markers targeting were targeted by the multiplex PCR in order to identify the bear individuals and assign gender (De Barba et al. 2017 and Supplementary information). Further information on genotyping error rate and probabilities of identity-by-descent can be found in De Barba et al. (2017), Beaumelle (2017), Bassi (2021) and Table S2.

Population abundance estimation using capture-recapture models

The results from all sources of individual identifications (genetic analyses and tracking of natural or artificial marks) of all bear signs for which the month when bear left the sign was known were then aggregated to compile the monthly detection history of each bear of the population through time from 2008 to 2020 (see Supplementary Materials).

We used the PCRD model (Kendall et al. 1997) to estimate population abundance while accounting for imperfect detection of individuals and temporary absence of some individuals from a sampling site (e.g., individuals may temporarily emigrate to areas where foraging conditions or breeding success are better or may be temporarily unavailable for capture because they are dormant, in torpor, or hibernate; Henle & Gruber 2017). PCRD models use a hierarchical sampling strategy, including widely-spaced "primary occasions," between which the population is considered as open (i.e. with births, deaths and temporary emigration), and repeated captures in a short timeframe (called "secondary occasions") between which the population is assumed to be closed to population changes. The population was assumed geographically closed, i.e. no emigration or immigration could occur between this population and another one outside the Pyrenees. We used years from 2008 to 2020 as primary occasions of capture (N = 13) and months from May to September as secondary occasions (N = 5), that is 65 occasions of capture in total. We chose these secondary occasions because no births occur in this time interval. We excluded months from October to April because of low activity of bears during hibernation and high mortality risks of cubs of the year during their first months of life (bear cubs are born in the den during January-February).

We used a classical frequentist approach to explore effects on survival, detection and temporary emigration structure. We fitted 24 different models in total, with four detection structures (constant, time-dependent considering variation between and within primary occasions and heterogeneous using finite mixtures), two survival structures (constant and age-dependent using three age classes: i.e. cubs < 2 year old, subadults = 2-3 years old and adults > 3 years old) and three emigration structures (constant, random and Markovian). We used the Akaike Information Criterion corrected for small sample size (AICc) to perform model selection (Burnham & Anderson 2002). These analyses were performed with the 'RMark' package (Laake 2013) that allows calling the Mark program (White & Burnham 1999) from R software (RCoreTeam 2013). Because we run into boundary estimates issues, we used a Bayesian approach to estimate annual population abundance, relying on the best supported model from the frequentist approach. These analyses were performed

using program Jags (Plummer 2003; and Riecke et al. 2018 for PCRD models in particular). Data and codes are available at https://github.com/oliviergimenez/pyrenean-brown-bear-abundance.

Results

Individual identification

From 2008 to 2020, we had in total 10,019 validated brown bear signs collected in the whole Pyrenees year-round. Among the 2,524 hair and scat samples, which were sent to genetic analyses in France over this period, 1,648 (about 65%) allowed individual identification. From 2008 to 2020, 98 different individuals (44 females, 41 males and 13 individuals with undetermined sex) were identified in the whole Pyrenees from May to September.

Model selection

The two top ranked models best supported by the data (with ΔAICc < 2) among the 24 fitted models both included age-dependent survival, heterogeneous detection and either random or Markovian emigration effects (Table 1). All other models had much higher AICc (ΔAICc > 6; Table 1). Survival estimates of cubs, subadults and adults were around 84%, 95% and 96%, respectively for both top ranked models (Table 2). Regarding the heterogeneous detection, 0.72 of individuals had a low detection probability of 42%, whereas 0.28 of individuals had a high detectable probability of 85% (Table 2). The probability of leaving the study area was <10% for both models, whereas the probability of remaining outside the study area was about 22% (Table 2).

Abundance estimation

Based on the best-supported model from the frequentist analysis (Table 2), Bayesian PCRD estimates of the Pyrenean brown bear population ranged from 13.0 with 95% credible interval =

[12.8, 13.3] in 2008 to 66.2 with 95% credible interval = [64.8, 67.8] in 2020 (Table 4), displaying a fivefold rise between the beginning and the end of the study (Fig. 2).

Discussion

Based on the combination of non-invasive genetic sampling of hair and scats and corresponding track size data, the Pyrenean brown bear population was shown to be composed at least of five individuals in 1995, indicating that population was then at the edge of extinction (Taberlet et al. 1997). To preserve the remaining Pyrenean gene pool and increase genetic diversity, the translocation of a total of 11 bears originating from Slovenia was performed from 1996 to 2018 (Quenette et al. 2019). To assess the effectiveness of these conservation efforts and the current conservation status of the Pyrenean brown bear population, it is important to evaluate how the population size has evolved since the first translocations. We used PCRD models applied to the cross-border non-invasive sampling data from France, Spain and Andorra to provide the first published annual abundance estimates of the critically endangered Pyrenean brown bear population and its trends over time from 2008 to 2020 since the first translocations that occurred in 1996. Our results suggest that annual size of the Pyrenean brown bear population increased and displayed a fivefold rise between 2008 and 2020, reaching > 60 individuals in 2020.

To date, the size of the Pyrenean brown bear population was annually estimated using the MDS index, defined as the minimum number of different individuals detected inside the study area over the year (Table S4). This method assumes that all individuals present in the population have a detection probability of one. Because the population size was so far very small compared to the intensive sampling effort (Table S1), the number of undetected individuals was considered each year as very small. As the population was assumed geographically closed, the MDS of the current year was used every year to correct the MDS of previous years (e.g., to add bears which were not detected the previous years but detect the current year) and defined what we called the Minimum

Retained Size (MRS; Sentilles et al. 2021a,b). MRS thus corresponded to a reassessment of the MDS in the light of the information newly collected in the following years. However, note that MRS estimation can be subject to sampling bias if some specific individual types (e.g., more detectable individuals or individuals still alive) are more prone to be detected a posteriori. While from 2008 to 2016, the MRS and MDS of the Pyrenean brown bear population remained very close from each other (mean difference ± SD = 0.9 ± 1.5), the difference between the two estimates becomes much larger from 2017 to 2020 (mean difference ± SD = 7.3 ± 3.2; Table S4 and Fig. 2). This suggests that the size and distribution range of the Pyrenean brown bear population have now reached a point that we cannot anymore neglect the risk of failing at detecting all individuals of the population over a year using MDS, especially for years, during which a limited number of samples can be sent to genetic analyses due to funding restrictions (such as in 2017 and 2018; see Table S1 for details). Consequently, it becomes crucial for the monitoring of the Pyrenean brown bear population to estimate population size using a method that account for individual heterogeneity in detection probabilities and to report uncertainty on estimates. This is why implementing a new reliable method of estimation of annual population abundance combining capture-recapture modelling and non-invasive sampling was particularly relevant for our study population at this stage.

