

Regulated hunting re-shapes the life history of brown 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 programmes and, although a number 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. Protection and sustainable management have led to numerical recovery of several populations of large carnivores, but managers and policymakers 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 intervention¹. 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 species² 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 Africa⁵, tigers (*Panthera tigris*) in Asia⁶ and brown bears in North America⁷ and Europe⁸. The latter is a particularly good example of enormous changes attributable to manipulation by humans. State-financed bounties introduced in the 1600s and 1700s aimed for, and nearly accomplished, complete eradication of bears from central and northern Europe by the early twentieth century⁹. Subsequent protective measures have allowed range expansion¹⁰ and numerical recovery to levels approximating those at the end of the industrial revolution in some regions⁹. Today, regulated, but intensive, hunting pressure has again resulted in a population decline in parts of northern Europe¹¹.

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 makeup¹², their interaction with current and future environments¹³, the realization of their ecological role¹⁴ and ultimately their trajectories and fates¹⁵. Although several individual-based longitudinal studies of carnivore demography have been carried out¹⁶ and examples of population dynamic effects of hunting have been reported¹⁷, 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 affects vital rates in some age and sex classes to a greater extent than in others²⁰. The resulting changes in survivorship and fertility schedules lead to modifications in 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 (Fig. 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 Fig. 1). Transitions between states were 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 (Figs. 2 and 3), with direct consequences for fitness.

Results and discussion

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 coexistence 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

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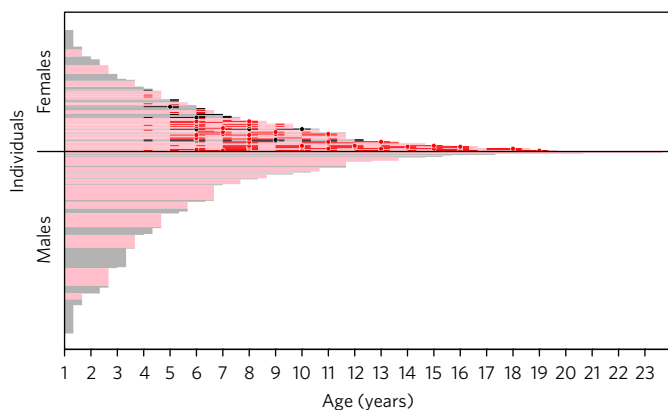


Fig. 1 | The lives and deaths of instrumented brown bears in Sweden. Each horizontal line represents the lifeline of a single bear from the time it reaches 1 year of age (the youngest age of capture) to its death (either detected or model-predicted). Only individuals (150 females and 190 males) that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

mortality risk early in life (Fig. 3). For cubs of the year, legal hunting is not a direct threat, because family groups are protected from hunting by law²⁸, although it may already play an indirect role at that early age, as infanticide is boosted by the removal of territorial males through hunting²⁹. 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 (Fig. 3). After this age, hunting mortality takes over as the leading cause of death, claiming 74% of instrumented adult (>3 yr) 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 mammals³⁰. 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 mortality³¹, thereby redefining not only how many individuals survive to live another year, but also which individuals and under what conditions (Figs. 2 and 3 and 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 hibernation³⁴. Indeed, den entry correlates with first snowfall and ambient temperature for male bears in our study area³⁵. Even in cases where the timing of den entry falls outside the hunting season, pre-denning behaviours, which include reduced movement³⁴, may decrease exposure to hunters. The potential modulating effect of winter weather on vulnerability to hunting is noteworthy. Increasingly

