Contributed Paper

Evaluating mortality rates with a novel integrated framework for nonmonogamous species

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Abstract: *The conservation of wildlife requires management based on quantitative evidence, and especially for large carnivores, unraveling cause-specific mortalities and understanding their impact on population dynamics is crucial. Acquiring this knowledge is challenging because it is difficult to obtain robust long-term data sets on endangered populations and, usually, data are collected through diverse sampling strategies. Integrated population models (IPMs) offer a way to integrate data generated through different processes. However, IPMs are female-based models that cannot account for mate availability, and this feature limits their applicability to monogamous species only. We extended classical IPMs to a two-sex framework that allows investigation of population dynamics and quantification of cause-specific mortality rates in nonmonogamous species. We illustrated our approach by simultaneously modeling different types of data from a reintroduced, unhunted brown bear (*Ursus arctos*) population living in an area with a dense human population. In a population mainly driven by adult survival, we estimated that on average 11% of cubs and 61% of adults died from human-related causes. Although the population is currently not at risk, adult survival and thus population dynamics are driven by anthropogenic mortality. Given the recent increase of human-bear conflicts in the area, removal of individuals for management purposes and through poaching may increase, reversing the positive population growth rate. Our approach can be generalized to other species affected by cause-specific mortality and will be useful to inform conservation decisions for other nonmonogamous species, such as most large carnivores, for which data are scarce and diverse and thus data integration is highly desirable.*

Keywords: hierarchical modeling, human-wildlife conflict, integrated population model, large carnivore, mortality rate, population ecology, two-sex model, *Ursus arctos*

Evaluación de las Tasas de Mortalidad bajo un Novedoso Marco de Trabajo Integrado para Especies No Monógamas

Resumen: *La conservación de la vida silvestre requiere de manejo basado en evidencia cuantitativa. Para los carnívoros, en especial, es crucial cuantificar las tasas de mortalidad por causas específicas y entender su impacto sobre las dinámicas poblacionales. Adquirir este conocimiento es un reto, ya que es complicado obtener bases de datos a largo plazo de poblaciones amenazadas y, usualmente, los datos provienen de distintas estrategias de muestreo. Los modelos de población integrados (MPIs) ofrecen una forma de integrar los datos generados por medio de procesos diferentes. Sin embargo, los MPIs son modelos basados en hembras que no tienen en cuenta de la disponibilidad de pareja y esta característica limita su aplicabilidad solamente a las especies monógamas. Extendimos los MPIs clásicos a un marco de trabajo de dos sexos que permite la investigación de las dinámicas poblacionales y la cuantificación de las tasas de mortalidad por causas*

específicas en especies no monógamas. Ilustramos nuestra estrategia modelando simultáneamente diferentes tipos de datos de una población de osos (Ursus arctos)*, reintroducida y no sujeta a caza, que vive en un área con una población humana densa. En una población impulsada principalmente por la supervivencia de adultos, estimamos que en promedio el 11% de los cachorros y el 61% de los adultos murieron por causas relacionadas con humanos. Aunque actualmente la población no se encuentra en riesgo, la supervivencia adulta y, por lo tanto, la dinámica poblacional están dirigidas por la mortalidad antropogénica. Debido al incremento reciente de los conflictos entre humanos y osos en la zona, la extracción de individuos por razones de manejo o por caza furtiva puede incrementar, lo que invertiría la tasa positiva de crecimiento poblacional. Nuestra aproximación analítica puede generalizarse a otras especies afectadas por distintas fuentes de mortalidad y será útil para informar las decisiones de conservación en otras especies no monógamas, como la mayoría de los grandes carnívoros, para las cuales los datos son escasos y diversos, y por lo tanto es deseable la integración de los sus datos.*

Palabras Clave: conflictos humanos – animal en conservación, ecología de poblaciones, grandes carnívoro, modelación jerárquica, modelo de dos sexos, modelo de población integrado, tasa de mortalidad, *Ursus arctos*

Introduction

Quantitative evidence is crucial for conservation of wildlife. For large carnivores, in particular, estimating cause-specific mortality rates is critical for understanding their impact on population dynamics. Integrated population models (IPMs) are useful tools for inferring population dynamics, especially when demographic data originating from different sources are available (Schaub & Abadi 2010). These models allow several types of information, such as capture-recapture, individual, and count data to be integrated into a single analysis through the use of a joint-likelihood function. The joint-likelihood analysis reduces parameter uncertainty and yields more robust and realistic estimates of demographic parameters, even in the case of parameters for which few or no data are available. The inherent hierarchical formulation of the IPMs explicitly separates the underlying (and unobservable) ecological mechanisms from the observation process, thus allowing one to disentangle process variation from sampling variation. This allows the estimation of demographic rates free from possible distorting patterns in the observation process, which involves imperfect detection and recovery. Integrated population models can thus help quantify cause-specific mortalities, necessary for conservation purposes when managing wild populations (Schaub et al. 2010; Tenan et al. 2012).

Two-sex models that include both sexes are required when vital rates differ between males and females and when the assumption that one sex determines population dynamics does not hold (Caswell 2001). Many carnivores such as brown bears have a polygamous mating system (Steyaert et al. 2012), and mate availability may play an important role in population viability, especially when populations are small (Gerber 2006). However, available IPMs are female based and cannot account for mate availability, rendering them useless for nonmonogamous species.

We developed a two-sex IPM, providing a new tool for ecologists to analyze population dynamics and cause-specific mortality rates in nonmonogamous species. We illustrated our approach by analyzing the dynamics of an unhunted brown bear (*Ursus arctos*) population in the central Alps. Even in unhunted populations, human presence is the most important determinant of bear ecology and behavior (Zedrosser et al. 2011), and conflicts with humans or traffic collisions represent important causes of mortality (Woodroffe & Ginsberg 1998). Large home ranges and the threat bears pose to livestock, crops, beehives and, in some cases, humans, makes coexistence between bears and humans a conservation challenge (Linnell et al. 2001). Unraveling cause-specific mortalities, assessing their magnitude and selectivity, and understanding their impact on population dynamics are thus crucial when addressing management and conservation of brown bear populations (Bischof et al. 2009). This is especially true in Europe, where human population densities can be extremely high and no wilderness areas are left at the relevant spatial scale for bears. The area inhabited by the study population has one of the highest human population densities (81 human inhabitants/km^2) among regions occupied by brown bears (De Barba et al. 2010*b*; Chapron et al. 2014). Direct persecution resulted in extirpation of the autochthonous bear population (Mustoni et al. 2003), and all bears currently in the study area originated from a reintroduction program. Currently, conflict with human activities and the consequent negative effect on public opinion are considered key factors that may jeopardize the success of the reintroduction (Mustoni et al. 2003). Such conflicts are likely to become more common as the bear population increases, thereby making it increasingly vital to understand bear population dynamics and the impact of human-related mortality to guide future conservation.

To this end, existing data collected through different sampling strategies could be used in an IPM framework that allows integration of such data. This approach can be particularly relevant for the estimation of mortality rates in charismatic species such as large carnivores.

Methods

Case Study

The study was conducted in 2002–2013 in the Italian Alps, where a brown bear population occurs over an area of approximately 16,000 km^2 (Groff et al. 2014). The study area is characterized by a mosaic of natural and human-modified habitats and a landscape that is fragmented by built areas and roads. By the end of the 1990s, the original brown bear population in the Italian Alps consisted of 3 animals (Mustoni et al. 2003). From 1999 to 2002, 9 bears were released as part of a project to reestablish a self-sustained population (Mustoni et al. 2003). From 2002 to 2013, a minimum of 2 bears emigrated to the Dinaric–Pindos population and no immigrants were observed (Groff et al. 2014).

BROWN BEAR DATA

Most data were obtained from a genetic monitoring program conducted in 2002–2013. Samples were collected noninvasively with hair traps (systematic sampling) and opportunistic collection of hair and feces (opportunistic sampling) (De Barba et al. 2010a, 2010b; Groff et al. 2014). Other data originated from radio tracking and visual observations of cubs with their radio-collared mother.

Systematic sampling was carried out each year in 2003–2013, except for 2009, 2011, and 2012 and consisted of an array of 26–114 hair traps deployed from the end of May or early June until August or October (see Supporting Information for sampling details). Opportunistic sampling was carried out throughout the year by agency personnel following notification by third parties and consisted of the collection of hair and feces taken at sites where bear damage occurred or from bears captured or found dead (see Supporting Information for sampling details) (De Barba et al. 2010b).