Differences between PCRD estimates of the annual abundance of the Pyrenean brown bear population and MRS or MDS values were relatively small (mean difference ± SD = -3.79 ± 3.77 and -1.02 ± 2.27, respectively), with PCRD estimates being either higher or smaller than MDS and MRS values depending on the year. Those differences could be explained by the fact that our PCRD framework includes temporary emigration, which means that a bear that is not found during an entire year will not be included in the total population size. Moreover, to use the PCRD framework, we excluded signs that were difficult to date, and those that fell outside of the secondary occasions (May to September), which left some individuals identified by MDS and MRS out of our database. Furthermore, MDS and MRS estimates performed so far always included the individuals that were

found dead in their yearly counts, while a PCRD model would only include them if the death occurred after the end of the primary occasion from October to December.

The model selection results highlighted two classes of individuals with significantly different detection probabilities (Table 2). A previous study on wolves highlighted the importance of accounting for individual heterogeneity in detection when estimating abundance of large carnivore populations (Cubaynes et al. 2010). Heterogeneity in the Pyrenean brown bears might stem from intraspecific home range disparities (McLoughlin, Ferguson & Messier 2000) making it more likely to find signs of individuals who move a lot, as well as from the fact that few bears were more easily visually identified due to their specific natural and/or artificial marks. The four individuals with long detection history (N > 20 occasions) that were detected more frequently over the study period were all big males with particularly large home ranges: Néré (detected at 61 of the 65 occasions during which it was present), Pyros (detected at 41 of the 45 occasions during which it was present), Goiat (detected at 22 of the 24 occasions during which it was present) and Balou (detected at 28 of the 32 occasions during which it was present). Another factor that might have caused heterogeneity is the efficiency of human agents when looking for bear signs. Some Pyrenean bears (e.g., dominant adult males and few adult females such as Caramelles and Nheu) displayed a stable spatial behavior over the years (Camarra et al. 2015), making their movements predictable in time and allowing the agents to become better at finding their signs (Fagen & Fagen 1996). Extending our approach to spatial capture-recapture models that account for individual heterogeneity in the detection process by estimating individual-specific activity could help alleviating those issues.

We found an age-dependent effect on survival, with cubs surviving less well (84%) than subadults (95%) and adults (96%; Table 2). These results are consistent with previous estimates from Chapron et al. (2009) in the same population (0.77 ± 0.11 for cubs, 0.90 ± 0.09 for yearlings, 1.00 for sub-adults, and 0.97 ± 0.03 for adults in the Central sub-population between 1993 and 2005). The lower survival rate in cubs compared to other age classes was expected, since cubs are known to suffer from many mortality risks such as infanticides, predations, mother death or

abandonments (Bunnell & Tait 1985) during their first year of life. These mortality risks are not restricted to their first four or five months of life (which were excluded from our analyses as we considered months from May to September as secondary occasions) but can also occur after April during late spring and summer.

The outputs of demographic analyses of the Pyrenean brown bear population are used to inform management decision-making and policies (e.g., regulation, reinforcements, compensation). In this context, the reporting of abundance estimates and trends can be particularly prone to political influence (Darimont et al. 2018) and stakeholder skepticism. Therefore, implementing sound population monitoring tools and robust statistical methods to convey the uncertainty associated to abundance estimates is crucial. Our results suggest that annual size of the Pyrenean brown bear population displayed a fivefold rise between 2008 and 2020, reaching > 60 individuals in 2020. This increase is mainly due to translocations of bears originated from Slovenia (1 male in 2016 and 2 females in 2018) combined with regular reproduction events during the study period (Sentilles et al. 2021b). While this is encouraging for the short-term viability of the population, the fate of this critically endangered population (UICN France et al. 2017) is still uncertain due to high consanguinity, geographic isolation, fragmentation and small population size, which makes it particularly vulnerable to demographic, environmental and genetic aleas (Chapron et al. 2009; Le Maho et al. 2013; Beaumelle 2016).

Although the number of individuals within a population is commonly considered as a fundamental ecological indicator, the trend in population abundance can be a poor predictor of population viability, especially when strong inbreeding occurs and total population size is much higher than the effective population size, as it is the case in the Pyrenean brown bear population (Beaumelle 2016; Bassi 2021). Brown bear females in Europe usually start reproducing at the age of four or five with an interbirth interval of at least two years (Schwartz et al. 2003, Swenson et al. 2007). Therefore, to improve the assessment of the conservation status and of the demo-genetic viability of this critically endangered population, using a set of indicators by monitoring the annual

number of females with cubs of the year (e.g., Palomero et al. 2007), the annual total number of ≥4-year-old females in the population, or the effective population size (Frankham 1995; Bassi 2021), in addition to PCRD estimates of the total population abundance, would be particularly relevant (Beissinger & Westphal 1998).

Our study provides evidence that the PCRD capture-recapture approach provides reliable estimates of the size of and trend in large mammal populations, while minimizing bias due to inter-individual heterogeneity in detection probabilities and quantifying sampling uncertainty surrounding these estimates. Such information is vital for informing management decision-making and assessing population conservation status. We recommend for monitoring the size of the Pyrenean brown bear population using this PCRD capture-recapture modelling approach in place of the former MDS metric, which increasingly failed over the last few years to detect all individuals of the population.

