Regulated hunting causes life history makeover in bears

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Management of large carnivores is among the most controversial topics in natural resource administration. Regulated hunting is a centrepiece of many carnivore management programs and, although a number of examples of hunting effects on population dynamics, body-size distributions, and life history in other wildlife have been observed, its effects on life history and demography of large carnivores remain poorly documented. We report results from a 30-year study of brown bears (*Ursus arctos*) analysed using an integrated hierarchical approach. Our study revealed that regulated hunting has severely disrupted the interplay between age-specific survival and environmental factors, altered the consequences of reproductive strategies, and changed reproductive values and life expectancy in a population of the world's largest terrestrial carnivore. Protective measures and sustainable management have led to numerical recovery of several populations of large carnivores, but managers and policy makers should be aware of the extent to which regulated hunting may be influencing vital rates, thereby reshaping the life history of apex predators.

Few organisms and natural processes remain untouched by human intervention [1]. Large carnivores and predation are no exception. Attempts to control and manage wildlife that compete with humans for the apex of shared food webs are responsible for the demise of some large carnivore species [2] and the present-day patterns in the abundance and distribution of those species that remain extant [3,4]. Well-known examples include declines in the distribution and abundance of lions (*Panthera leo*) in Africa [5], tigers (*Panthera tigris*) in Asia [6], and brown bears in North America [7] and Europe [8]. The latter is a particularly good example of enormous changes attributable to manipulation by humans. State-financed bounties introduced in the 1600-1700s aimed for, and nearly accomplished, complete eradication of bears from central and northern Europe by the early 20th century [9]. Subsequent protective measures have allowed range expansion [10] and numerical recovery to levels approximating those at the end of the industrial revolution in some regions [9]. Today, regulated, but intensive, hunting pressure has again resulted in a population decline in parts of northern Europe [11].

Less conspicuous than effects on abundance and distribution, yet important, are the effects that management has on the interaction between vital rates and their intrinsic and extrinsic determinants. Individual variation in recruitment and survival in the context of various drivers governs the dynamics of wild animal populations; their demographic makeup [12], their interaction with current and future environments [13], the realization of their ecological role [14], and ultimately their trajectories and fates [15]. Although several individual-based longitudinal studies of carnivore demography have been carried out [16] and examples of population dynamic impacts of hunting have been reported [17], we still lack comprehensive documentation of how hunting, in concert with individual and environmental factors, influences vital rates in hunted carnivore populations. These effects are better documented and understood in ungulate populations, where hunting, particularly highly selective trophy hunting, has been the subject of intensive study for decades [18,19]. Selective hunting impacts demographic rates in some age and sex classes to a greater extent than in others [20]. Such change alters survivorship and fertility schedules, inevitably impacting population dynamics, life history and the distribution of body and trophy trait sizes [21,22]. It is not surprising that corresponding examples and insights for carnivore populations are mostly lacking, considering the difficulty of monitoring rare and elusive species and analysing sparse ecological data. Taking advantage of a unique individual-based dataset from a hunted brown bear population that has been monitored continuously and intensively in Sweden since 1985 (Figure 1), we estimated cause-specific mortality and recruitment parameters jointly, as well as the effects of key intrinsic and extrinsic factors on these parameters. We did so using a Bayesian multistate capture-recapture model that combined information from physical captures, telemetry, re-sightings, and dead recoveries (Supplementary Figure 1). Transitions between states are modelled across multiple years and between three annual biological seasons (mating, hyperphagia, and denning) consistent with the timing of major life history events during a year. The integrated approach for estimating vital rates revealed pronounced influences of individual attributes and environmental characteristics on both survival and reproduction. Most striking is the central role of hunting in the interplay between vital rates and their drivers (Figures 2 and 3), with direct consequences for fitness.

Once they have reached adulthood, the risk of predation that apex predators experience from non-human sources is typically low [23-25]. Legal hunting, one of the primary tools for defraying, or at least mitigating the socioeconomic and political costs of the co-existence of humans with wildlife [26,27], maintains a source of mortality that is unique in how it selects its targets. Bears are exposed to the highest mortality risk early in life (Figure 3). For cubs-of-the-year, legal hunting is not a direct threat, because family groups are protected from hunting by law [28], although it may already play an indirect role at that early age, as infanticide is boosted by the removal of territorial males through hunting [29]. During the second year of life, death due to legal hunting becomes a factor, but other sources of mortality, although substantially reduced, are still the primary threat (Figure 3). After this age, hunting mortality takes over as the leading cause of death, claiming 74% of instrumented adult (>3y) male bears and 72% of adult females. This positive relationship between hunting mortality risk and age counters the natural pattern of reduced mortality during adulthood in large mammals [30]. Increased adult mortality can change the demographic makeup of wild populations, lead to social instability, alter life histories, and cause evolutionary changes [31-33].

Regulated hunting has profoundly altered the severity and the shape of age-specific mortality [31], thereby redefining not only how many individuals survive to live another year, but also which individuals and under what conditions (Figures 2 and 3, Supplementary Tables

2 and 8). Aside from a positive age effect on mortality, legal hunting mortality was also influenced by hunting pressure (Supplementary Tables 2 and 8), and, at least for females, increased with yearling body size and road density (Supplementary Table 2). Even climatic conditions affected a bear's probability of making it through the fall hunting season; male bears experienced a reduced risk when winters were more severe (Supplementary Table 8), presumably due to earlier entry into a winter den for hibernation [34]. Indeed, den entry correlates with first snowfall and ambient temperature for male bears in our study area [35]. Even in cases where the timing of den entry falls outside of the hunting season, pre-denning behaviours, which include reduced movement [34], may decrease exposure to hunters. The potential modulating effect of winter weather on vulnerability to hunting is noteworthy. Increasingly short and milder winters may extend the period during which bears are vulnerable to legal hunting. Early start of hibernation has been hypothesized as a strategy for predator avoidance in small mammals, as well as in female brown bears [36,37]. This would explain why severe winters had no discernible effect on hunting mortality of female bears in our study, who usually start to hibernate earlier than male bears [34,37]. Additionally, previous studies have shown that bears try to avoid human disturbance during hibernation by selecting den sites far from roads or in concealed and rugged terrain. [38-40]. Changing environmental conditions, that affect denning and possibly other aspects of bear ecology, could be taken into account when setting hunting seasons and regulations, but uncertainty about future climatic conditions and increased climate variability [41] may pose a challenge for planning and setting hunting seasons.