Samples were genetically analyzed for individual identification and pedigree reconstruction. Eight to 10 loci were used for individual identification (De Barba et al. 2010a, 2010b). We used the following data in the IPM (Fig. 1): annual counts of the total number of individuals observed in the population (census, Fig. 1), annual counts of the total number of cubs (fecundity), male harem size, capture-recapture-recovery (CRR) data, and annual counts of the total number of recovered individuals that died from natural or anthropogenic causes (mortality).

To obtain annual counts of the total number of individuals observed in the population in 2002–2013 split into age- and sex-specific classes, we pooled genotype data from systematic and opportunistic sampling and complemented this with available data from radio tracking and sightings (Fig. 1; see Supporting Information for sampling details).

We calculated annual counts of the total number of cubs by adding the maximum number of cubs (i.e., individuals in their first year) detected for each breeding female of known genotype in each year. We derived this information from the wild pedigree or from data on visual observations of cubs with their radio collared, and thus genetically identified, mother (Fig. 1; Supporting Information). We used parentage analyses of individual genotypes to reconstruct the pedigree, as described in De Barba et al. (2010a). We used the wild pedigree to derive male harem size (i.e., number of female mates per male [Caswell 2001]). We used a polygynous mating system as an approximation of the brown bear mating system (Steyaert et al. 2012).

We derived CRR data from the systematic sampling performed with hair traps (capture-recapture component) and from radio-tracking data (recovery component). Recovery data for a subset of individuals (both collared or not) detected with the systematic sampling and found dead were incorporated into the capture-recapture data set. We assigned records of bear mortality due to unknown causes to the natural-causes' category so as to obtain conservative estimates of human-induced mortality rates while considering all available data (see Supporting Information for details on mortality causes and necropsy analyses).

The annual numbers of individuals that were opportunistically found dead in 2002–2013, genetically identified, and had not been detected previously through systematic sampling were used to estimate anthropogenic mortality along with the CRR data. In accordance with CRR data, we placed records of bears dead due to unknown causes in the natural-causes category (Supporting Information). All individuals were randomly recovered except for those removed for management purposes. No bears recovered dead were radio collared except for 3 individuals in the systematic sampling and 1 individual from the opportunistic sampling (for details on radio-collared individuals and mortality causes, see Supporting Information). We considered recovery probability was close to 1 for individuals killed or removed by local authorities, killed due to vehicle collision, or wearing an active radio collar. This implies recovery probability for individuals killed by humans reflects the recovery processes resulting from both intentional removal by wildlife management authorities and random recovery of individuals that died from other human-related causes (e.g., car accidents or poaching). No animals that died from natural causes wore radio collars.

The Integrated Population Model

We simultaneously analyzed the different data sets by combining them into an IPM (e.g., Tenan et al. 2012) to estimate population sizes and demographic rates. In IPMs, inference is based on the joint likelihood derived
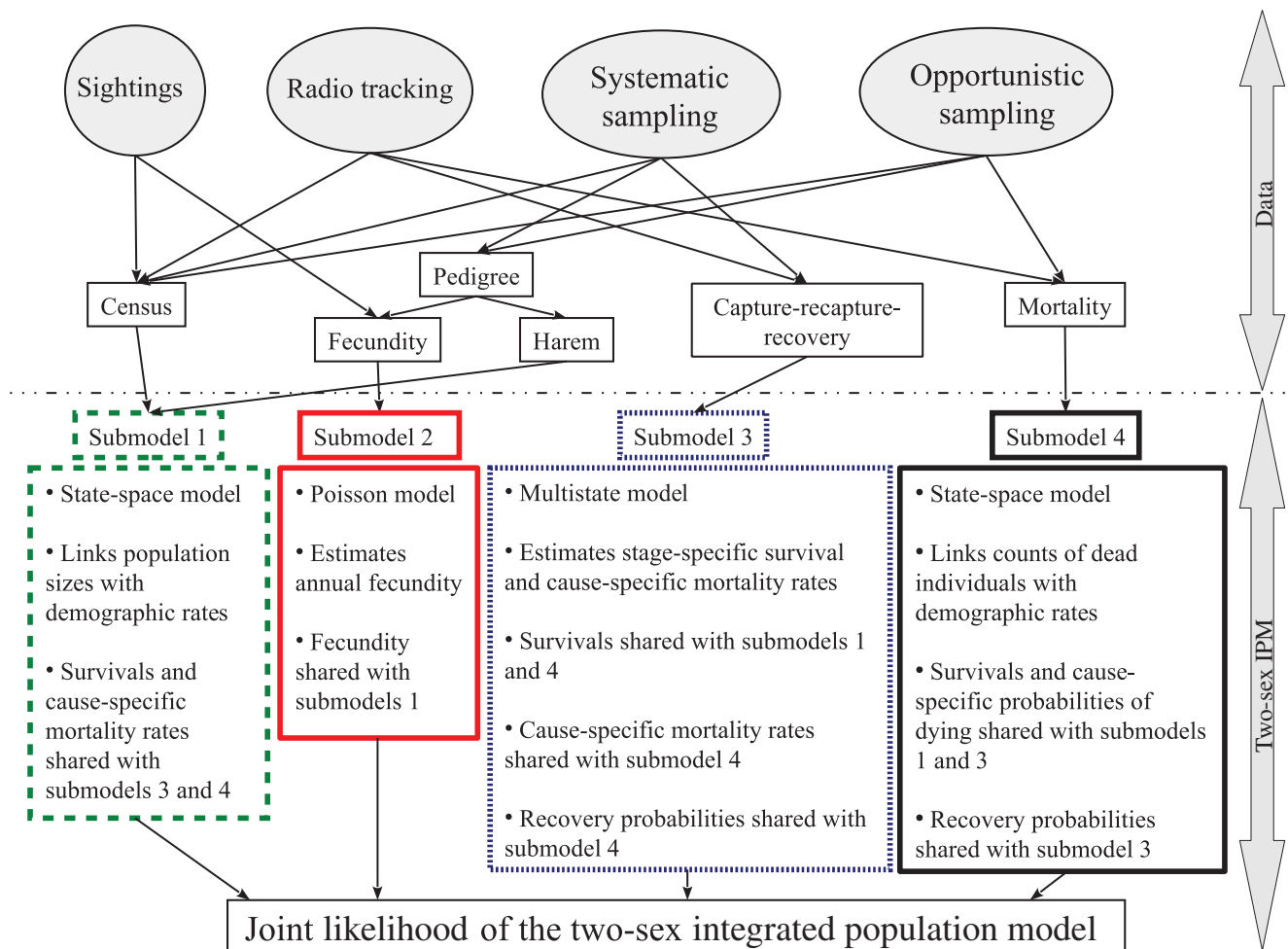
Figure 1. Graphical representation of the data involved in the analysis of the brown bear population and the different components (i.e., submodels) of the two-sex integrated population model.

from the multiplication of the likelihoods for all the data sets. The different submodels that compose the IPM have one or more parameters in common; thus, information from more than one data source can be used to estimate demographic parameters (Schaub & Abadi 2010). Below we describe the different likelihood components and how they are linked in the integrated framework (Figs. 1 & 2).