Acknowledgements

We would like to acknowledge all field co-workers from the Brown Bear Network (ROB) and from Spanish and Andorran teams. Financial and logistical support for this study was provided by the ONCFS / OFB in France. OG was supported by a grant from 'Mission pour l'interdisciplinarité' of CNRS, through its 'Osez l'interdisciplinarité' call.

References

Bassi, C. (2021). *Etude de la taille efficace et de la diversité génétique de la population d'ours brun, Ursus arctos, des Pyrénées.* Rapport de stage de Master 2e année, Université Aix-Marseille, France.

Beaumelle, C. (2016). *Evolution génétique et généalogie de la population des ours bruns (Ursus arctos) dans les Pyrénées.* Rapport de stage de Master 1ere année, Université Grenoble Alpes, France.

Beissinger, S.R. & Westphal, I. (1998). On the use of demographic models of population viability in endangered species management. *J. Wildl. Manag.* 62, 821-841.

Bischof, R., Brøseth, H. & Gimenez, O. (2016). Wildlife in a politically divided world: Insularism inflates estimates of brown bear abundance. *Conserv. Lett.* 9, 122-130.

Blanc, L., Marboutin, E., Gatti, S. & Gimenez, O. (2013). Abundance of rare and elusive species: empirical investigation of closed versus spatially explicit capture–recapture models with lynx as a case study. *J. Wildl. Manag.* 77(2), 372-378.

Boulanger, J., White, G.C., McLellan, B.N., Woods, J., Proctor, M. & Himmer, S. (2002). A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia, Canada. *Ursus* 137-152.

Bunnell, F.L. & Tait, D.E.N. (1985). Mortality rates of North American bears. *Arctic* 38, 316-323

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.* 2nd edition. New York: Springer-Verlag.

Camarra, J.J., Sentilles, J., Bombillon, N., Gastineau, A. & Quenette, P.Y. (2015). *Suivi de l'ours brun dans les Pyrénées françaises (Sous-populations occidentale et centrale) - Rapport annuel, Année 2015.* Vincennes, France: Office National de la Chasse et de la Faune Sauvage.

Castro□Arellano, I., Madrid□Luna, C., Lacher Jr, T. E. & Léon□Paniagua, L. (2008). Hair□trap efficacy for detecting mammalian carnivores in the tropics. *J. Wildl. Manag.* 72(6), 1405-1412.

Chapron, G., Quenette, P.Y., Legendre, S. & Clobert, J. (2003). Which future for the French Pyrenean brown bear (*Ursus arctos*) population? An approach using stage-structured deterministic and stochastic models. *C. R. Biol.* 326, 174-182.

Chapron, G., Wielgus, R., Quenette, P.Y. & Camarra, J.J. (2009). Diagnosing mechanisms of decline and planning for recovery of an endangered brown bear (*Ursus arctos*) population. *PloS One* 4, e7568.

Couturier, M.A.J. (1954). *L'ours brun: Ursus arctos* L. (Vol. 1). Grenoble, France: Arthaud.

Creel, S., Spong, G., Sands, J.L., Rotella, J., Zeigle, J., Joe, L., Murphy, K.M. & Smith, D. (2003). Population size estimation in Yellowstone wolves with error□prone noninvasive microsatellite genotypes. *Mol. Ecol.* 12(7), 2003-2009.

Cubaynes, S., Pradel, R., Choquet, R., Duchamp, C., Gaillard, J.M., Lebreton, J.D., Marboutin, E., Miquel, C., Reboulet, A.M., Poillot, C., Taberlet, P. & Gimenez, O. (2010). Importance of accounting for detection heterogeneity when estimating abundance: the case of French wolves. *Conserv. Biol.* 24(2), 621-626.

Dahle, B. & Swenson, J.E. (2003). Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *J. Zool.* 260(4), 329-335.

Darimont, C.T., Paquet, P.C., Treves, A. & Artelle, K.A. (2018). Political populations of large carnivores. *Conserv. Biol.* 32(3), 747-749.

De Barba, M., Miquel, C., Lobréaux, S., Quenette, P.Y., Swenson, J.E. & Taberlet, P. (2017). High□throughput microsatellite genotyping in ecology: Improved accuracy, efficiency,

standardization and success with low quantity and degraded DNA. *Mol. Ecol. Res.* 17(3), 492-507.

De Barba, M., Waits, L.P., Garton, E.O., Genovesi, P., Randi, E., Mustoni, A. & Groff, C. (2010). The power of genetic monitoring for studying demography, ecology and genetics of a reintroduced brown bear population. *Mol. Ecol.* 19, 3938-3951.

Fagen, R. & Fagen, J.M. (1996). Individual distinctiveness in brown bears, *Ursus arctos* L. *Ethology* 102, 212-226.

Forney, K.A. (2000). Environmental models of cetacean abundance: reducing uncertainty in population trends. *Conserv. Biol.* 14(5) 1271-1286.

Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: a review. *Genet. Res.* 66(2), 95-107.

Gervasi, V., Brøseth, H., Gimenez, O., Nilsen, E. B., Odden, J., Flagstad, Ø. & Linnell, J. D. (2016). Sharing data improves monitoring of trans-boundary populations: the case of wolverines in central Scandinavia. *Wildl. Biol.* 22(3), 95-106.

Gervasi, V., Ciucci, P., Davoli, F., Boulanger, J., Boitani, L. & Randi, E. (2010). Addressing challenges in non invasive capture-recapture based estimates of small populations: a pilot study on the Apennine brown bear. *Conserv. Genet.* 11(6), 2299-2310.

Henle, K. & Gruber, B. (2018). Performance of multistate mark–recapture models for temporary emigration in the presence of survival costs. *Methods Ecol. Evol.* 9(3), 657-667.

UICN France, MNHN, SFEPM & ONCFS (2017). *La Liste rouge des espèces menacées en France – Chapitre Mammifères de France métropolitaine.* Paris, France.

Keating, K.A., Schwartz, C.C., Haroldson, M.A. & Moody, D. (2002). Estimating numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. *Ursus* 13, 161-174.