In contrast to the central role of hunting in the interplay between vital rates and their determinants, only age, among the factors we tested, had an influence on the risk of mortality due to causes other than legal hunting; this was the case for both males and females. Cubs-of-the-year were the exception; their mother's age and the severity of the preceding winter appeared to play some role in survival (Supplementary Table 4). Older females survived better during spring (outside the hunting season), reproduced more often (Figure 3b, Supplementary Table 5), produced larger litters (Figure 3b, Supplementary Table 7), and their cubs had a higher probability of surviving their first spring (Figure 3b, Supplementary Table 3). For most of their lives, male bears were more vulnerable to hunting and other mortalities, than females. This was particularly pronounced during the subadult and early adult stage (Figure 3c), usually a time of dispersal and thus elevated risk in a male bear's life [42].

The protection of family groups from hunting creates a strong link between survival and reproduction, further amplifying the influence of management on the life history of bears. Although legal hunting mortality for solitary females increases with age, females are accompanied by offspring for a substantial proportion (29 %) of hunting seasons they experience during their life (>5y, Figure 1), an effective protection against legal hunting, which is limited to solitary individuals by regulation. Interestingly, although most cubs are weaned during their second spring, some litters stay with their mother for an extra year. This creates the setting for a trade-off between the increased protection afforded females and their offspring during the hunting season and the loss in reproductive opportunities, as females with yearling cubs have a markedly lower probability of reproducing during the following year than solitary females. Perhaps we are already observing the results of intensive human-caused selection on life history strategies: It has previously been suggested [43] that contrasting average litter sizes in different brown bear populations may be partially explained by differences in the duration and intensity of human persecution. In our study population, the proportion of litters that remains with their mother for an extra year has increased during the past 30 years, from 12% during the first, 14% during the second, and 34% during the third and most recent decade (Supplementary Figure 3, Supplementary Table 6). However, this change in maternal care duration also coincides with a period of population growth (Supplementary Figure 2), and further study is needed to disentangle the potential effects of density dependence and hunting.

Changes in two important age-specific life history descriptors, life expectancy and reproductive value, further attest to the magnitude of the demographic impact of hunting. For example, between 1992 and 2014, the life expectancy of yearlings dropped from 8.8 years during years with low hunting pressure to 5.2 years at times when hunting pressure was at its highest (Figure 4). Reproductive value, the number of future female offspring born to a female of a given age, was similarly depressed by hunting pressure (Figure 4).

The example of the Scandinavian brown bear shows that numerical success manifested in the partial recovery of European [10] and North American [44] carnivore populations after a reprieve from centuries of persecution bent on extirpation does not automatically imply the re-establishment of untouched apex predator demography and life history. These results do not inform the debate whether unaltered “wild” carnivore populations are a desired or even attainable goal of management [45]. They should, however, raise awareness among managers and policy makers to the pronounced and comprehensive effect of regulated hunting on carnivore ecology, even in partially recovered and sustainably managed populations. Although hunted populations may be stable or growing under sustainable management regimes, changes in vital rates and a modulating effect on the influence of intrinsic and extrinsic determinants can alter the fitness consequences of life history strategies, ultimately transforming the makeup of populations, modifying traits represented within, and potentially driving evolutionary change.

Methods

Capture and telemetry The study area consist of 13,000 km^2 of rolling low mountainous terrain in Dalarna and Gävleborg counties in south-central Sweden (approximately 61° N, 14° E). The elevations range from about 200m a.s.l. in the southeastern part to about 1.000 m a.s.l. in the western part, but only a minority of the area is above timberline, which is about 750m a.s.l. The area is covered by an intensively managed boreal forest interspersed with natural bogs and lakes. The dominating tree species are Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*), but deciduous trees like mountain birch (*Betula pubsecens*), silver birch (*Betula pendula*), aspen (*Populus tremula*) and grey alder (*Alnus incana*) are common [46]. The mean temperatures in January and July are -7° C and 15° C, respectively. Snow cover lasts from late October until early May and the vegetation period is about 150-180 days [47]. Average precipitation is ~ 600-1.000 mm annually [48]. In the study area, human settlements are concentrated in the north and south, with only few high-traffic roads (i.e., main public roads; 0.14 km/km^2). However, isolated houses (mainly cabins) and both paved and gravel roads with low traffic volumes (e.g., roads used for forestry, or roads to private property, with very little traffic compared with high-traffic roads) are distributed throughout the study area (0.3 and 0.7 km/km^2 for cabins and low-traffic roads, respectively) [49]. Bears are intensively hunted in the entire area.

During the study period (1985 - 2014), brown bears were darted from a helicopter using a remote drug delivery system shortly after den emergence in late April and beginning of May. Most bears were first captured as yearlings while accompanying their radiomarked mothers, or by detection of tracks in the snow from helicopter or snowmobile.

We exclusively used VHF-radio-transmitters (Telonics®, model 500) for adult (≥4 years) bears from 1985 until 2002. Since 2003, mainly GPS-GSM-collars (GPS Plus, Vectronic Aerospace GmbH, Germany) were used on adult bears. Yearling brown bears were not fitted with a radio-collar, due to their fast growth pattern. Instead, a sterile peretonial radiotransmitter (Telonics®, model IMP/400/L HC) was implanted in their peritoneal cavity. Also all adult bears fitted with a GPS-collar were implanted with a peretonial transmitter to serve as back-up in case of battery or technical failure of the collar. For details regarding capture and handling of bears in our study refer to Arnemo et al. [50]. All capture and handling conformed to the current laws regulating the treatment of animals in Sweden and were approved by the appropriate Swedish management agency (Naturvårdsverket) and ethical committee (Djuretiska nämden i Uppsala).