POPULATION COUNT AND HAREM-SIZE DATA

We modeled count data with a state-space approach in which the observation process is conditional on the state process (submodel 1, Fig. 2). The state process describes how population size changes across time as a function of demographic rates. We described the state process with a two-sex population model (Caswell 2001), in which the number of breeding individuals at year $t = 1, \dots, 12$ was determined by explicitly modeling access to reproduction (i.e., the probability that females and males breed) as a function of the availability of opposite-sex individuals

(Jenouvrier et al. 2010). We used a mating function for polygynous species to define year-specific female (u_t^F) and male (u_t^M) mating probabilities from the total number of potentially breeding (i.e., sexually mature) females (N_{PB}^F) and males (N_{PB}^M), and the average harem size ($\bar{b}$):

$$u_t^F = \frac{\bar{b} \min \left(\left(N_{PB, t}^F / \bar{b} \right), N_{PB, t}^M \right)}{N_{PB, t}^F} \quad \text{and}$$

$$u_t^M = \frac{\min \left(\left(N_{PB, t}^F / \bar{b} \right), N_{PB, t}^M \right)}{N_{PB, t}^M}. \quad (1)$$

We assumed females and males can start breeding from 3 and 4 years of age onward, respectively. We accounted for demographic stochasticity by modeling the development of the population with Poisson and binomial processes. The total number of breeders ($N_{BR, t}^{TOT}$) was derived by summing the number of mated individuals for the two sexes in year t ($N_{BR, t}^F$ and $N_{BR, t}^M$), and the expected values were defined as the number of potentially reproductive individuals multiplied by their mating probability:
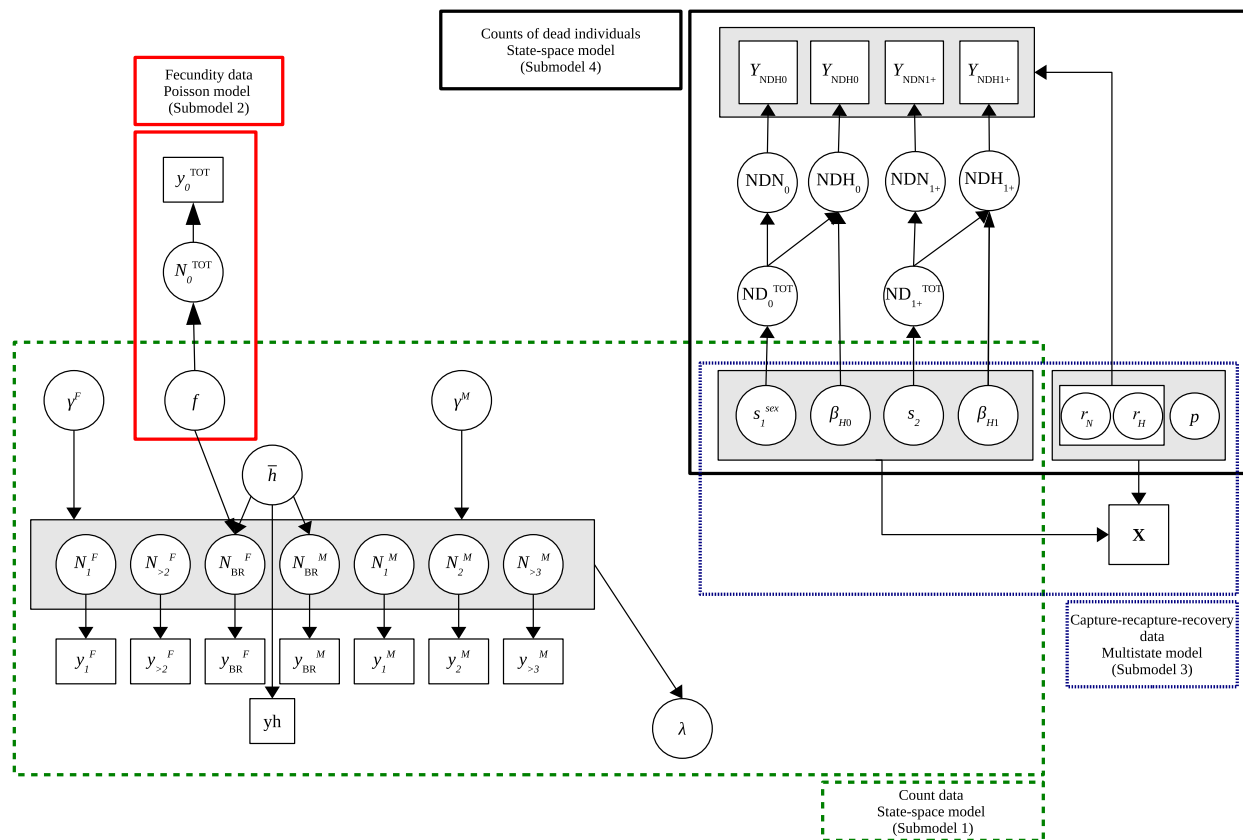
Figure 2. Directed acyclic graph of the two-sex integrated population model for the brown bear application (circles, estimated parameters; squares, data; arrows, dependences between nodes; nodes: y_0^{TOT}, number of cubs detected; y_1^{sex}, $y_{>2}^F$, y_2^M, $y_{>3}^M$, $y_{\text{BR}}^{\text{sex}}$, stage- and sex-specific count data; yh, harem-size data; $\mathbf{X}$, capture-recapture-recovery data; y_{NDN0}, y_{NDH0}, $y_{\text{NDN1+}}$, $y_{\text{NDH1+}}$, counts of dead individuals; N_0^{TOT}, number of cubs; N_1^{sex}, sex-specific number of 1-year-old individuals; $N_{>2}^F$, number of nonbreeding females over 2 years of age; N_2^M, number of 2-year-old males; $N_{>3}^M$, number of nonbreeding males over 3 years of age; $N_{\text{BR}}^{\text{sex}}$, sex-specific number of breeding individuals; ND_0^{TOT}, total number of dead cubs in the population; $\text{ND}_{1+}^{\text{TOT}}$, total number of dead adults in the population; NDN_0, number of cubs killed by natural causes; NDH_0, number of cubs killed by anthropogenic causes; NDN_{1+}, number of adults killed by natural causes; NDH_{1+}, number of adults killed by anthropogenic causes; λ, population growth rate; f, $\bar{b}$, γ^{sex}, s_1^{sex}, s_2, β_{H0}, β_{H1}, r_H, r_N, and p are defined in Table 1's footnote.

$$N_{\text{BR},t}^F \sim \text{Pois}\left(\bar{b}\min\left(\left(N_{\text{PB},t}^F/\bar{b}\right), N_{\text{PB},t}^M\right)\right) \quad \text{and}$$

$$N_{\text{BR},t}^M \sim \text{Pois}\left(\min\left(\left(N_{\text{PB},t}^F/\bar{b}\right), N_{\text{PB},t}^M\right)\right). \quad (2)$$

The expected total number of births produced by the population at time t was $E[B_t] = N_{\text{BR},t}^{\text{TOT}}(1 - \rho_2)f_t$, where ρ_2 is the proportion of males among breeding pairs and f_t is fecundity. If mating was strictly monogamous, then ρ_2 would be 0.5; however, a polygamous mating system implies a dependence on the relative number of breeding individuals of the sexes: $\rho_2 = (1/\bar{b})/[(1/\bar{b}) + 1]$, where $\bar{b}$ is the average number of females with which a single male mates, or harem size (Caswell & Weeks 1986). Observed harem size ($\text{yh}_{i,t}$) for male $i = 1, \ldots, 7$ at time t was modeled as $\text{yh}_{i,t} \sim \text{Pois}(E[b_{i,t}])$, $\log(E[b_{i,t}]) = \mu_b$ and $\bar{b} = \exp(\mu_b)$. The number of cubs (N_0) of each sex was then derived from

the total number of cubs $N_{0,t}^{\text{TOT}} \sim \text{Pois}(E[B_t])$ as $N_{0,t}^F \sim \text{bin}(N_{0,t}^{\text{TOT}}, (1 - \rho))$ and $N_{0,t}^M = N_{0,t}^{\text{TOT}} - N_{0,t}^F$, where ρ is the proportion of males at birth.

Changes in the remaining stage-specific population sizes were stochastically modeled with binomial processes. The number of 1-year-old individuals of each sex was $N_{1,t+1}^{\text{sex}} \sim \text{Bin}(N_{0,t}^{\text{sex}}, s_{1,t}^{\text{sex}})$, where $s_{1,t}^{\text{sex}}$ is the sex-specific probability that a cub survives from year t to $t + 1$. Similarly, the number of 2-year-old males was $N_{2,t+1}^M \sim \text{bin}(N_{1,t}^M, s_{2,t})$, where $s_{2,t}$ is the sex-independent probability than an individual survives from year t to $t + 1$. The total number of potentially reproductive females at year t ($N_{\text{PB},t}^F$) was the summation of 3 components: number of sexually immature females ($N_{\text{NR},t-1}^F$, 2 years old or older) with probability $s_{2,t-1}\gamma^F$, where γ is the probability of becoming sexually mature; number of potentially breeding females with no access to reproduction in the

previous year ($N_{NA,t-1}^F = N_{PB,t-1}^F - N_{BR,t-1}^F$) who survived with probability $s_{2,t-1}$; and number of females that skipped reproduction in the previous year ($N_{NB,t-1}^F$) that had bred 2 years before. Annual numbers of potentially breeding males ($N_{PB,t}^M$) were derived from the number of sexually immature individuals ($N_{NR,t-1}^M$, 3 years old or older) with probability $s_{2,t-1}\gamma^M$; the number of sexually mature males with no access to reproduction in the previous year ($N_{NA,t-1}^M = N_{PB,t-1}^M - N_{BR,t-1}^M$) who survived with probability $s_{2,t-1}$; and the number of males that mated in the previous breeding season whose proportion of the total number of mated individuals was ρ_2 and who survived with probability $s_{2,t-1}$.