Kendall, W.L., Nichols, J.D. & Hines, J.E. (1997). Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology* 78, 563-578

Laake, J.L. (2013). *RMark: An R interface for analysis of capture-recapture data with MARK*. AFSC Processed Rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Le Maho, Y., Boitani, L., Clobert, J., Quenette, P.Y., Sarrazin, F. & Savouré-Soubelet, A. (2013). *Expertise collective scientifique « L'Ours brun dans les Pyrénées »*. Paris, France: Muséum National d'Histoire Naturelle.

Long, R.A., Zielinski, W.J., Long, R., MacKay, P., Zielinski, W. & Ray, J. (2008). Designing effective noninvasive carnivore surveys. In *Noninvasive survey methods for carnivores*: 8-44. Long, R.A., MacKay, P., Ray, J. & Zielinski, W. (Eds.). Washington, USA: Island Press.

Lukacs, P.M. (2005). *Statistical aspects of using genetic markers for individual identification in capture-recapture studies.* Ph.D. thesis, Colorado State University, USA.

Lukacs, P.M. & Burnham, K.P. (2005). Review of capture–recapture methods applicable to noninvasive genetic sampling. *Mol. Ecol.* 14(13), 3909-3919.

McGowan, C.P., Runge, M.C. & Larson, M.A. (2011). Incorporating parametric uncertainty into population viability analysis models. *Biol. Conserv.* 144(5), 1400-1408.

Mcloughlin, P.D., Ferguson, S.H. & Messier, F. (2000). Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evol. Ecol.* 14(1), 39-60.

Miquel, C., Bellemain, E., Poillot, C., Bessiere, J., Durand, A. & Taberlet, P. (2006). Quality indexes to assess the reliability of genotypes in studies using noninvasive sampling and multiple tube approach. *Mol. Ecol. Notes* 6(4), 985-988.

Mowat, G. & Strobeck, C. (2000). Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. *J. Wildl. Manag.* 183-193.

Nichols, J.D. & Williams, B.K. (2006). Monitoring for conservation. *Trends Ecol. Evol.* 21(12), 668-673.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* (62), 3-135.

Palomero, G., Ballesteros, F., Nores, C., Blanco, J.C., Herrero, J. & García-Serrano, A. (2007). Trends in number and distribution of brown bear females with cubs-of-the-year in the Cantabrian Mountains, Spain. *Ursus* 18(2), 145-157.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd international workshop on distributed statistical computing*: 1-10. Hornik, K., Leisch, F. & Zeileis, A. (Eds.). Vol. 124, No. 125.10. Vienna, Austria.

Quenette, P.Y., Jonozovic, M. & Marinsic, A., Camarra, J.J., Guinot-Ghestem, M., Sentilles, J., Steinmetzn J., Vanpé, C. & Alban, N. (2019). First translocation of females in the French Western Pyrenees: a new step in the long process of brown bear restoration in the Pyrenees Mountains. *Int. Bear News* 28, 11-13.

Rankin, R.W., Nicholson, K.E., Allen, S.J., Krützen, M., Bejder, L. & Pollock, K.H. (2016). A full-capture hierarchical Bayesian model of Pollock's Closed Robust Design and application to dolphins. *Front. Mar. Sci.* 3, 25.

RCoreTeam (2013). *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing.

Riecke, T.V., Leach, A.G., Gibson, D. & Sedinger, J.S. (2018). Parameterizing the robust design in the BUGS language: Lifetime carry□over effects of environmental conditions during growth on a long□lived bird. *Methods Ecol. Evol.* 9(11), 2294-2305.

Schofield, M.R. & Barker, R.J. (2011). Full open population capture–recapture models with individual covariates. *J. Agric. Biol. Environ. Stat.* 16(2), 253-268.

Schwartz, C.C., Keating, K.A., Reynolds III, H.V., Barnes Jr, V.G., Sellers, R.A., Swenson, J.E., Miller, S.D., McLellan, B.N., Keay, J., McCann, R., Gibeau, M., Wakkenin, W.F., Mace, R. D., Kasworm, W. & Smith, R. (2003). Reproductive maturation and senescence in the female brown bear. *Ursus* 109-119.

Sentilles J., Lemaître P.L., Vanpé C. & Quenette P.Y. (2021a). *Rapport annuel du réseau ours brun 2020*. Paris, France: Office Français de la Biodiversité.

Sentilles, J., Vanpé, C. & Quenette, P.Y. (2021b). Benefits of incorporating a scat-detection dog into wildlife monitoring: a case study of Pyrenean brown bear. *J. Vertebr. Biol.* 69(3), 20096-1.

Solberg, K.H., Bellemain, E., Drageset, O.M., Taberlet, P. & Swenson, J.E. (2006). An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. *Biol. Conserv.* 128(2), 158-168.

Støen, O.G., Bellemain, E., Sæbø, S. & Swenson, J.E. (2005). Kin-related spatial structure in brown bears Ursus arctos. *Behav. Ecol. Sociobiol.* 59(2), 191-197.

Swenson, J.E., Adamič, M., Huber, D. & Stokke, S. (2007). Brown bear body mass and growth in northern and southern Europe. *Oecologia* 153(1), 37-47.

Swenson, J.E., Gerstl, N., Dahle, B. & Zedrosser, A. (2000). Action plan for the conservation of the brown bear (*Ursus arctos*) in Europe. *Nat. Environ.* 114, 1-69.

Taberlet, P., Camarra, J.J., Griffin, S., Uhres, E., Hanotte, O., Waits, L.P., Dubois-Paganon, C., Burke, T. & Bouvet, J. (1997). Noninvasive genetic tracking of the endangered Pyrenean brown bear population. *Mol. Ecol.* 6(9), 869-876.

Thompson, W. (2013). *Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters.* Washington, D.C., USA: Island Press.

Vanpé, C., Sentilles, J., Lemaître, P.L., Desbarax, R., Bibal, D., Darmani, G., Labal, P. & Quenette, P.Y. (2021). *Cartographie quinquennale (2016-2020) de l'aire de répartition de l'ours brun dans les Pyrénées françaises.* Vincennes, France: Office Français de la Biodiversité.