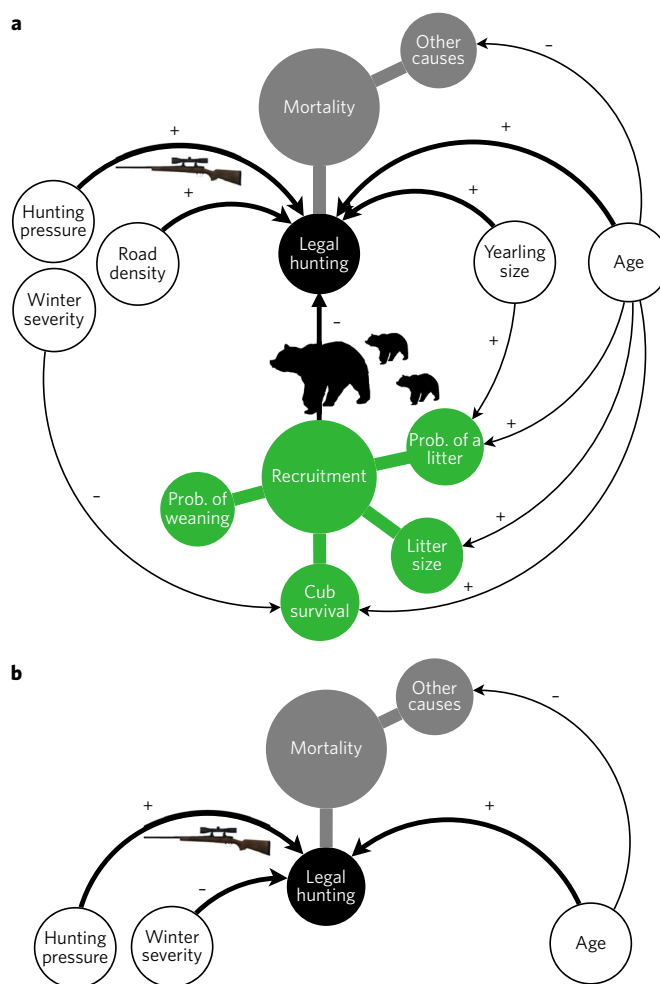


Fig. 2 | Vital rates and important determinants for brown bears in Scandinavia. **a, b**, Path diagrams for females (**a**) and males (**b**) show the effects of intrinsic and extrinsic factors on survival (grey circles, both females and males) and recruitment parameters (green circles, only females). Arrows are associated with a plus or minus sign signifying the direction of significant effects (95% credible interval of effects estimates do not overlap 0). Hunting takes a central role; both 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 (as per regulation).

short and mild 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 the males^{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 variability⁴¹ 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

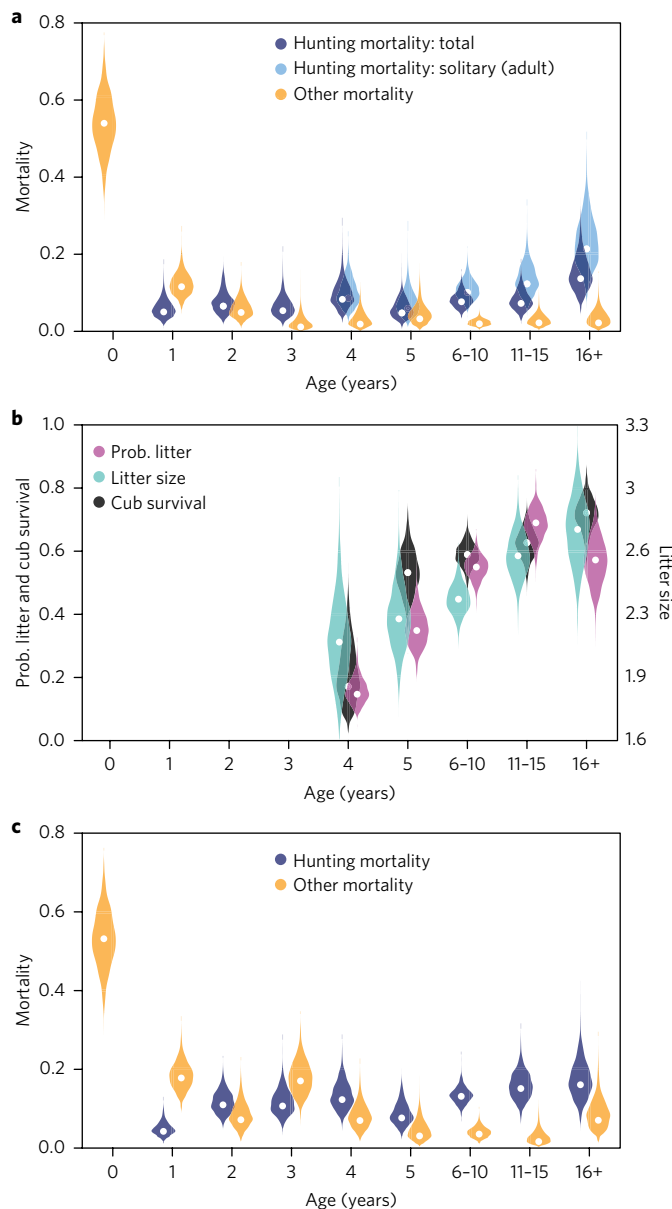


Fig. 3 | Age-specific vital rates in brown bears. **a**, Cause-specific mortality of female bears ($N=189$ for ages ≥ 1 yr). Hunting mortality is shown for all females irrespective of reproductive status (dark blue) and for adult females once individuals with dependent young during the hunting season have been excluded (light blue). **b**, Age-dependent estimates of the probability of emerging from the winter den with a litter of newborn 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 ≥ 1 yr). Estimates for cubs of the year (0 yr, $N=557$) in **a, c** are joint estimates for male and female cubs, as sex was not identified until capture (1 yr at the earliest). The relative width of each violin along the y axis indicates the posterior density distribution of the parameter (shorter violins = narrower credible intervals); means are indicated by white dots. Violins are associated with discrete age classes, but are offset slightly along the x axis to aid visibility.