In the observation model, we described the relationship between the available stage- and sex-specific counts ($y_{stage,t}^{sex}$) and the true population size: $y_{1,t}^F \sim \text{Pois}(N_{1,t}^F)$ for 1-year-old females; $y_{BR,t}^F \sim \text{Pois}(N_{BR,t}^F)$ for breeding females; $y_{>2,t}^F \sim \text{Pois}(N_{>2,t}^F)$ for nonbreeding females over 2 years of age, with $N_{>2,t}^F = (N_{NR,t}^F + N_{NA,t}^F + N_{NB,t}^F)$; $y_{1,t}^M \sim \text{Pois}(N_{1,t}^M)$ for 1-year-old males; $y_{2,t}^M \sim \text{Pois}(N_{2,t}^M)$ for 2-year-old males; $y_{BR,t}^M \sim \text{Pois}(N_{BR,t}^M)$ for breeding males; and $y_{>3,t}^M \sim \text{Pois}(N_{>3,t}^M)$ for nonbreeding males over 3 years of age, with $N_{>3,t}^M = N_{NR,t}^M + N_{NA,t}^M$. We used a Poisson distribution to account for random observation error in population counts, but other error assumptions can be made (Kéry & Schaub 2012). The observation model for count data cannot entirely account for systematic patterns in the observation error, such as a temporal trend in the related sampling effort (Kéry & Schaub 2012).

FECUNDITY DATA

In each year, we recorded the total number of cubs (y_0^{TOT}) produced by a sample (of size R) of breeding females for which litter size was observed. The annual fecundity (f_t) was modeled using a Poisson regression model (submodel 2 in Fig. 2): $y_{0,t}^{TOT} \sim \text{Pois}(R_t f_t)$. In our application, litter size was available for all detected breeding females and thus $R_t = y_{BR,t}^F$.

CAPTURE-RECAPTURE-RECOVERY DATA

We used a multistate CRR model to combine recaptures of live individuals and recoveries to estimate survival parameters and mortality due to natural or anthropogenic causes while accounting for the probability of finding and reporting an animal that died from a particular cause (Servanty et al. 2010) (submodel 3 in Fig. 2). We assumed individuals can move through 3 main states: alive (first year of life A_1 or later A_{2+}), recently dead due to natural causes (RD_N), and recently dead due to anthropogenic causes (RD_H). We also considered an unobservable dead state (D); all recently dead individuals at time t moved to the dead state at $t + 1$. Individual i can change state ($z_{i,t}$) according to transition matrix Ψ (Supporting Information) with a state equation $z_{i,t+1} | z_{i,t} \sim \text{cat}(z_{i,t} \Psi_{i,t})$. Given that individual i is alive at time t, it can survive to time $t + 1$ with sex-specific probability $s_{1,t}^{sex}$ during

its first year of life or with probability $s_{2,t}$ if older than 1 year. Alternatively, the individual may die from natural causes with probability $\beta_{N0} = (1 - \beta_{H0})$ (if 1 year old) or $\beta_{N1} = (1 - \beta_{H1})$ (if over 1 year of age) or may die because of anthropogenic causes with probability β_{H0} or β_{H1}. Recovery probabilities for individuals killed due to either natural (r_N) or anthropogenic causes (r_H) were included in the state transition matrix to ensure the parameters were properly updated (Supporting Information) (Kéry & Schaub 2012).

Five types of mutually exclusive events ($x_{i,t}$) could be observed and were arbitrarily coded as follows: 1, seen alive in the first year of life; 2, seen alive at over 1 year of age; 3, recovered dead due to natural causes; 4, recovered dead due to anthropogenic causes; 5, not seen. The events were then included in the observation matrix Θ (Supporting Information) containing the detection probability p_t. The related equation was $x_{i,t} | z_{i,t} \sim \text{cat}(x_{i,t} \Theta_{i,t})$. To account for the variability in the annual number of active hair traps and sampling occasions, we considered annual estimates of detection probability originated from a random process with a common mean (μ_p) and a constant temporal variance (σ_p^2): $\text{logit}(p_t) = \mu_p + \varepsilon_{p,t}$, where $\varepsilon_{p,t} \sim N(0, \sigma_p^2)$ for $t = \{1, 2, 3, 4, 5, 7, 10\}$. In the years when no sampling activity was carried out, $t = \{6, 8, 9\}$, we considered $p_t = 0$. Cause-specific recovery probabilities (r_H and r_N) were kept constant across years (Supporting Information).

COUNTS OF DEAD INDIVIDUALS

We also considered a model component for the yearly counts of dead individuals recovered by local authorities and not previously detected through capture-recapture sampling (submodel 4 in Fig. 2). In the state process, the total number of dead cubs in the population (i.e., individuals that died during their first year of life (ND_0^{TOT})) was defined by summing the related abundances for each sex represented by $ND_{0,t+1}^F \sim \text{bin}(N_{0,t}^F, (1 - s_{1,t}^F))$ and $ND_{0,t+1}^M \sim \text{bin}(N_{0,t}^M, (1 - s_{1,t}^M))$; thus, $ND_{0,t+1}^{TOT} = ND_{0,t}^F + ND_{0,t}^M$. In other words, for each sex, the total number of cubs that died in year t ($ND_{0,t}^{sex}$) was derived from the total number of cubs in the population in the previous year ($N_{0,t-1}^{sex}$) and the probability of dying between $t-1$ and t ($1 - s_{1,t-1}^{sex}$), which is the complement of survival probability. Because dead individuals can be recovered anywhere, not just in the study area, survival probability was true and not apparent (Kéry & Schaub 2012). From the total number of dead cubs in the population (ND_0^{TOT}), we estimated the number of cubs killed by anthropogenic causes, $NDH_{0,t} \sim \text{bin}(ND_{0,t}^{TOT}, \beta_{H0})$, and by natural causes, $NDN_{0,t} = ND_{0,t}^{TOT} - NDH_{0,t}$. Similarly, the total number of dead non-cubs (ND_{1+}^{TOT}) was derived from the total number of non-cubs alive in the previous year (N_{1+}^{TOT}): $ND_{1+,t+1}^{TOT} \sim \text{bin}(N_{1+,t}^{TOT}, (1 - s_{2,t}))$. The estimated number of non-cubs that died from

anthropogenic causes was $NDH_{1+,\,t} \sim bin(ND_{1+,\,t}^{TOT}, \beta_{H1})$, whereas the number of non-cubs that died from natural causes was $NDN_{1+,\,t} = ND_{1+,\,t}^{TOT} - NDH_{1+,\,t}$. The observation model for the recovery process describes the link between the available counts of individuals recovered dead for each mortality cause and stage (y_{NDH0}, y_{NDN0}, y_{NDH1+}, and y_{NDN1+} for cubs that died from human-related causes and natural causes, non-cubs that died from human-related causes and natural causes, respectively), the true total number of individuals dead in the population (NDH_0, NDN_0, NDH_{1+}, and NDN_{1+}), and the cause-specific recovery probabilities (r_H and r_N). Recovery probabilities are shared with the multistate capture-recapture submodel (Figs. 1 & 2; see Supporting Information for details on the implementation of the IPM). The observation process is summarized with binomial processes as follows: $y_{NDH0,\,t} \sim bin(NDH_{0,\,t}, r_H)$, $y_{NDN0,\,t} \sim bin(NDN_{0,\,t}, r_N)$, $y_{NDH1+,\,t} \sim bin(NDH_{1+,\,t}, r_H)$ and $y_{NDN1+,\,t} \sim bin(NDN_{1+,\,t}, r_N)$.