Bears equipped with VHF-collars or only implants were located weekly by telemetry using standard triangulation methods from the ground or from an aircraft (helicopter or fixed-wing) during their nondenning period. The GPS collars were scheduled to take one position every 30 minutes. These positions were stored in the collar until seven relocations had been collected, which then were transferred as a text message via the GSM network to a ground station. The implantable radio-transmitters had a battery life of approximately 4-5 years, which assured that specific bears could be relocated and recaptured even after transmitter loss or failure [51].

We included in this study data from 424 telemetried brown bears (189 females, 235 males) and 244 litters (557 cubs-of-the-year) associated with 82 females.

Hunting and dead recovery Anyone with a general hunting license who has passed the annual shooting test, has hunting rights to an area, and a weapon legal for big game hunting can kill bears in Sweden. An annual quota limits the harvest of bears. These quotas have increased steadily during the study period (1981-1989: 46.2 ± 9.8 bears/year (mean ± SD), 1990-1999: 56.9 ± 9.6, 2000-2009: 127.9 ± 70.9, 2010-2014: 296.4 ± 17.7; overall range: 36-319) [11]. At the same time, the Swedish bear population also increased in size (nationwide population size estimates: 1975-1976: 400-600 bears; 1991: 771; 1993: 834; 1994: 950-1200; 2000: 2006-2465; 2005: 2350-2900; 2008: 2968-3667; 2013: 2782; Supplementary Figure 2) [11]. There was some regional variation in the starting dates for the bear hunting season until 2001, with starting dates usually between late August and early September. In 2002, the national authorities set a common start date of 21 August throughout the country [11]. The bear hunting season in Sweden generally lasts 1-2 months and stops either at the scheduled season end date or when the quota is reached [28]. Until the quota has been filled, hunters may shoot any solitary bear encountered, regardless of sex and age, although in some years and regions sex-specific quotas were used. Since 1986, all members of bear family groups, i.e., mothers and their accompanying offspring of any age, are protected from hunting, which strengthened the previous regulation that only protected cubs of the year and their mothers [11].

By regulation, successful hunters are required to report their kill to the authorities on the day of the kill and provide information on date and location of death of the bear, as well as age, sex, body measurements, and a tooth for age determination to official inspectors by the county government. In addition, every bear found dead must be reported to the police and is examined by the Swedish State Veterinary Institute to determine cause of death. Location of death, sex, age, and body measurements are recorded. In addition to legal hunting, brown bears in Sweden die from a variety of other causes, such as intraspecific predation, vehicle collision, depredation control, and poaching [28]. A tally over dead recoveries (N=313) by cause is provided in Supplementary Table 1.

Individual attributes. In addition to their reproductive states, we used sex, age, and body size as individual attributes in the analysis. For bears not captured as yearlings with their mother, a vestigial first premolar was extracted during capture for age determination [52]. We used head circumference at the yearling age as a surrogate measure of overall size of a bear [53]. We measured head circumference in cm (at the widest part of the zygomatic arch between eyes and ears) with a tape measure. For bears that were captured for the first time when they were older than 1y, we used the mean individual deviation from a general population growth curve [54] to estimate head-circumference at age 1.

Environmental attributes. Climate data were obtained from the Swedish Meteorological and Hydrological Institute (SMHI). Station-specific time series within the study area were converted using the R package *mba* [55] to interpolated raster series (1985-2014; 5-day temporal resolution; 5-km spatial resolution) for each of the following climate variables: minimum daily temperature, maximum daily temperature, average daily temperature, daily precipitation, and average daily snow depth. From the base climate variable rasters, we then derived new annual or seasonal rasters of quantities which we believed to be particularly relevant for hibernating species such as the brown bear: winter severity (number of days below -10°C between Nov and Apr) and days of frost after last snow melt in spring

[56]; In addition, using the same raster dimensions and resolution, we extracted rasters of road density estimates (Swedish National Road Database, NVDB; obtained from the Swedish Transport Administration, www.trafikverket.se) and an annual bear density index. The later was derived by combining bear genetics from scat collection efforts and the Swedish Large Carnivore Observation Index (LCOI) [57]. County-specific density index distributions were created based on scats, and LCOI was used to apply a temporal correction. From these, annual density grids were created from 1998-2015, with a 1-km spatial resolution. For individuals preceding 1998, the 1998 grid was used, as similar data from earlier were not available. Hunting statistics suggest quite stable population estimates before 1998 [11]. Finally, to account for variation across our study area, we averaged raster values of the aforementioned environmental variables associated with the area inhabited by each bear using a circular home range with a sex-specific average home range diameter (18.33 km for males and 8.31 km for females and unweaned males [58]) around either the median of that individual's relocations or the center of the individual's 100% adaptive Local Convex Hull (*a*-LoCoH) polygon. The method used was chosen based on a visual inspection of how well the circle covered the individual's recorded positions. We used the number of bears killed by hunters annually as a proxy for hunting pressure across the study entire area. To capture the potential additional effect of large-scale changes in management and the population, we divided the study period into decades, and used "period" as a temporal covariate in our models.

Multi-state capture recapture model. We developed Bayesian multi-state hierarchical models to jointly estimate survival and reproductive parameters for females, as well as the influence of individual and environmental covariates on vital rates in both sexes. At the core of each model were three primary processes: (I) transitions between the states a bear could be in, (II) covariate effects on the constituent vital rates (cause-specific survival and reproductive parameters), and (III) the observation process. Due to differences in life history patterns between the sexes, separate models were fitted for males and females, with the male model a simplified version of the female model (recruitment component removed, Supplementary Figure 1).

For females, we modeled transitions between 6 possible states:

- State 1: alive and solitary
- State 2: alive with cubs-of-the-year
- State 3: alive with yearling cubs
- State 4: newly dead due to legal hunting
- State 5: newly dead due to other causes (natural and human-caused)
- State 6: dead

The entire study period consisted of 30 years. Each year was divided into three seasons reflecting the biology and major events in the life of bears in Scandinavia:

- *Mating season* (1 May – 31 July): Emergence form the winter den, separation from yearling and older cubs, mating.
- *Berry season* (1 Aug – 31 Oct): Hyperphagia and elevated fat storage in preparation for hibernation, hunting season
- *Denning season* (1 Nov – 30 Apr). Den entry, hibernation, parturition.