Waits, L.P. & Paetkau, D. (2005). Noninvasive genetic sampling tools for wildlife biologists: a review of applications and recommendations for accurate data collection. *J. Wildl. Manag.* 69(4), 1419-1433.

White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird study* 46(sup1), S120-S139.

Wilson, G.J. & Delahay, R.J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildl. Res.* 28(2), 151-164.

Woods, J.G., Paetkau, D., Lewis, D., McLellan, B.N., Proctor, M. & Strobeck, C. (1999). Genetic tagging of free-ranging black and brown bears. *Wildl. Soc. Bull.* 616-627.

Wroe, S. & Milne, N. (2007). Convergence and remarkably consistent constraint in the evolution of carnivore skull shape. *Evol. Int. J. Org. Evol.* 61(5), 1251-1260.

Figure captions

Figure 1. Map of the transboundary range area (on squares of 10 x 10 km) of the Pyrenean brown bear population for the year 2020.

Figure 2. Variation in the annual population size of the Pyrenean brown bear from 2008 to 2020, estimated from the Bayesian Pollock's robust design capture-recapture approach (PCRD, black full circles and black full line, with the associated 97.5% credible interval in grey), compared to the Minimum Retained population Size (MRS, grey open squares and grey full line) and Minimum Detected population Size (MDS, black open circles and black dashed line) values.

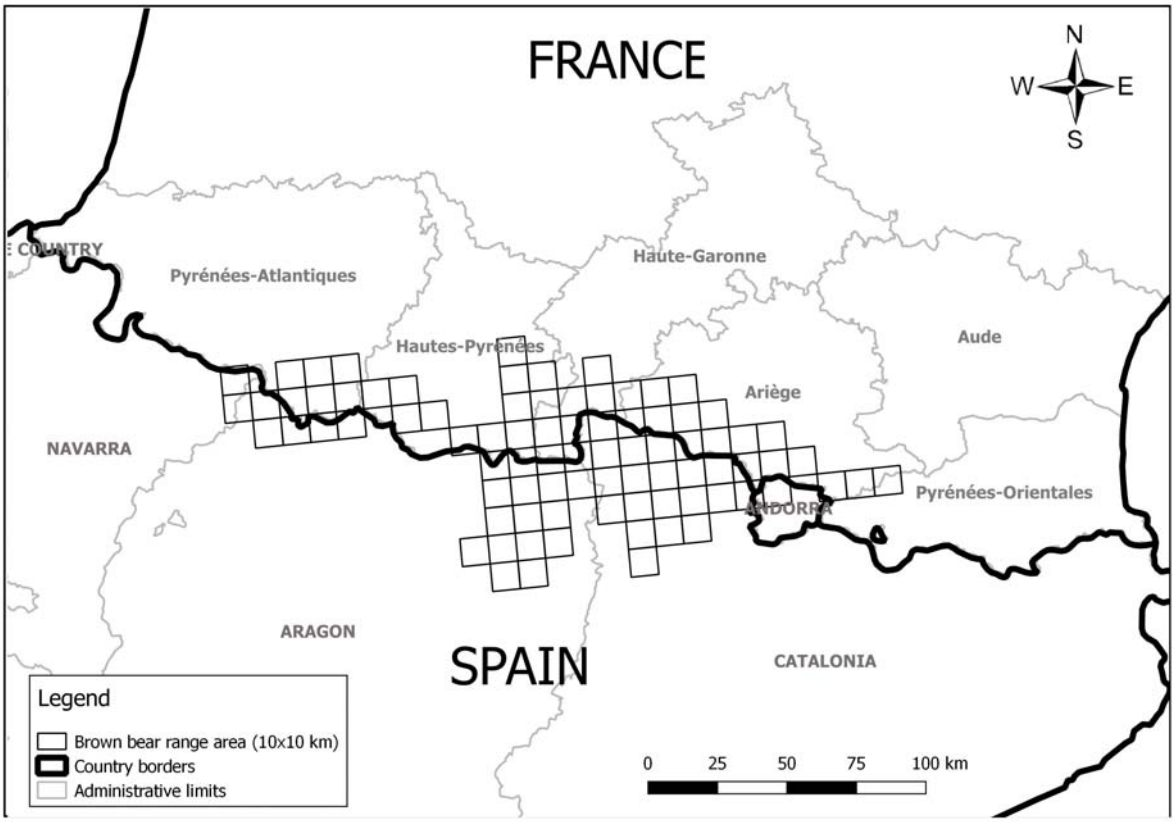
FRANCE
N
W
E
S
Pyrénées-Atlantiques
Haute-Garonne
Hautes-Pyrénées
Aude
Ariège
NAVARRA
Pyrénées-Orientales
ANDORRA
ARAGON
SPAIN
CATALONIA
Legend
Brown bear range area (10x10 km)
Country borders
Administrative limits
0
25
50
75
100 km

Figure 1.