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 (Fig. 3b and Supplementary Table 5), produced larger litters (Fig. 3b and

Supplementary Table 7), and their cubs had a higher probability of surviving their first spring (Fig. 3b and Supplementary Table 3). For most of their lives, male bears were more vulnerable than females to hunting and other mortalities. This was particularly pronounced during the subadult and early adult stages (Fig. 3c), usually a time of dispersal and thus elevated risk in a male bear's life⁴².

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 (>5 yr; Fig. 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 to 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 suggested⁴³ 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 remain 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 Fig. 3 and Supplementary Table 6). However, this change in maternal care duration also coincides with a period of population growth (Supplementary Fig. 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 yr during years with low hunting pressure to 5.2 yr at times when hunting pressure was at its highest (Fig. 4). Reproductive value, the number of future female offspring born to a female of a given age, was similarly depressed by hunting pressure (Fig. 4).

The example of the Scandinavian brown bear shows that numerical success manifested in the partial recovery of European¹⁰ and North American⁴⁴ 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 management⁴⁵. They should, however, raise awareness among managers and policymakers 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 consists of 13,000 km² of rolling low mountainous terrain in Dalarna and Gävleborg counties in south-central Sweden (approximately 61° N, 14° E). The elevations range from about 200 m above sea level (a.s.l.) in the southeastern part to about 1000 m a.s.l. in the western part, but only a minority of the area is above timberline, which is about 750 m a.s.l. The area is covered by an intensively managed boreal forest interspersed with natural