Transitions in the model follow this seasonal schedule, with season-specific parameter estimates and biologically appropriate constraints. Transitions are estimated as state changes from the beginning of one season to the beginning of the next. For females, state transitions from the mating to the berry season are captured by the following matrix, with rows corresponding to states of departure and columns states of arrival:

$$\Psi = \begin{bmatrix} (1-w) & 0 & 0 & 0 & w & 0 \\ (1-w)(1-S)^n & (1-w)(1-(1-S)^n) & 0 & 0 & w & 0 \\ (1-w)P & 0 & (1-w)(1-P) & 0 & w & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \qquad (1)$$

Here, w represents the probability of dying due to causes other than legal hunting, *S* is the survival of cubs-of-the-year, *n* the size of the litter, and *P* the joint probability of weaning or losing an entire litter of yearling cubs. Use of the "newly dead" states (S4 and S5) allowed us to distinguish between cause-specific mortalities. S6 ("dead") is an absorbent state.

Transitions from the berry season to the denning season include legal hunting as an additional source of mortality h:

$$\Psi = \begin{bmatrix} (1-w-h) & 0 & 0 & h & w & 0 \\ (1-w-h)(1-S)^n & (1-w-h)(1-(1-S)^n) & 0 & h & w & 0 \\ (1-w-h)P & 0 & (1-w-h)(1-P) & h & w & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \qquad (2)$$

Transitions from winter to spring differ from the other seasonal transition, as this time-step includes recruitment (females may emerge from the winter den with cubs-of-the-year) and aging (mothers in state 2 with dependent cubs-of-the-year transition to state 3 with to yearling litters).

$$\Psi = \begin{bmatrix} (1-w)(1-f) & (1-w)f & 0 & 0 & w & 0 \\ (1-w)(1-S)^n & 0 & (1-w)(1-(1-S)^n) & 0 & w & 0 \\ (1-w) & 0 & 0 & 0 & w & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \qquad (3)$$

The additional fecundity parameter *f* is the probability that a female that was in state 1 during the previous season emerges from the winter den with dependent cubs-of-the-year. This in turn is the joint probability of parturition and survival of the cubs to shortly after den exit.

For males, reproductive states were excluded from the model, thereby reducing transitions to a 4x4 matrix, with the following states:

- State 1: alive and solitary
- State 2: newly dead due to legal hunting
- State 3: newly dead due to other causes (natural and human-caused)
- State 4: dead

Transitions from the mating season to the berry season, as well as from the denning season to the mating season, contain only mortality due to causes other than legal hunting:

$$\Psi = \begin{bmatrix} (1-w) & 0 & w & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{bmatrix} \tag{4}$$

Legal hunting becomes an additional source of mortality in the matrix defining transitions from the berry season to the denning season.

$$\Psi = \begin{bmatrix} (1-w-h) & h & w & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{bmatrix} \tag{5}$$

Recruitment parameters and cub survival.

At the earliest (with few exceptions), individuals were first captured and instrumented during their second spring (i.e. age 1y). Consequently, survival of cubs-of-the-year had to be estimated using a different procedure than for older, marked bears. Throughout the project, a substantial effort was made to observe all adult females several times throughout the year to determine and monitor their reproductive status. Litter size was determined by counting cubs-of-the-year accompanying instrumented mothers from the air or the ground 3 times annually, after den emergency in early May, after the mating season in early July, and shortly before hibernation in September and October [59]. We used these observations of instrumented females with dependent offspring to estimate all recruitment parameters and the season-specific survival of cubs-of-the-year.

Litter size $N_{COY,spring}$ (at den emergence from the winter den, cubs-of-the-year) was modeled as a truncated Poisson distribution with mean λ. The truncation was used to permit only observable litter sizes

$$N_{COY,mating\ season} \sim Poisson(\lambda), \quad \text{with } 0 < N_{COY,mating\ season} < 5 \tag{6}$$

During the first year following den emergence, observed seasonal litter sizes wer modeled as draws from binomial distributions:

$$N_{COY,berry\ season} \sim Binomial(N_{COY,mating\ season}, S_{mating\ season}) \tag{7}$$

$$N_{COY,denning\ season} \sim Binomial(N_{COY,berry\ season}, S_{berry\ season}) \tag{8}$$

$$N_{C1Y,matging\ season} \sim Binomial(N_{COY,denning\ season}, S_{denning\ season}) \tag{9}$$

Due to a lack of pronounced sexual dimorphism in brown bear cubs and the fact that observations took place before cubs were old enough for capture and marking, we did not estimate sex-specific survival rates for cubs-of-the-year. Survival of offspring that lived to age 1y, can be estimated directly via the transition matrix. Although most offspring separate from their mother during their second spring, some females retain their litters for an additional year. In order to account for the resulting variation in reproductive states, we estimated the joint probability P of either weaning a litter of yearlings or losing the entire litter to other causes as part of the state transition process (see equations 1 and 2).

Covariates and variable selection

Effects of extrinsic and intrinsic covariates on key parameters were incorporated into the model via logistic regression, with the exception of effects on litter size, which was realized through a Poisson regression with the litter size parameter as the response, followed by truncation (equation 6). All continuous variables were standardized ($x_{st} = (x - \bar{x})/sd(x)$). In order to identify variables whose impact warranted inclusion in the model, we utilized Bayesian variable selection based partially on Kuok & Mallick [60,61]. This approach employs an inclusion parameter for each predictor term, which captures the probability that the coefficient associated with that term differs from 0. Once a full version of the model had been fitted and inclusion parameters estimated, we refit a simplified version of the model with parameter retention guided by review of the posterior distribution of both the parameter in question and the inclusion parameter.