ESTIMATION OF TEMPORAL VARIABILITY

We used a hierarchical formulation of the IPM to estimate the temporal random variance of parameters. We assumed annual estimates originated from a random process with a common mean (μ) and a constant temporal variance (σ^2). Fecundity and survival rates (s_1^{sex} and s_2) were modeled as follows: $\log(f_t) = \mu_f + \varepsilon_{f,\,t}$ with $\varepsilon_{f,\,t} \sim N(0, \sigma_f^2)$, $logit(s_{1,\,t}^{sex}) = \mu_{s1,\,sex} + \varepsilon_{s1,\,t}$ with $\varepsilon_{s1,\,t} \sim N(0, \sigma_{s1}^2)$, and $logit(s_{2,\,t}) = \mu_{s2} + \varepsilon_{s2,\,t}$ with $\varepsilon_{s2,\,t} \sim N(0, \sigma_{s2}^2)$. We assumed a common temporal variance for male and female cub survival. We calculated population growth rate (λ_t) as N_{t+1}^{TOT}/N_t^{TOT} and the geometric mean of all year-specific values.

Bayesian Analyses

The two-sex IPM was fitted using a Bayesian formulation and the Markov chain Monte Carlo framework. We used uniform(0,1) prior distributions for the mean survival probabilities and for the other probabilities (mortality, skipping, recruitment, detection, and recovery). For further details of the prior specification of other model parameters, see the model code in Supporting Information. Posterior parameter distributions were assessed for prior sensitivity (King 2009) by using a second set of priors with normal(0,100) probabilities for the mean survival and detection probabilities on the logit scale. The two sets of priors yielded similar posterior parameter distributions. We discuss estimates obtained under the first prior set.

Summaries of the posterior distribution were calculated from 3 Markov chains initialized with random starting values and run 1,000,000 times after a 500,000 burn-in and resampling every 50 draws, resulting in 20,000 posterior samples per chain. The $\hat{R}$ diagnostic (Brooks & Gelman 1998) used to assess convergence was < 1.02

for all parameters. Models were implemented in JAGS (Plummer 2003) executed from R (R Core Team 2012).

Demographic Effects of Anthropogenic Mortality

We assessed the demographic consequences of human-related mortality with a periodic two-sex model (Caswell 2008) with parameter estimates obtained from the IPM. Specifically, we computed the sensitivity of the population growth rate and population structure to changes in demographic rates and to the proportional decrease in survival due to anthropogenic mortality. The latter was derived from $\delta_1^{sex} = 1 - (\bar{s}_1^{sex}/s_{1NH}^{sex})$ for cubs and $\delta_2 = 1 - (\bar{s}_2/s_{2NH})$ for non-cubs, where s_{1NH}^{sex} and s_{2NH} are the survival rates in the absence of anthropogenic mortality. These survivals were expressed as a function of the mean survival probability $\bar{s} = expit(\mu_s)$, where expit is the inverse-logit function, and the proportion of deaths from human-related causes for cubs was $s_{1NH}^{sex} = 1 - (1 - \bar{s}_1^{sex})(1 - \beta_{H0})$ and for non-cubs was $s_{2NH} = 1 - (1 - \bar{s}_2)(1 - \beta_{H1})$. Further details on sensitivity and elasticity analysis are in Supporting Information.

Results

The estimated brown bear annual population ranged from 14 (95% CRI 10–20 in 2003) to 46 individuals (95% CRI 37–57 in 2012) from 2002 to 2013 (Fig. 3f) (and Supporting Information for additional results). We estimated the population increased on average by 8.6% during the 12-year study (geometric mean growth rate $\lambda = 1.086$ [95% CRI $1.039 - 1.136$] [Fig. 3a]). A projection of the population from 2013 to 2016 showed an increase in median size, but the associated uncertainty increased considerably over time (Fig. 3f).

Systematic sampling yielded identification of 8–24 different individuals per year, 44 captures, and 91 recaptures (Supporting Information). Nine individuals (all non-cubs) detected within the systematic sampling were found dead (1 from natural causes, 2 from unknown causes, and 6 from anthropogenic causes) and were included in the capture-recapture data set (see additional information on mortality causes in Supporting information). Opportunistic sampling yielded identification of 5–34 different individuals per year. Annual counts of individuals opportunistically found dead and not previously detected by the systematic sampling included 6 individuals dead due to unknown causes and 5 individuals dead due to anthropogenic causes (Supporting Information).

Survival probability during the first year of life did not substantially differ between sexes ($\bar{s}_1^F = 0.650$, 95% CRI $0.380 - 0.907$; $\bar{s}_1^M = 0.727$, 95% CRI $0.372-0.984$). Individuals over 1 year old had a sex-independent survival probability $\bar{s}_2 = 0.903$
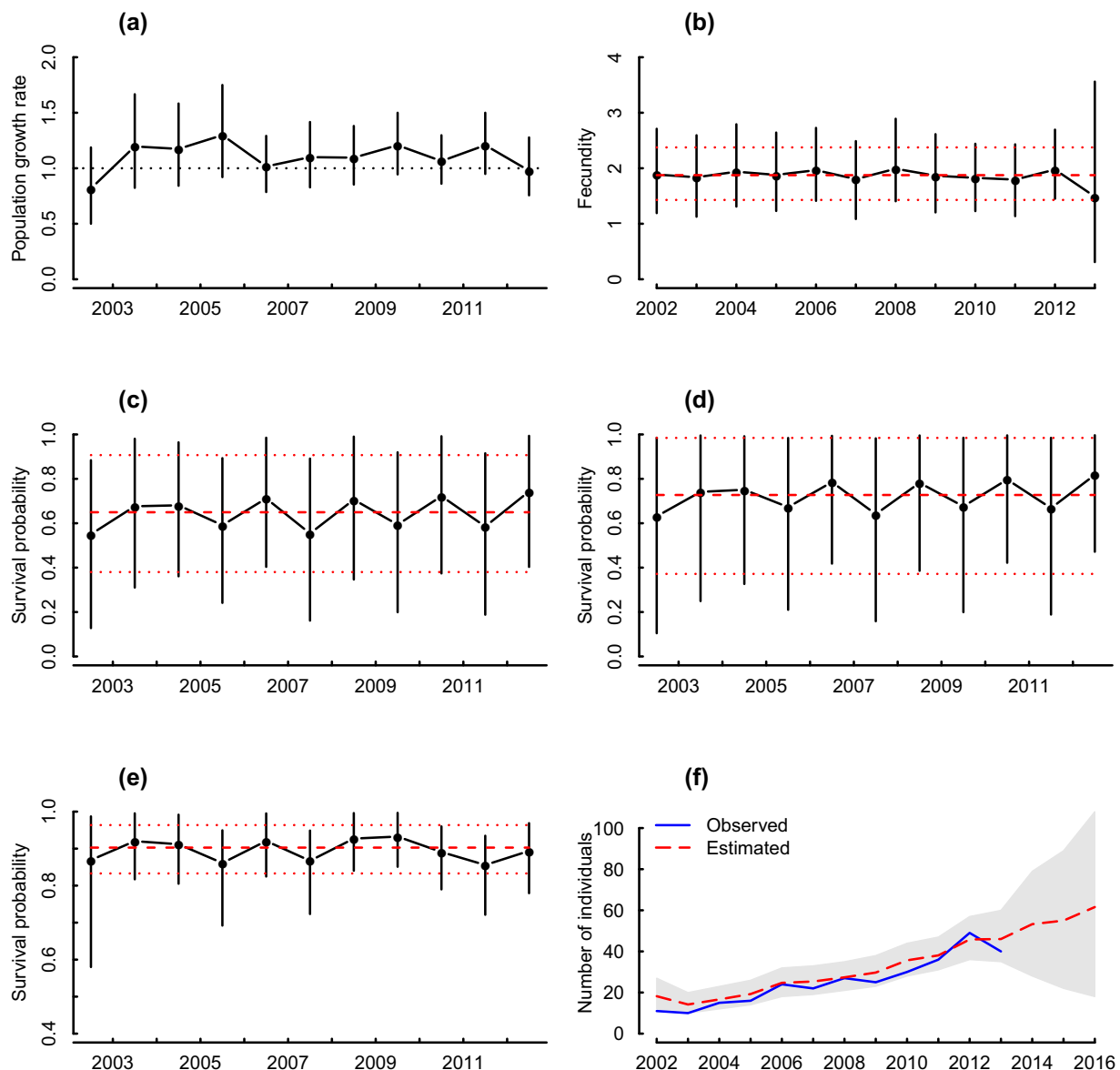
Figure 3. Estimates of (a) population growth λ_t; (b-e) demographic rates of the brown bear population in the central Italian Alps; and (f) estimated and observed population size in 2002–2013 (vertical lines in [a-e], 95% credible intervals; horizontal dotted line in [a], population stability; dashed line in [b-e], mean from the random effects model; dotted lines in [b-e], 95% credible intervals of the mean). In (f), the estimated population size is projected onto the period 2014–2016 and the shaded area is 95% credible interval for the estimates.