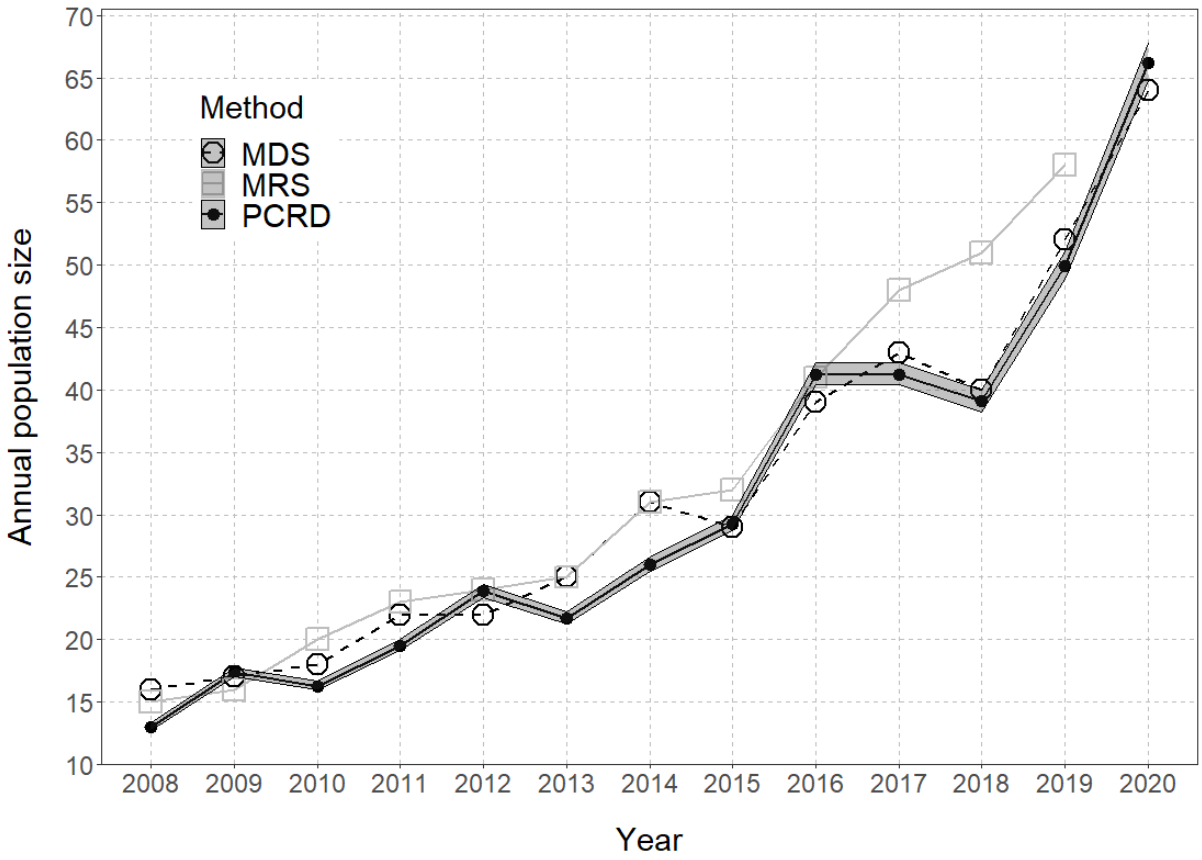
Method
MDS
MRS
PCRD
Annual population size
Year
70
65
60
55
50
45
40
35
30
25
20
15
10
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020

Figure 2.

Table 1. Model selection from the frequentist capture-recapture approach using a Pollock's robust design (PCRD) capture-recapture modelling approach.

Model	Survival structure	Detection structure	Emigration structure	AICc	ΔAICc
1	Age-dependent	Heterogeneous	Random	1496.43	0.00
2	Age-dependent	Heterogeneous	Markovian	1496.90	0.47
3	Constant	Heterogeneous	Random	1503.48	7.04
4	Constant	Heterogeneous	Markovian	1503.76	7.33
5	Age-dependent	Heterogeneous	No	1520.68	24.25
6	Constant	Heterogeneous	No	1528.73	32.30
7	Age-dependent	Time-dependent (within primary occasions)	Random	1548.00	51.57
8	Age-dependent	Time-dependent (between primary occasions)	Random	1548.28	51.85
9	Age-dependent	Time-dependent (between primary occasions)	Markovian	1548.58	52.14
10	Age-dependent	Time-dependent (within primary occasions)	Markovian	1549.03	52.60
11	Constant	Time-dependent (within primary occasions)	Random	1555.00	58.56
12	Constant	Time-dependent (between primary occasions)	Random	1555.31	58.87
13	Constant	Time-dependent (between primary occasions)	Markovian	1555.41	58.98
14	Constant	Time-dependent (within primary occasions)	Markovian	1555.85	59.42
15	Age-dependent	Constant	Random	1562.58	66.15
16	Age-dependent	Constant	Markovian	1562.86	66.43
17	Constant	Constant	Random	1569.64	73.21
18	Constant	Constant	Markovian	1569.73	73.30
19	Age-dependent	Time-dependent (within primary occasions)	No	1611.84	115.40
20	Constant	Time-dependent (within primary occasions)	No	1619.97	123.54
21	Age-dependent	Time-dependent (between primary occasions)	No	1625.67	129.23
22	Constant	Time-dependent (between primary occasions)	No	1634.10	137.66
23	Age-dependent	Constant	No	1637.98	141.54
24	Constant	Constant	No	1646.44	150.01

Table 2. Parameter estimates for the two best-supported models from the frequentist capture-recapture approach using a robust design, in which temporary emigration is either random or Markovian.

	Temporary emigration			
	Random		Markovian	
	Estimate	SE	Estimate	SE
Cub survival probability	0.844	0.038	0.844	0.038
Subadult survival probability	0.954	0.028	0.955	0.029
Adult survival probability	0.962	0.015	0.962	0.015
Probability of leaving the study area	0.105	0.023	-	-
Probability of leaving the study area given presence in the study area at the previous sampling occasion	-	-	0.097	0.023
Probability of leaving the study area given absence in the study area at the previous sampling occasion	-	-	0.217	0.103
Proportion of individuals in class 1 of mixture	0.722	0.053	0.723	0.053
Detection probability of class 1 individuals	0.421	0.023	0.422	0.023
Detection probability of class 2 individuals	0.850	0.034	0.850	0.034

Supplementary Information

Genetic analyses from 2017 to 2020

From 2017 to 2020, genetic analyses were conducted in our laboratory at ANTAGENE (https://www.antagene.com/en). DNA extraction was conducted according to a sterile process in a designated extraction room free of DNA. For each sample, disposable sterile tools were used and bench was cleaned with bleach to avoid cross-contamination. Each sample was transferred to a sterile labelled microtube to proceed to DNA extraction. Sample tubes were surrounded by positive and negative extraction controls and lysed overnight at 56°C according to manufacturer's instructions (Nucleospin 96 Tissue Kit, Macherey-Nagel, Düren, Germany). DNA was isolated and purified using purification columns and vacuum filtration (Nucleospin 96 Tissue Kit, Macherey-Nagel, Düren, Germany). DNA was eluted with 100 µL of elution buffer to obtain final concentrations between 20-100 ng/µl. Extracts were stored in labelled 96-tube strips plates in a -20°C freezer.