Imperfect detection

States and fates of individual bears are not always observable. Instrumented animals may lose their telemetry collars, devices may fail, or batteries become depleted before recapture/recollaring. Similarly, mortalities due to causes other than legal hunting are not always detected (collar drop/loss/failure before or during death). We therefore used a hierarchical approach that models states as latent variables

$$z_{i,t} \sim Multinomial(\psi[z_{i,t-1}, i, t-1,]) \tag{10}$$

and links them with the data through an explicitly modeled observation process:

$$y[i,t] \sim Bernoulli(p[z_{i,t}, i, t]) \tag{11}$$

By definition, the detection of individuals “newly dead due to legal hunting” is perfect. Recovery of individuals that died due to other causes is < 1, and is estimated following Kéry & Schaub [62] by including an additional parameter R in the transition matrix (e.g. here shown as an example for the case based on female state transitions from the mating season to the berry season, equation 1) such that:

$$\Psi = \begin{bmatrix} (1-w) & (1-w) & 0 & 0 & wR & w(1-R) \\ (1-w)(1-S)^n & (1-w)(1-(1-S)^n) & 0 & 0 & wR & w(1-R) \\ (1-w)P & 0 & (1-w)(1-P) & 0 & wR & w(1-R) \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \qquad (12)$$

The recovery probability r signifies the probability that a bear that has died is detected (i.e. enters the state “newly dead due causes other than legal hunting”), instead of transitioning directly from a live state into the “dead” state for which $p = 0$. Illegal hunting is among these alternative sources of mortality, and it has targeted large carnivores in Scandinavia, including our study area [63]. As has been shown [64], both perfectly known mortalities and cryptic poaching can lead to biases, when it is assumed that individuals lost to monitoring are dying for the same reasons and at the same rate as animals with known fates. In the case of perfectly documented deaths, the bias can stem from the fact that, by definition, animals without know fates cannot fall victim to this source of mortality. This bias is not of concern in the present study, as the Bayesian multistate hierarchical model estimates states for all individuals, including individuals that have been lost to monitoring and for which fates are unknown. Since the detection (recovery) probability of individuals in state “newly dead due to legal hunting” is 1, individuals without known fates – i.e. with a trailing sequence of unknown states – are not permitted to enter that state. The model-estimated vital rates (state transitions) are the result of both observed and predicted states, and therefore account for the fact that only individuals with observed fates could have died due to legal hunting. Not as readily excluded is the second cause of bias, caused by the potential link between an individual’s probability to being lost to monitoring and its probability of dying due to an imperfectly documented cause of death. However, only one source of mortality – illegal hunting – is liable to produce unexplained loss during monitoring. By definition, illegal hunting is a highly cryptic cause of death, as poachers go to lengths to avoid discovery and prosecution [63]. Cryptic poaching was estimated to contribute half (51%) of total mortality among wolves in Sweden, with as many as 2 illegal kills missed for every one detected. Rates of poaching are area specific and are much lower for bears in the area pertinent to the study than in Scandinavian wolves. This is presumably in part due to long-standing and generous hunting season for the bears and due to significantly lower levels of controversy surrounding bear management. Twenty-five of 424 instrumented bears (5.9%) included in the study have unknown fates, and illegal hunting was confirmed as the cause of mortality for 7 (2.2%) of 313 bears that died during the study period (Supplementary Table 1). Just as telling, out of a total of 39 instrumented bears that were lost to monitoring during the study period, 14 were eventually recovered dead (56%, often several years after having lost contact), with only one of these due to confirmed illegal hunting (Supplementary Table 1).

Our approach did not allow us to identify separate rates of competing risks in the “other” category, as these rates cannot be distinguished from cause-specific recovery probabilities. Therefore, the parameter r represents the joint recovery probability for deaths due to any death aside from legal hunting and w the corresponding probability of mortality. Illegal hunting is liable to contribute only a fraction to this joint class of mortalities, likely limiting its biasing effect.

Nonetheless, more work is needed to help untangle the effect of different sources of mortality and to isolate potential biases introduced by cryptic poaching. A promising approach for accomplishing this has already been described [63], which estimates a latent cryptic poaching parameter to explain changes in population size. However, this approach requires population size estimation, which we did not incorporate in our model, where vital rates were estimated directly as individual transitions.

Model implementation. Bayesian models were fitted using JAGS [65] via the R2jags package [66] in R [67]. Uniform or flat priors were used for all unknown parameters. Probabilities were sampled on the logit scale, therefore their priors were informative after inverse-logit transformation. We ran 10 parallel chains for each model implementation, with a burn-in of 10,000 iterations and another 3000 iterations post-convergence. Chains were thinned by utilizing every 10th element in each chain. This configuration resulted in 3000 samples from posterior distributions of all parameters estimated by the model. We assessed convergence to a stationary distribution using trace plots for model parameters to ensure adequate mixing and by using the Gelman and Rubin diagnostic R-hat; [68]. We summarized posterior distributions of the unknown parameters by their means and 95% credible intervals.

Parameter estimates Supplementary Tables 2 – 9 show coefficient estimates from regressions with focal ecological parameters as the response. Regressions were implemented within the Bayesian integrated population dynamic model and selection of predictor terms was guided by Bayesian variable selection, partially following the approach by Kuo & Mallick [60,61]. All continuous variables were standardized ($x_{st} = (x - \bar{x})/sd(x)$); levels for categorical variables are indicated. We calculated the average proportion of hunting seasons experienced by females (>4y) accompanied by dependent cubs as follows. We populated missing cells in the state history matrix (individuals and years represented by rows and columns respectively) with the most common trajectory (sequence of states for a given individual) predicted by the Bayesian model. We then divided the total time spent by all female bears with cubs during the hunting season by the time spent without cubs.