(95% CRI $0.833 - 0.964$) (Table 1, Figs. 3c–e). The probability of dying from anthropogenic causes was age dependent and was higher for individuals over 1 year of age ($\beta_{H1} = 0.611$, 95% CRI $0.317 - 0.868$) than for cubs ($\beta_{H0} = 0.105$, 95% CRI $0.002 - 0.461$).

Harem size was observed for 7 males and ranged from 1 to 5 females (median 1.5). Observed mean fecundity for the study period was 1.75 cubs/breeding pair. The estimated average harem size ($\bar{b}$) was 1.920 (95% CRI $1.407 - 2.525$) females/male, and average fecundity ($\bar{f}$) was 1.876 (95% CRI $1.429 - 2.376$) cubs/breeding pair and year (Fig. 3b). Mating probability

for females (u^F) increased on average over time, whereas the trend for males (u^M) was the opposite (Supporting Information).

Our two-sex IPM improved precision in parameter estimates for both mortality and recovery rates relative to the estimates obtained under the same multistate model included in the IPM but fitted separately. Under the IPM, the SD for the estimates was reduced from 0.299 to 0.121 for human-induced cub mortality (β_{H0}), from 0.152 to 0.146 for human-induced adult mortality (β_{H1}), from 0.193 to 0.180 for recovery probability of individuals that died from human-induced causes (r_H), and from

Table 1. Posterior estimates of demographic parameters of the brown bear population in the central Italian Alps.

Parameter[*]	Quantiles				
	Mean	*SD*	*0.025*	*0.500*	*0.975*
$\bar{s}_1^F$	0.650	0.136	0.380	0.650	0.907
$\bar{s}_1^M$	0.727	0.169	0.372	0.744	0.984
σ_{s1}	0.926	0.822	0.036	0.729	3.003
$\bar{s}_2$	0.903	0.035	0.833	0.905	0.964
σ_{s2}	0.764	0.686	0.031	0.603	2.488
β_{H0}	0.105	0.121	0.002	0.060	0.461
β_{H1}	0.611	0.146	0.317	0.620	0.868
$\bar{f}$	1.876	0.242	1.429	1.866	2.376
σ_f	0.144	0.119	0.005	0.116	0.443
$\bar{h}$	1.920	0.286	1.407	1.902	2.525
ρ	0.529	0.106	0.324	0.528	0.734
ρ_2	0.346	0.034	0.284	0.345	0.416
γ^F	0.671	0.203	0.266	0.685	0.984
γ^M	0.615	0.251	0.109	0.643	0.983
$\bar{p}$	0.747	0.141	0.395	0.770	0.952
σ_p	2.205	1.354	0.606	1.860	5.956
r_H	0.451	0.180	0.181	0.422	0.875
r_N	0.222	0.102	0.083	0.203	0.475

[*] *Mean survival probabilities for cubs ($\bar{s}_1^{\mathrm{sex}}$) and individuals over 1 year of age ($\bar{s}_2$) are given on probability scale; that is, $\bar{s}_1^{\mathrm{sex}} = expit(\mu_{s1,\,\mathrm{sex}})$ and $\bar{s}_2 = expit(\mu_{s2})$, where expit is the inverse-logit function and the related σs are on logit scale. The sex $= \{M, F\}$ indicates males and females, respectively. Mean fecundity, $\bar{f} = exp(\mu_f)$, is given along with its temporal random variation (σ_f, on log scale). The β_{H0} and β_{H1} are the probabilities of death due to anthropogenic causes if an animal dies in its first year of life or later, respectively; $\bar{h}$ is the mean harem size; ρ is the proportion of males at birth; and ρ_2 is the proportion of males among breeders. Sex-specific recruitment probabilities are denoted as γ^{sex}. Mean detection probability ($\bar{p}$) is on probability scale; that is, $\bar{p} = expit(\mu_p)$, and σ_p is on logit scale. The r_H and r_N are recovery probabilities for animals that died due to anthropogenic or natural causes, respectively.*

0.212 to 0.102 for recovery probability of individuals that died from natural causes (r_N; Fig. 4). The estimated mean r_H shifted from 0.665 (95% CRI 0.295 − 0.981) in the multistate model to 0.451 (95% CRI 0.181 − 0.875 in the IPM), and r_N mean estimates shifted from 0.458 (95% CRI 0.131 − 0.932) to 0.222 (95% CRI 0.083 − 0.475).

The deterministic projection of the periodic two-sex model showed a population increase of 8.7% per year ($\hat{\lambda} = 1.087$). Elasticity analyses showed a positive relationship between the population growth rate at equilibrium ($\hat{\lambda}$) and both fecundity and adult survival (Supporting Information). Adult survival probability fell by 6.2% as a result of anthropogenic mortality ($\delta_2 = 0.062$), assuming this type of mortality is additive. Given current demographic rates, if adult survival were to fall 16% ($s_2 = 0.811$), the population would decrease ($\hat{\lambda} < 1$) (Fig. 5). However, a negative growth rate would also occur if average fecundity drops to 1.5 cubs and adult survival is reduced by 13% ($s_2 = 0.836$) or, similarly, if fecundity drops to 1.0 and adult survival falls by 8.9% ($s_2 = 0.877$). A reduction in adult survival of >19% could not be compensated

for by even the maximum fecundity reported for brown bears in Europe (mean litter size 2.4 cubs [Steyaert et al. 2012]).

Discussion

A Two-Sex Integrated Population Model

We developed a two-sex IPM that contains a nonlinear mating function (Caswell 2001) to account for the fact that mate availability can affect population growth and viability. Additionally, we modeled male harem size in the mating function as a random variable, instead of fixing default values as is classically done.

Estimating human-induced mortality separately from natural mortality while accounting for different recovery probabilities requires CRR information, which can be difficult to obtain. However, simple records of dead individuals are not sufficient for estimating unbiased cause-specific mortality rates. We are not aware of any previous study on large carnivores that jointly exploits both sources of information to improve estimates of mortality rates. Bischof et al. (2009) used CRR data to determine mortality caused by legal hunting of brown bears but did not estimate the effects of other human-induced causes of mortality. Other researchers used the observed proportions of cause-specific mortalities and ignored the bias generated by the observation process (e.g., Krofel et al. 2012).