For each DNA sample, 13 microsatellites and 3 sex identification markers (ZFX, 318.2 and SMCY) were amplified by two multiplex PCRs (polymerase chain reaction) four times and analyzed in two runs (one for each multiplex) with an automated sequencer (Table S5).

PCR reactions were prepared step-by-step according to a unidirectional workflow starting in a clean room with positive air pressure to prepare sensitive reagents (enzymes and DNA primers) and continuing in a pre-PCR room for combining DNA and reagents using filtered tips. Three negative and positive controls were included per PCR reaction. PCR amplifications were then performed in a dedicated post-PCR area in 96-well microplates at 10 µl final volumes containing 5 µl of mastermix Taq Polymerase (Type-It Microsatellite PCR Kit, Qiagen, Hilden, Germany), and either 0.80 µL of a first pool of 8 pairs of primers or 0.36 µl of a second pool of 8 pairs of primers at a concentration from 0.08 to 0.60 µM each, and a mean of 30 ng of genomic DNA (Table S5). Each pair of primers was coupled with a fluorescent dye (Table S5). Our PCR thermal protocol consisted of 95°C for 15

min, followed by 8 touchdown cycles of 95°C for 30 s, 62°C to 55°C for 90 s (decreasing 1°C per cycle), and 72°C for 30 s, then followed by 35 cycles of 95°C for 30 s, 55°C for 90 s, and 72°C for 30 s, ending with an extension of 60°C for 30 min. PCR products were resolved on an ABI PRISM 3130 XL capillary sequencer (ThermoFisher Scientific, Waltham, Massachusetts) under denaturing conditions (Hi-DiTM Formamide, ThermoFisher Scientific, Waltham, Massachusetts) with an internal size marker prepared once and dispatched equally in all sample wells of each multiplex run. The four electropherograms for each sample were analyzed using GENEMAPPER 4.1 (ThermoFisher Scientific, Waltham, Massachusetts) and analyzed independently by two analysts to determine the allele sizes for each marker of each individual. When the genotypes determined by each analyst did not agree, the electropherograms were read again, reading errors were resolved, and in case of persistent disagreement, ambiguous results were considered as missing data.

Dating of bear signs

For photos and videos, we used the metadata from the automatically triggered camera traps or cameras to define accurately the date of bear presence. For hair collected on baited hair traps, we used photo data collected on camera traps set up in front of baited hair traps when available to identify date when hair were left. From those specific bear signs, month of bear presence could be determined accurately based on the date when signs were left.

For other types of bear signs, we could not know precisely the date when signs were left and we relied on an evaluation of the time period when sign could have been left by the bear. More specifically, when hair collected on baited hair trap were not associated with any photo or video, we considered that the bear had left the hair during the time period included between the date of the last visit of the hair trap when barbed wire was cleaned and the date of the visit when hair were collected. If this time period was larger than 2 months, we discarded the hair sample from our analyses. We also discarded hair samples collected spontaneously outside systematic monitoring

design, because the time interval during which they might have been left by the bear could not be evaluated precisely (bear hair deteriorate very slowly in the field), except in the case hair were associated with a damage on livestock or beehives, in which case the estimated date of the damage provided the estimated date of hair deposition. Finally, we estimated the time interval when scats were dropped by evaluating the freshness of the scat when collected in the field. When the time period during which hair or scat could have been left overlapped two different months, we considered as a proxy the month of the median date between maximum and minimum date of the time period as the month of bear presence, since this should not affect much our estimation of population size with capture-recapture analyses.

Compilation of monthly detection history of bears

Matching genotypes were considered to arise from the same individual and classified as recaptures as the combined non-exclusion probability of the 13 microsatellites for independent individuals and for sibships were negligeable (Lukacs & Burnham 2005). Importantly, we did not consider location data from GPS collar or VHF transmitters to compile detection history to avoid large inter-individual differences in monitoring pressure between bears. Orphan cubs that were captured in the field and kept in captivity for a while for care before being released in the wild were considered as still present and detected in the population during the months of captivity (N = 1). For individuals for which we knew the date of death (N = 9), we used this information and right censored them in the corresponding detection histories. For translocated bears originated from Slovenia (N = 3), the first month of potential detection was the month of release in the Pyrenees.

Table S1. Systematic monitoring effort in the French Pyrenees in terms of number of transects (including 6 hair traps per transect in average), total length of transects (km), number of camera traps, number of baited hair traps and number of genetically analysed samples per year between 2008 and 2020.

Year	# transects	total length of transects (km)	# camera traps	# baited hair traps	# analysed samples
2008	30	300*	7	59	125
2009	36	360*	10	73	84
2010	60	600*	12	86	167
2011	68	615	26	90	209
2012	68	615	18	0	224
2013	48	426	49	0	137
2014	50	411	39	0	193
2015	44	358	40	0	152
2016	47	376	48	0	179
2017	53	414	45	0	134
2018	57	441	45	0	158
2019	56	424	59	0	314
2020	58	428	60	0	448

Note: * Estimated based on an average transect length of 10 km. The number of analysed samples corresponds to the number of scat or hair samples (collected in France, Spain or Andorra) analysed by the French molecular laboratory (LECA or our laboratory) per year.

Table S2. Summary statistics of the 58 different genotypes found in the Pyrenean brown bear population in 2020 for each of the 13 microsatellite loci provided by the allele frequency analysis of CERVUS software (Marshall et al. 1998).