Calculation of life history metrics. We used parameters estimated by the Bayesian hierarchical multi-state model to populate a stage (reproductive) and age-structured population projection matrix. Multi-annual age classes were expanded into annual age classes, with the last class (16y+) extending from 16 to 35 to include the maximum observed life span of bears in our study population. Together with cubs-of-the-year (0-1), this yielded a total number of age classes x_{max} of 36. Probabilities populating this 108 x 108 projection matrix (3 reproductive states x 36 age classes) were derived from model-predicted vital rate estimates; with seasonal survival probabilities multiplied to yield annual probabilities. Using the matrix, we then calculated age-class specific life expectancy and reproductive values for female bears [69]. We used R package popbio [70] for population projection and to determine the stable age/stage distribution. The proportion of individuals that survive to the beginning of age class *x* was calculated as:

$$l_x = n_x/n_0 \tag{13}$$

based on a starting population size of n_0 and n_x individuals that survive to the beginning of subsequent age classes *x*. For the remainder of the analysis, reproductive states were aggregated within age classes. We calculated the mid-point survivorship, i.e. the proportion of individuals that survive to the midpoint between age class *x* and *x*+1 as

$$L_x = (l_x + l_{x+1})/2 \tag{14}$$

The sum of age classes T_x remaining to all individuals *k* that have survived to the beginning of age class *x* is

$$T_x = T_{x-1} - Lx - 1; \quad T_0 = \sum_{i=0}^{k} T_x - L_{x-1} \tag{15}$$

Finally, we calculated the average life expectancy of an individual that has survived to the beginning of age class x as

$$e_x = T_x/l_x \tag{16}$$

To obtain the reproductive value [71], we used two additional variables: the expected number of female offspring m_x produced by an individual during age x and the intrinsic rate of natural increase *r*, obtained from the population projection matrix. Reproductive value v_x, the number of future female offspring born to a female that has survived to the beginning of age class *x*, can then be calculated as

$$v_x = \frac{\sum_y^{x_{max}} e^{-ry} l_y m_y}{e^{-rx} l_x} \tag{17}$$

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Author contributions RB and CB conceived the study with JES, AM, and TC. JES, AZ, AF coordinated collection and compilation of field data. RB, IMR, and AZ extracted and formatted intrinsic and extrinsic covariates. RB and CB developed, implemented and analysed the model. RB wrote the first draft of the paper; all authors contributed to subsequent versions.

Competing financial interests

The authors declare no competing financial interests.

Figure legends

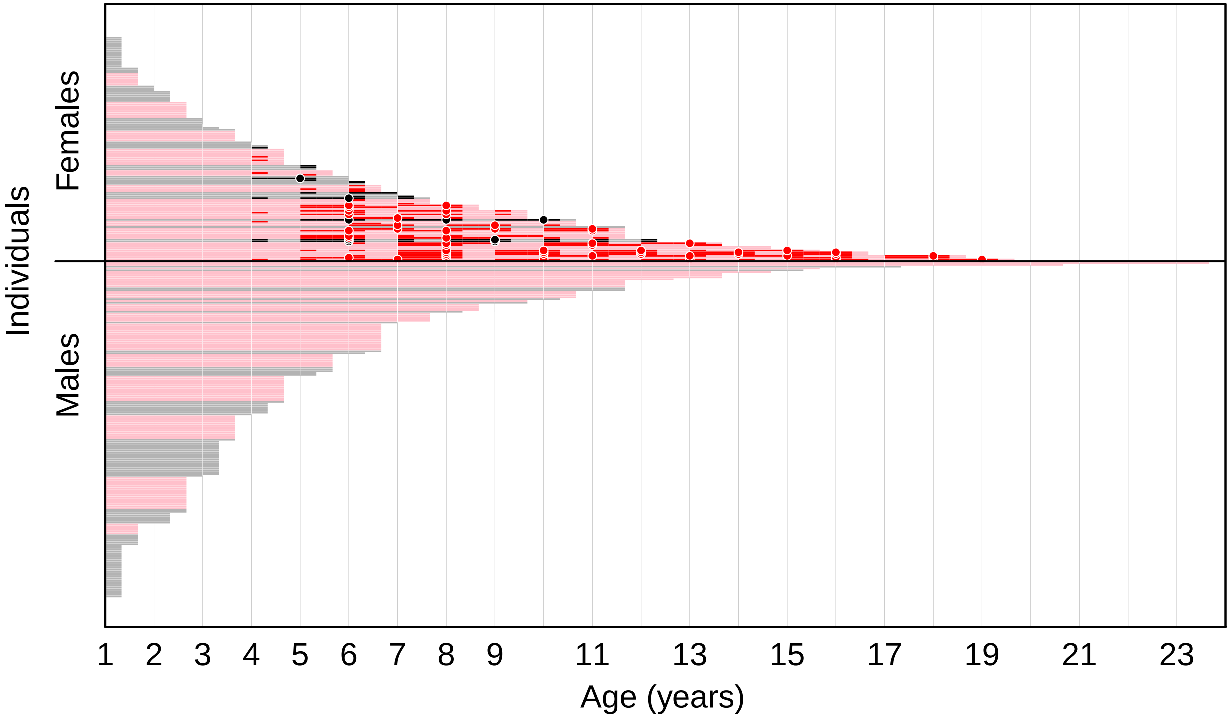
Fig. 1. The lives and deaths of instrumented brown bears in Sweden. Each horizontal line represents the lifeline of a single bear from the time it reaches 1 year of age (the youngest age of capture) to its death (either detected or model-predicted). Only individuals (150 females, 190 males) are included that were recovered dead (N=313) or were lost from monitoring and for which death was predicted by the model to have occurred within the study period (N=27). The cause of death is indicated with pink (legal hunting) and grey (other causes) line colours. Whereas most young bears die from other causes, hunting becomes increasingly prevalent as the cause of death with progressing age. For females, periods associated with dependent offspring are represented by darker horizontal lines tracking the lifeline; recruitment events (i.e. when offspring reach 1 year of age) are indicated by dots. Females may reproduce as young as 4 years, but are rarely successful in raising offspring before they are 5 or 6 years old. Only bears first captured before age 5y are included.

Figure 2. Vital rates and important determinants for brown bears in Scandinavia. Path diagrams for females (**a**) and males (**b**) show effects of intrinsic and extrinsic factors on survival (grey circles, females and males) and recruitment parameters (green circles, only females). Arrows are associated with a plus or minus sign signifying the direction of significant effects. Hunting takes a central role; intrinsic and extrinsic factors influence hunting mortality directly (thicker black arrows) and, in females (**b**), also indirectly through variables that affect recruitment, association with dependent offspring, and therefore exemption from legal hunting per regulation.