By comparing estimates obtained under the IPM and the multistate capture-recapture model, we demonstrated how our integrated framework can improve precision in the estimation of key demographic and nuisance parameters, namely cause-specific mortality and recovery rates, which would otherwise be difficult to estimate with a single data source due to the lack of information available. Our estimates of anthropogenic cub mortality and recovery probability associated with natural mortality achieved the greatest accuracy in the IPM (60% and 52% reduction in SD of the estimate, respectively) (Fig. 4). This improvement in precision was related to the fact that the CRR data set alone contained a small number of records on cub mortality and on recoveries of individuals that died from natural causes, making the estimation of the related parameters difficult under the multistate model. That parameters otherwise not estimable become estimable is possible because population size (and thus counts) contains information about all demographic processes in the population, and this information can be extracted with IPMs. In the same way, the size of the fraction of the population that died due to specific mortality causes (and counts of recovered individuals) contains information about the death process (and complement survival). Thus, our integrated framework can provide estimates of mortality rates that account for cause-specific recovery processes and nonmonogamy of a species. This
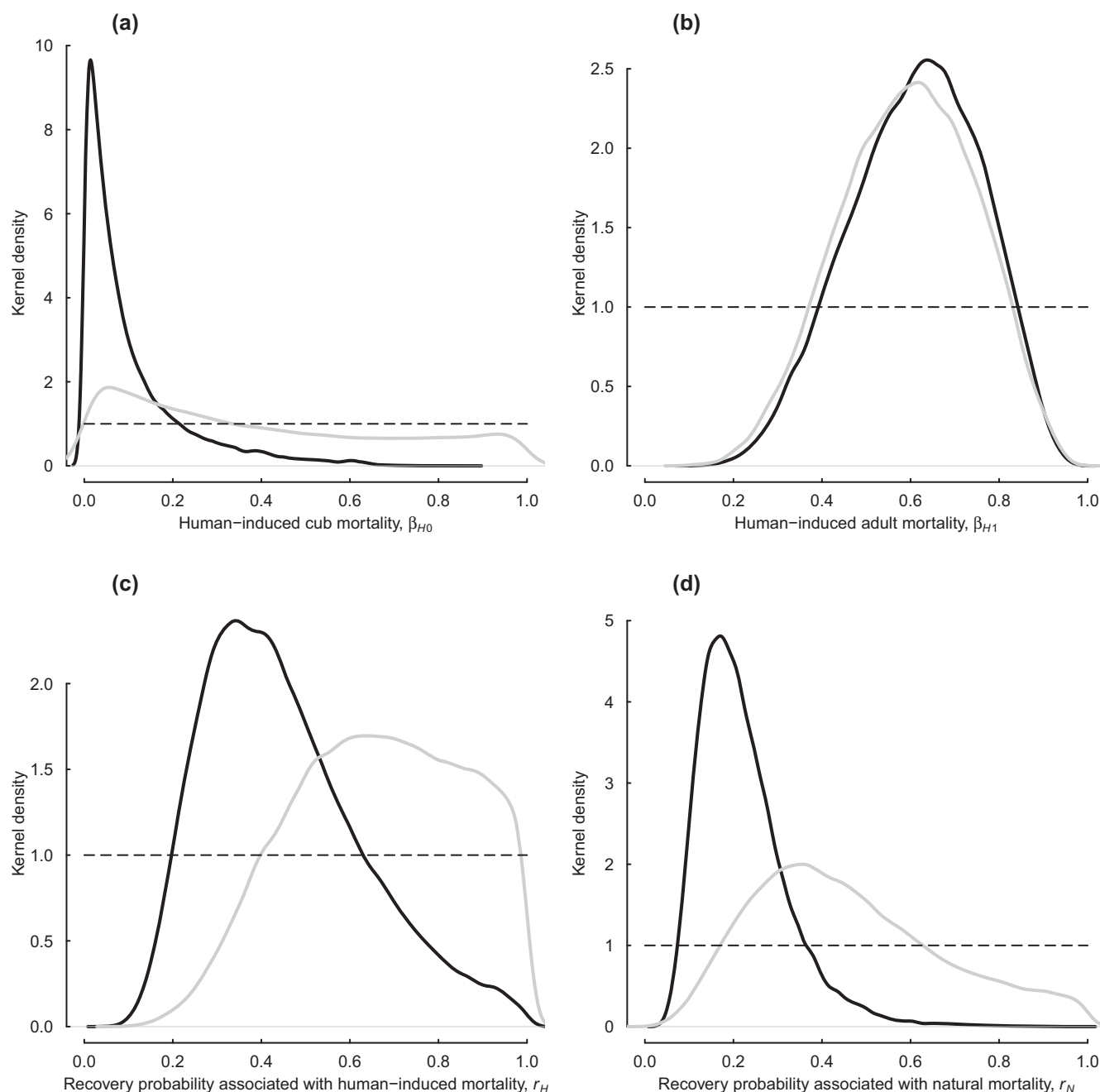
(a)

(b)

(c)

(d)

Figure 4. Posterior densities for human-induced cub and adult bear mortality and for recovery probabilities obtained under the two-sex integrated population model (black lines) and the multistate model fitted to the capture-recapture-recovery data alone (gray lines) (dashed lines, uniform [0,1] prior distribution).

is particularly useful in the case of small populations of endangered species for which there are limited data, and a combination of multiple sources of information is highly desirable to increase precision of parameter estimates.

Integrated population models offer a way to integrate the few data available that have been collected with different sampling strategies. However, data must be carefully evaluated before analysis, and potential sources of bias must be considered. For instance, the state-space models

used to infer the true but unknown population trajectory from population count data, or the true number of individuals that died from specific causes from counts of recovered individuals, can account for random observation error but cannot adjust for systematic patterns of sampling error (e.g., a temporal trend in sampling effort) and do not allow estimation of detection probability (Kéry & Schaub 2012). The same logic applies for fecundity data, especially when the representativeness of the sample of
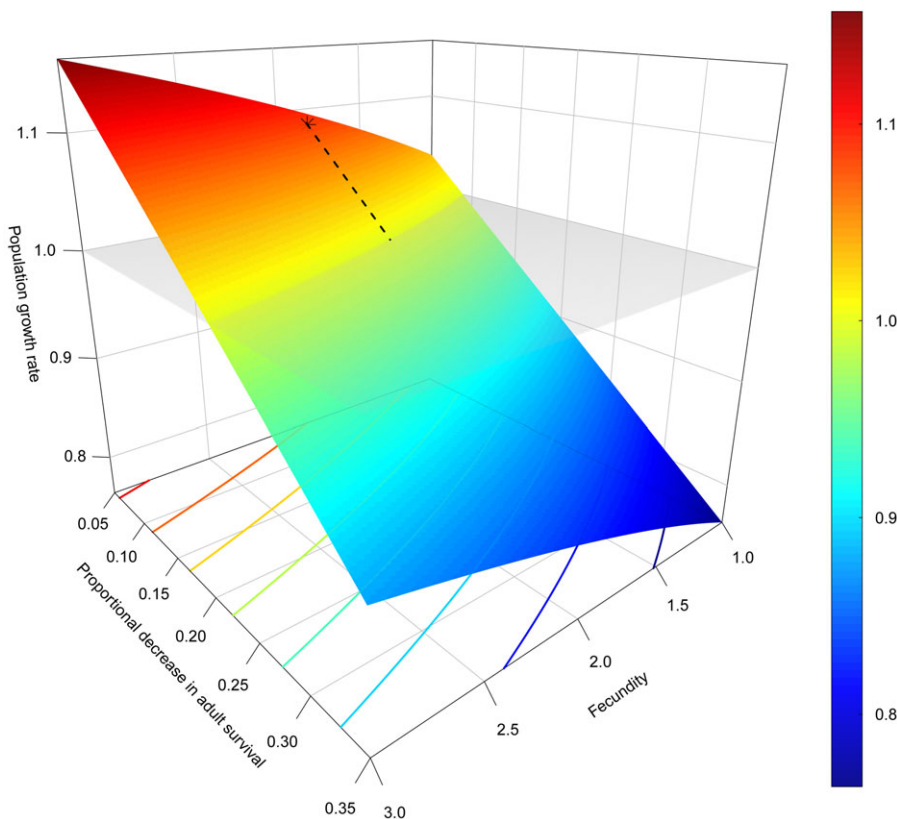
Figure 5. Proportional change in survival probability of adult bears due to anthropogenic causes of mortality (δ_2) in relation to fecundity and population growth rate (asterisk, current parameter estimates; dashed line, theoretical decrease in adult survival that would lead to population stability [i.e., population growth rate $\lambda = 1$]). Contour lines and shading indicate different values of population growth rate in relation to the proportional decrease in adult survival and fecundity. The horizontal plane indicates population stability.

breeding females (and related counts of cubs) is low or changes across time and space.

The Brown Bear Case Study

Accurate demographic assessments are particularly important for populations located in densely inhabited areas, such as this brown bear population. Bischof et al. (2009) stressed that assessing the magnitude and selectivity of cause-specific mortality is crucial to understanding the dynamics of managed populations. We estimated the proportion of deaths due to natural and anthropogenic causes while accounting for the different probability of recovering individuals that died because of one or the other of these two factors. About 61% of adults and 11% of cubs were estimated to have died from human-related causes. Given current demographic rates, the population will decrease if adult survival is reduced by 16% because of anthropogenic mortality (assuming this type of mortality is additive). However, both inbreeding, which is a serious concern in the study population (De Barba et al. 2010a), and density-dependent effects may lower reproductive performance, thereby leaving much less leeway for the anthropogenic mortality rate to increase before the population begins to decline. Furthermore, our results are conservative because all records of unknown causes of death were regarded as natural deaths.