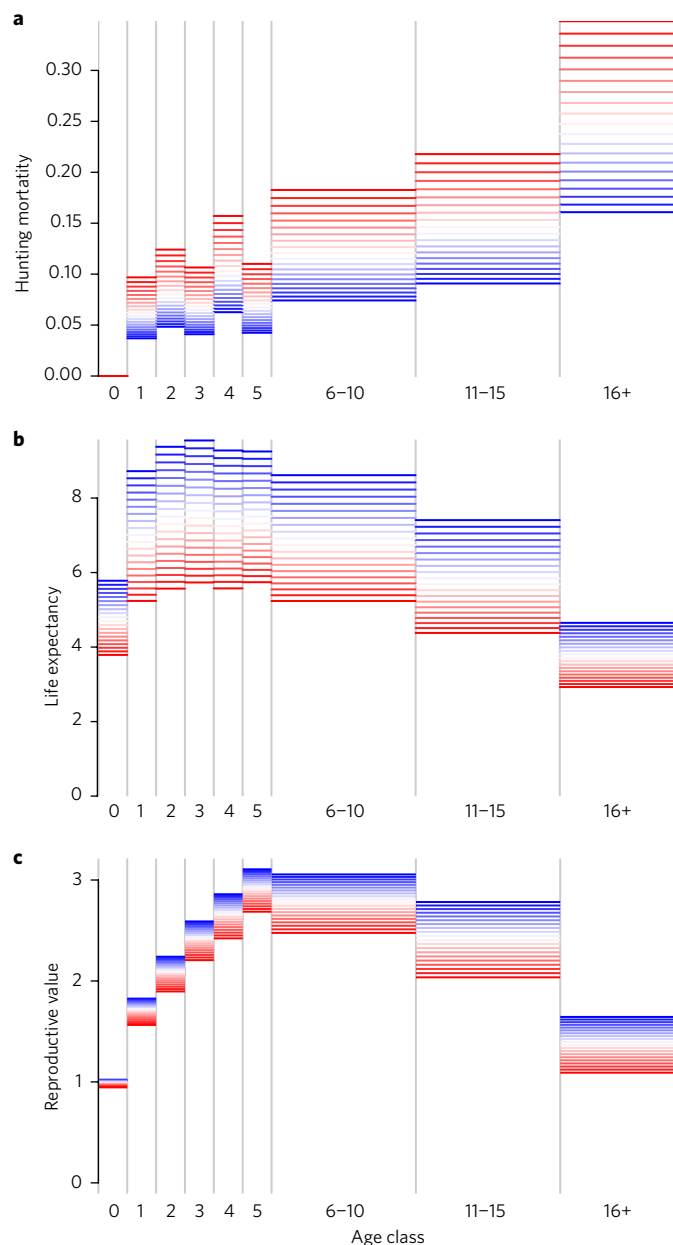


Fig. 4 | Changes in life history descriptors for female bears in response to different levels of hunting pressure. **a**, Hunting mortality experienced by a given age class at different levels of hunting pressure. Mortality estimates are shown for female bears without dependent young; bears accompanied by offspring are exempt from hunting. **b,c**, Panel **a** serves as a reference for **b,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 number of future female offspring expected to be produced by a female in a given age class.

bogs and lakes. The dominating tree species are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), but deciduous trees such as mountain birch (*Betula pubescens*), silver birch (*Betula pendula*), aspen (*Populus tremula*) and grey alder (*Alnus incana*) are also common⁴⁶. 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 days¹⁷. Average precipitation is ~ 600 – 1000 mm annually⁴⁸. In the study area, human settlements are concentrated in the north and south, with only few high-traffic roads (main public roads; 0.14 km km⁻²). However, isolated houses (mainly cabins) and both paved and gravel

roads with low traffic volumes (such as 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 early May. Most bears were first captured as yearlings while accompanying their radiomarked mothers, or by detection (from helicopter or snowmobile) of tracks in the snow.

We exclusively used VHF radio transmitters (Telonics, model 500) for adult (≥ 4 yr) bears from 1985 to 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 peritoneal radiotransmitter (Telonics, model IMP/400/L HC) was implanted in their peritoneal cavity. Furthermore, all adult bears fitted with a GPS collar were implanted with a peritoneal transmitter to serve as backup in case of battery or technical failure of the collar. For details regarding capture and handling of bears in our study, refer to previously published work³⁰. 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 nämnden 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 aircraft) during their non-denning 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 radiotransmitters had a battery life of approximately 4–5 years, which assured that specific bears could be relocated and recaptured even after transmitter loss or failure⁵¹.

We included in this study data from 424 brown bears (189 females and 235 males) tracked with VHF/GPS 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 per year (mean \pm s.d.); 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 size¹¹ (Supplementary Fig. 2). 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 country¹¹. 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 reached²⁸. 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, that is, 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 mothers¹¹.

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 poaching²⁸. A tally of 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 determination⁵². We used head circumference at the yearling age as a surrogate measure of overall size of a bear⁵³. We measured head circumference in cm (at the widest part of the zygomatic arch between the eyes and ears) with a tape measure. For bears that were captured for the first time when they were older than 1 yr, we used the mean individual deviation from a general population growth curve⁵⁴ 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 that we believed to be particularly relevant for hibernating species such as the brown bear: winter severity (number of days below -10°C between November and April) and days of frost after the last snow melt in spring⁵⁶. 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 latter 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 1998⁵¹. 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 males⁵⁸) around either the median of that individual's relocations or the centre 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 entire study 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.

Multistate capture–recapture model. We developed Bayesian multistate 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: (1) transitions between the states a bear could be in; (2) covariate effects on the constituent vital rates (cause-specific survival and reproductive parameters); and (3) the observation process. Owing to differences in life history patterns between the sexes, separate models were fitted for males and females, with the male model being a simplified version of the female model (with recruitment component removed; Supplementary Fig. 1).

For females, we modelled 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 to 31 July): emergence from the winter den, separation from yearling and older cubs, and mating.

Berry season (1 Aug to 31 Oct): hyperphagia and elevated fat storage in preparation for hibernation; hunting season.

Denning season (1 Nov to 30 Apr): den entry, hibernation and 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:

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

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 is 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 absorbing state.

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

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

Transitions from the denning to the mating season 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 ageing (mothers in S2 with dependent cubs of the year transition to S3 with yearling litters).