Figure 3. Age specific vital rates in brown bears. (**a**) Cause-specific mortality of female bears (N=189 for ages ≥ 1y). Hunting mortality is shown for all females irrespective of reproductive status (dark blue) and for adult females once individuals with dependent young during the hunting season have been excluded (light blue). (**b**) Age-dependent estimates of the probability of emerging from the winter den with a litter of new-born cubs, litter size, and the survival of cubs-of-the-year during the mating season. (**c**) Cause specific mortality of male bears (N= 235 for ages ≥ 1y). Estimates for cubs-of-the-year (0y, N=557) in (**a**) and (**c**) are joint estimates for male and female cubs, as sex was not identified until capture (1y at the earliest). The relative width of each violin along its longitudinal axis indicates the posterior density distribution of the parameter (shorter violins =

narrower credible interval); means are indicated by white dots. Violins are associated with discrete age classes, but are offset slightly along the x-axis to aid visibility.

Fig. 4. Changes in life history descriptors for female bears in response to different levels of hunting pressure. (**a**) Hunting mortality experienced by a given age class at different levels of hunting pressure. Mortality estimates are shown for female bears without dependent young; bears accompanied by offspring are exempt from hunting. Panel (**a**) serves as a reference for (**b**) and (**c**): line colours correspond to different hunting mortality levels, increasing from dark blue (lowest) to dark red (highest). Life expectancy (**b**) is the number of years remaining in an individual’s life once it has reached the age class indicated on the x-axis, and reproductive value (**c**) is the future number of female offspring expected to be produced by a female in a given age class.


Females
Males
Individuals
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17
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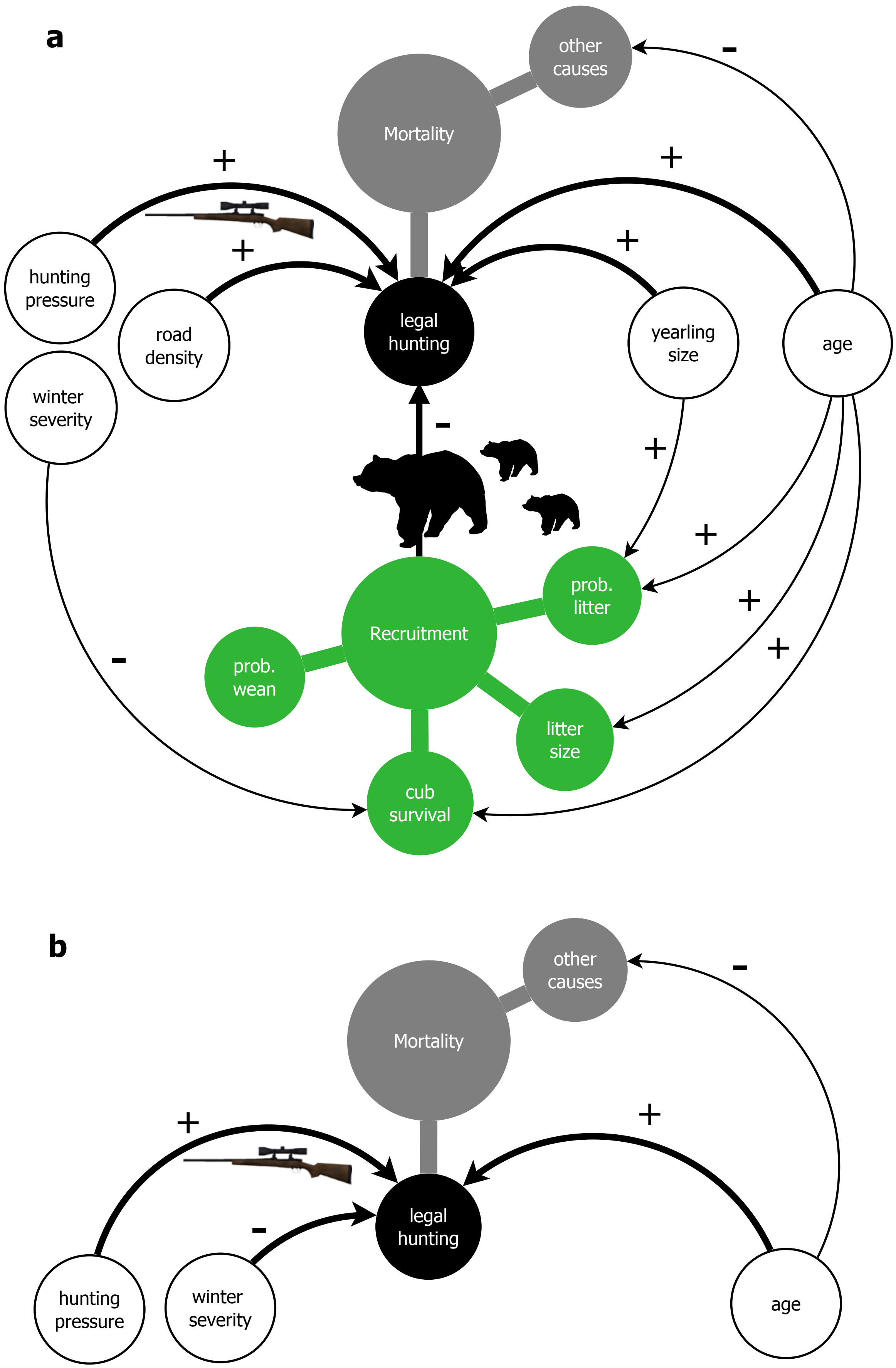
23
Age (years)