A rigorous scientific approach to conservation acknowledges that single-value estimates, such as the mean value of mortality rates, do not sufficiently represent demographic quantities; thus, a full consideration of the uncertainty in the estimates is needed. The range of uncertainty around the average estimate of anthropogenic cub and adult mortality ($0 - 46\%$ and $32 - 87\%$, respectively for the 95% Bayesian credible interval) could dramatically change the inherent demographic scenario. In our case, the uncertainty in cause-specific mortality estimates can be ascribed to the few recovery data available. This, however, does not diminish the potential of our approach; rather, it highlights the need to have available a fair amount of recovery data ascribable to known causes of death and collected under standardized protocols. When standardized protocols cannot be implemented, systematic errors in the recovery process (e.g., from spatiotemporal heterogeneity in sampling effort) must be reduced. Alternatively, augmenting the number of radio-collared individuals would allow collection of detailed mortality data, especially for natural and illegal causes of death.

Because our data set was small, we included bears that died from unknown causes in the natural-causes category to obtain conservative estimates of human-induced mortality rates while considering all available data. In this way, we minimized the risk of overestimating anthropogenic mortality. Alternatively, the model could be extended in order to estimate unknown causes of death by expressing these data as missing values (Gimenez et al. 2009; Rovero et al. 2015). A key question in the

assessment of demographic consequences of cause-specific mortality is whether compensatory mortality or depensation occurs. Multistate capture-recapture models are useful tools to address this question because they allow estimation of the temporal correlation between mortalities, where compensatory mortality is modeled with a common mean and a constant temporal variance and residuals are treated as a realization from a multivariate normal distribution with a variance–covariance matrix (Servanty et al. 2010). We were unable to test whether mortality was compensatory because of problems in the estimation of temporal variances in mortality, probably due to the small data sets involved and the lack of systematic sampling in 3 years of the study. Thus, a continuous and standardized effort to collect individual longitudinal data is highly desirable especially when dealing with small populations.

Our integrated framework can also be employed in the case of reintroduction or recovery programs for threatened species because it can be used to contrast estimated trends and population size of the study with projections provided in feasibility studies. Unfortunately, no projections are available from the feasibility study of the brown bear reintroduction program. The study only mentions the availability of sufficient habitat for a minimum viable population of at least 50 individuals. Although current anthropogenic mortality rates do not appear to represent a threat to population persistence, management that seeks to improve social acceptance of bears, and large carnivores in general, is urgently needed. The mitigation of social and human-bear conflicts is also a priority as a means of establishing a self-sustained Alpine population and, eventually, restoring a meta-population network that includes the Dinaric–Pindos population (De Barba et al. 2010*b*; Peters et al. 2015). In the meantime, the study of population dynamics should be based on analytical approaches capable of exploiting all available sources of information in order to increase reliability and precision.

Acknowledgments

Supporting Information

Details of sampling design, sample sizes, and genotyping success (Appendix S1); details on the implementation of the two-sex IPM (Appendix S2) and sensitivity and elasticity analyses (Appendix S3); additional plots on population size of different stage classes and mating probabilities (Appendix S4); R and JAGS script for the two-sex IPM (Appendix S5); R code to project an initial population structure to its equilibrium (Appendix S6); MATLAB code to obtain the relevant derivatives of the 2 mating functions (Appendix S7); and MATLAB code to perform the whole elasticity analysis (Appendix S8) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Bischof R, Swenson JE, Yoccoz NG, Mysterud A, Gimenez O. 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. Journal of Animal Ecology **78:**656–665.

Brooks SP, Gelman A. 1998. Alternative methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics **7:**434–455.

Caswell H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts.

Caswell H. 2008. Perturbation analysis of nonlinear matrix population models. Demographic Research **18:**59–116.

Caswell H, Weeks DE. 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. The American Naturalist **128:**707–735.

Chapron G, et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science **346:**1517–1519.

De Barba M, Waits L, Garton E, Genovesi P, Randi E, Mustoni A, Groff C. 2010*a*. The power of genetic monitoring for studying demography, ecology and genetics of a reintroduced brown bear population. Molecular Ecology **19:**3938–3951.

De Barba M, Waits LP, Genovesi P, Randi E, Chirichella R, Cetto E. 2010*b*. Comparing opportunistic and systematic sampling methods for non-invasive genetic monitoring of a small translocated brown bear population. Journal of Applied Ecology **47:**172–181.

Gerber LR. 2006. Including behavioral data in demographic models improves estimates of population viability. Frontiers in Ecology and the Environment **4:**419–427.

Gimenez O, Bonner SJ, King R, Parker RA, Brooks SP, Jamieson LE, Grosbois V, Morgan BJ, Thomas L. 2009. Modeling demographic processes in marked populations. Pages 883–915 in Thomson DL, Cooch EG, Conroy MJ, editors. WinBUGS for population ecologists: Bayesian modeling using Markov Chain Monte Carlo methods. Springer, New York.

Groff C, Bragalanti N, Rizzoli R, Zanghellini P. 2014. 2013 Bear report. Technical report. Forestry and Wildlife Department of the Autonomous Province of Trento, Trento, Italy.

Jenouvrier S, Caswell H, Barbraud C, Weimerskirch H. 2010. Mating behavior, population growth, and the operational sex ratio: a

periodic two-sex model approach. The American Naturalist **175:**739–752.

Kéry M, Schaub M. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Oxford, United Kingdom.

King R. 2009. Bayesian analysis for population ecology. CRC Press, Boca Raton, Florida.

Krofel M, Jonozovic M, Jerina K. 2012. Demography and mortality patterns of removed brown bears in a heavily exploited population. Ursus **23:**91–103.

Linnell JD, Swenson JE, Anderson R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation **4:**345–349.

Mustoni A, et al. 2003. Planning the brown bear *Ursus arctos* reintroduction in the Adamello Brenta Natural Park. A tool to establish a metapopulation in the central-eastern Alps. Hystrix **14:**3–27.

Peters W, Hebblewhite M, Cavedon M, Pedrotti L, Mustoni A, Zibordi F, Groff C, Zanin M, Cagnacci F. 2015. Resource selection and connectivity reveal conservation challenges for reintroduced brown bears in the Italian Alps. Biological Conservation **186:**123–133.

Plummer M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 1–10 in Kurt H, Friedrich L, Achim Z, editors. Proceedings of the 3rd international workshop on distributed statistical computing. Technische Universität Wien, Vienna.

R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rovero F, Mtui A, Kitegile A, Jacob P, Araldi A, Tenan S. 2015. Primates decline rapidly in unprotected forests: evidence from a monitoring program with data constraints. PLOS ONE **10** (e0118330) DOI: 10.1371/journal.pone.0118330.

Schaub M, Abadi F. 2010. Integrated population models: a novel analysis framework for deeper insights into population dynamics. Journal of Ornithology **152:**227–237.

Schaub M, Aebischer A, Gimenez O, Berger S, Arlettaz R. 2010. Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. Biological Conservation **143:**1911–1918.

Servanty S, Choquet R, Baubet É, Brandt S, Gaillard JM, Schaub M, Toïgo C, Lebreton JD, Buoro M, Gimenez O. 2010. Assessing whether mortality is additive using marked animals: a Bayesian state-space modeling approach. Ecology **91:**1916–1923.

Steyaert SM, Endrestøl A, Hacklaender K, Swenson JE, Zedrosser A. 2012. The mating system of the brown bear *Ursus arctos*. Mammal Review **42:**12–34.

Tenan S, Adrover J, Navarro AM, Sergio F, Tavecchia G. 2012. Demographic consequences of poison-related mortality in a threatened bird of prey. PLOS ONE **7** (e49187) DOI: 10.1371/journal.pone.0049187.

Woodroffe R, Ginsberg JR. 1998. Edge effects and the extinction of populations inside protected areas. Science **280:**2126–2128.

Zedrosser A, Steyaert SM, Gossow H, Swenson JE. 2011. Brown bear conservation and the ghost of persecution past. Biological Conservation **144:**2163–2170.