Locus	N	k	HObs	HExp	NE-I	NE-SI	PIC	F(Null)
UA03	58	4	0.655	0.622	0.215	0.495	0.549	-0.0218
UA06	58	4	0.724	0.657	0.173	0.467	0.6	-0.0653
UA14	58	4	0.759	0.705	0.144	0.437	0.645	-0.0458
UA16	58	6	0.414	0.461	0.328	0.604	0.424	0.0908
UA17	58	3	0.517	0.497	0.308	0.581	0.442	-0.0189
UA25	58	5	0.483	0.427	0.364	0.629	0.392	-0.0989
UA51	58	4	0.603	0.537	0.269	0.551	0.483	-0.0608
UA57	58	3	0.552	0.45	0.399	0.627	0.354	-0.1089
UA63	57	6	0.719	0.694	0.146	0.442	0.639	-0.0178
UA64	58	2	0.534	0.492	0.381	0.601	0.369	-0.0455
UA65	58	4	0.621	0.595	0.246	0.516	0.513	-0.0358
UA67	58	3	0.517	0.571	0.266	0.533	0.488	0.0589
UA68	58	5	0.724	0.734	0.121	0.417	0.68	-0.0054
MEAN		4.08	0.602	0.572	0.258	0.531	0.506	-0.0289

Note: N: number of individuals typed, k: the number of alleles, Hobs: observed heterozygosity, Hexp: expected heterozygosity, NE-I: average exclusion probabilities for each locus for identity, NE-SI: average exclusion probabilities for each locus for sib identity, PIC: polymorphic information content, F(Null): the frequency of null alleles. The combined non-exclusion probabilities for identity and sib identity were 9.10^{-9} and 0.000235, respectively.

Table S3. Parameters of the model, in which temporary emigration is random, survival is age-dependent survival and there is heterogeneity in the detection process, estimated using a Bayesian robust-design capture-recapture approach.

	Mean	SD	Naive SE	Time-series SE
beta[1]	8.52E-01	0.0402	0.8991	0.0014
beta[2]	9.33E-01	0.0333	0.0007	0.0009
beta[3]	9.46E-01	0.0175	0.0004	0.0004
deviance	2.31E+03	17.9349	0.4010	0.5163
gamma	6.62E-02	0.0218	0.0005	0.0006
mean.p	4.29E-01	0.0272	0.0006	0.0019
pstar[1]	8.50E-01	0.0188	0.0004	0.0009
pstar[2]	8.50E-01	0.0188	0.0004	0.0009
pstar[3]	8.50E-01	0.0188	0.0004	0.0009
pstar[4]	8.50E-01	0.0188	0.0004	0.0009
pstar[5]	8.50E-01	0.0188	0.0004	0.0009
pstar[6]	8.50E-01	0.0188	0.0004	0.0009
pstar[7]	8.50E-01	0.0188	0.0004	0.0009
pstar[8]	8.50E-01	0.0188	0.0004	0.0009
pstar[9]	8.50E-01	0.0188	0.0004	0.0009
pstar[10]	8.50E-01	0.0188	0.0004	0.0009
pstar[11]	8.50E-01	0.0188	0.0004	0.0009
pstar[12]	8.50E-01	0.0188	0.0004	0.0009
sdeps	2.10E-01	0.0214	0.0005	0.0007

Note: beta[i]: age-specific survival for age i (with 1: cubs, 2: subadults, 3: adults), gamma: probability of emigration; mean.p: mean detection probability, sdeps: SD of the random effect, pstar[j]: averaged detection over individuals for year j, with j ranging from 2008 to 2019.

Table S4. Comparison of the annual abundance of the Pyrenean brown bear population, estimated from a Bayesian Pollock's robust design (PCRD) capture-recapture approach (with associated 97.5% Credible Interval), with Minimum Detected Size (MDS, total number of different individuals detected in the population during the year) and Minimum Retained Size (MRS, reassessment of the MDS in the light of the information newly collected in the following years) values from 2008 to 2020.

Year	PCRD Estimate	97.5% CI	MDS value	MRS value
2008	13.0	12.8 - 13.3	16	15
2009	17.4	17.0 - 17.8	17	16
2010	16.3	15.9 - 16.7	18	20
2011	19.5	19.1 - 20.0	22	23
2012	23.9	23.4 - 24.4	22	24
2013	21.7	21.3 - 22.2	25	25
2014	26.0	25.5 - 26.7	31	31
2015	29.3	28.7 - 30.0	29	32
2016	41.2	40.4 - 42.2	39	41
2017	41.2	40.4 - 42.2	43	48
2018	39.1	38.3 - 40.0	40	51
2019	49.9	48.9 - 51.1	52	58
2020	66.2	64.8 - 67.8	64	NA

Table S5. Combinaison of microsatellite markers used in each PCR mix and type of fluorescent dye used for each microsatellite marker from 2017 to 2020.

Mix	Locus name	Dye	Publication
A	UA03	6FAM	De Barba *et al*. 2017
A	UA06	6FAM	De Barba *et al*. 2017
A	UA25	NED™	De Barba *et al*. 2017
A	UA67	NED™	De Barba *et al*. 2017
A	UA64	PET™	De Barba *et al*. 2017
A	UA63	PET™	De Barba *et al*. 2017
A	UA16	VIC™	De Barba *et al*. 2017
A	UA14	VIC™	De Barba *et al*. 2017
B	UA17	6FAM	De Barba *et al*. 2017
B	UA57	6FAM	De Barba *et al*. 2017
B	UA51	NED™	De Barba *et al*. 2017
B	UA65	PET™	De Barba *et al*. 2017
B	UA68	VIC™	De Barba *et al*. 2017
B	Our-ZFX	6FAM	Bidon *et al*. 2013
B	Our-318	6FAM	Bidon *et al*. 2013
B	Our-SMCY	6FAM	Bidon *et al*. 2013

De Barba, M., Miquel, C., Lobréaux, S., Quenette, P. Y., Swenson, J. E., & Taberlet, P. (2017). High-throughput microsatellite genotyping in ecology: Improved accuracy, efficiency, standardization and success with low-quantity and degraded DNA. Molecular Ecology Resources, 17(3), 492-507.

Bidon, T., Frosch, C., Eiken, H. G., Kutschera, V. E., Hagen, S. B., Aarnes, S. G., ... & Hailer, F. (2013). A sensitive and specific multiplex PCR approach for sex identification of ursine and tremarctine bears suitable for non-invasive samples. Molecular Ecology Resources, 13(3), 362-368.