a
other causes
Mortality
-
+
+
hunting pressure
road density
legal hunting
+
+
yearling size
age
winter severity
-
+
+
prob. litter
+
+
Recruitment
prob. wean
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litter size
cub survival
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Mortality
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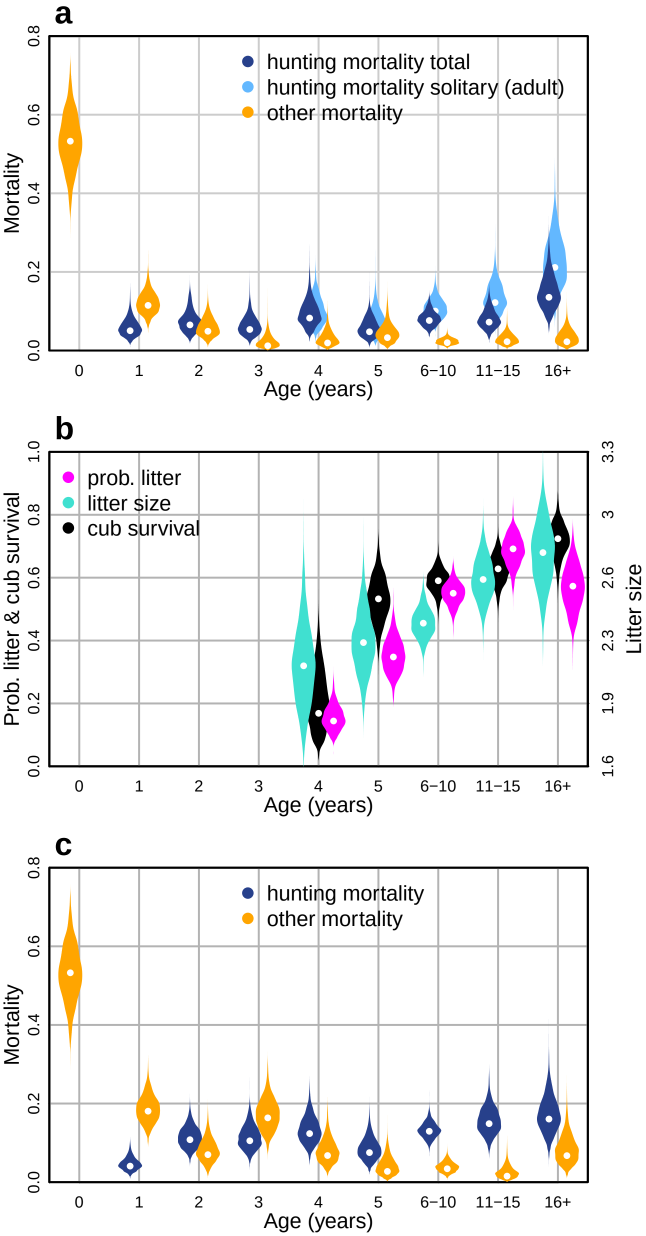
legal hunting
-
hunting pressure
winter severity
age


a
hunting mortality total
hunting mortality solitary (adult)
other mortality
Mortality
0.0
0.2
0.4
0.6
0.8
0
1
2
3
4
5
6−10
11−15
16+
Age (years)
b
prob. litter
litter size
cub survival
Prob. litter & cub survival
0.0
0.2
0.4
0.6
0.8
1.0
Litter size
1.6
1.9
2.3
2.6
3
3.3
0
1
2
3
4
5
6−10
11−15
16+
Age (years)
c
hunting mortality
other mortality
Mortality
0.0
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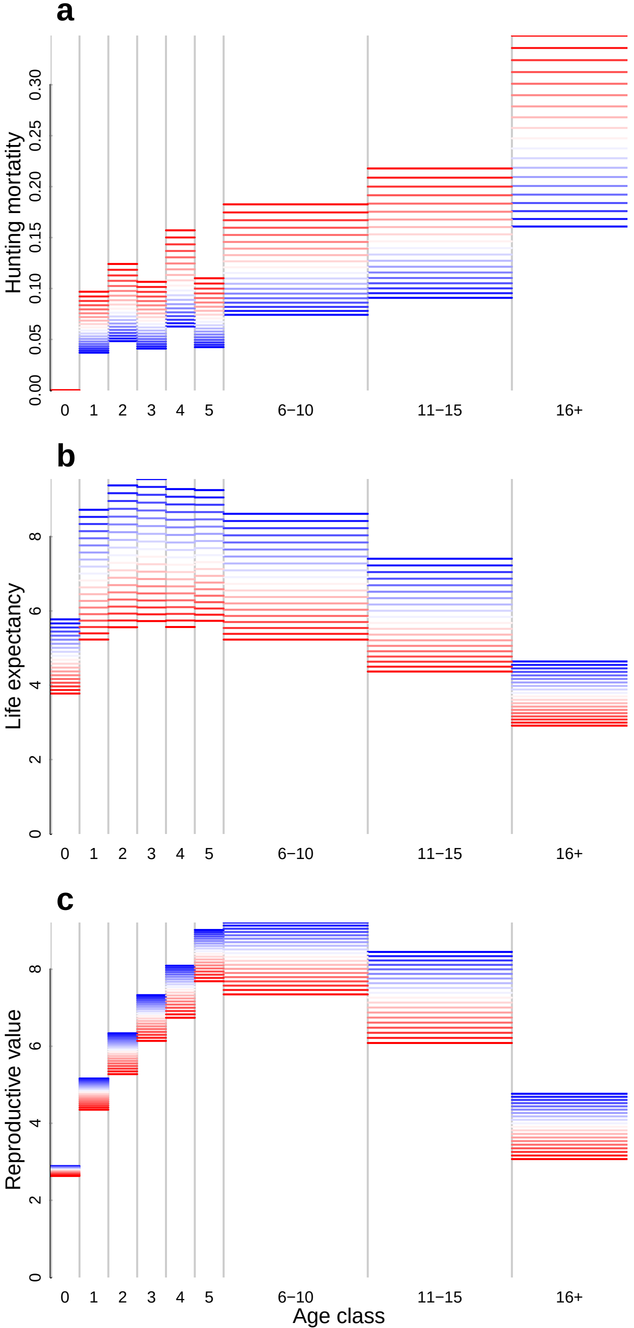
16+
Age (years)


a
Hunting mortatity
0.00
0.05
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0.20
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0.30
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1
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3
4
5
6−10
11−15
16+
b
Life expectancy
0
2
4
6
8
0
1
2
3
4
5
6−10
11−15
16+
c
Reproductive value
0
2
4
6
8
0
1
2
3
4
5
6−10
11−15
16+
Age class