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

The additional fecundity parameter f is the probability that a female that was in S1 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 4×4 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:

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

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

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

Recruitment parameters and cub survival. At the earliest (with few exceptions), individuals were first captured and instrumented during their second spring (aged 1 yr). 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 three times annually: after den emergence in early May, after the mating season in early July, and shortly before hibernation in September and October⁵⁹. 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 $N_{\text{COY, spring}}$ (at den emergence from the winter den; COY, cubs of the year) was modelled as a truncated Poisson distribution with mean λ . The truncation was used to permit only observable litter sizes

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

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

$$N_{\text{COY, berryseason}} \sim \text{Binomial}(N_{\text{COY, matingseason}}, S_{\text{matingseason}}) \quad (7)$$

$$N_{\text{COY, denningseason}} \sim \text{Binomial}(N_{\text{COY, berryseason}}, S_{\text{berryseason}}) \quad (8)$$

$$N_{\text{CIY, matingseason}} \sim \text{Binomial}(N_{\text{COY, denningseason}}, S_{\text{denningseason}}) \quad (9)$$

Owing 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 1 yr 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. To account for the resulting variation in reproductive states, we estimated the joint probability P of either weaning a litter of yearlings (CIY) 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 ($x_{st} = (x - \bar{x})/s.d.(x)$). To identify variables whose impact warranted inclusion in the model, we used Bayesian variable selection based partially on previous work^{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 refitted 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 (due to collar drop/loss/failure before or during death). We therefore used a hierarchical approach that models states $z_{i,t}$ as latent variables

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

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

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

where p is the detection probability conditional on an individual's state at time t . 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 previous work⁶² by including an additional parameter R in the transition matrix (shown here as an example for the case based on female state transitions from the mating season to the berry season, equation 1) such that:

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

The recovery probability R signifies the probability that a bear that has died is detected (that is, enters the state 'newly dead due to 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 area⁶³. As has been shown⁶⁴, 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 known 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 the state 'newly dead due to legal hunting' is 1, individuals without known fates—those 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 of 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 prosecution⁶⁵. Cryptic poaching was estimated to contribute half (51%) of total mortality among wolves (*Canis lupus*) in Sweden, with as many as two 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 may in part be due to the longstanding and generous hunting season for bears and due to significantly lower levels of controversy surrounding bear management. 25 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, probably 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 described⁶³, 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 JAGS⁶⁵ via the R2jags package⁶⁶ in R⁶⁷. Uniform or flat priors were used for all unknown parameters. Probabilities were sampled on the logit scale, and so 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 2000 iterations post-convergence. Chains were thinned by utilizing every 20th element in each chain. This configuration resulted in 1000 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 $R\text{-hat}$ 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 a previously published approach^{60,61}. All continuous variables were standardized; levels for categorical variables are indicated. We calculated the average proportion of hunting seasons experienced by females (> 4 yr) 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 multistate 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 (16+ yr) 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 yr), this yielded a total number of age classes $k = 36$. Probabilities populating this 108×108 projection matrix (3 reproductive states \times 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 bears⁶⁹. 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 age class x . For the remainder of the analysis, reproductive states were aggregated within age classes. We calculated the midpoint survivorship, that is, 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 that have survived to the beginning of age class x is

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

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 value⁷¹, 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

$$v_x = \frac{\sum_{y=x}^k e^{-ry} l_y m_y}{e^{-rx} l_x} \quad (17)$$

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Code availability. The JAGS code for the Bayesian hierarchical multistate model is available in the Supplementary Information.

Data availability. The data used to generate figures displaying quantitative information are available in the Supplementary Information. The individual-based brown bear monitoring data are available from the corresponding author upon reasonable request.

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Author contributions

R.B. and C.B. conceived the study with J.E.S., A.M. and T.C. J.E.S., A.Z. and A.F. coordinated collection and compilation of field data. R.B., I.M.R. and A.Z. extracted and formatted intrinsic and extrinsic covariates. R.B. and C.B. developed, implemented and analysed the model. R.B. wrote the first draft of the paper; all authors contributed to subsequent versions.

Competing interests

The authors declare no competing financial interests.

Additional information

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▶ Experimental design

1. Sample size

Describe how sample size was determined.

The data used for the analysis were obtained during a longterm (30 years) monitoring study. Each year an effort was made to capture and VHF/GPS collar as many bears as logistically and economically possible, although female bears were prioritized, due management aspects of the research and because this yielded additional information on dependent offspring. Annual sample sizes increased as time progressed, due to development in capture methodology and growing population size.

2. Data exclusions

Describe any data exclusions.

We excluded data associated with individuals for which year of birth or sex was unknown at the time of the analysis, as these were essential individual attributes needed in the analysis.

3. Replication

Describe whether the experimental findings were reliably reproduced.

The data were obtained during an observational study. No experiments were conducted.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

The data were obtained during an observational study. No experiments were conducted. Almost all female bears and a substantial portion of male bears in the study area were captured. Although we cannot be certain that the captured portion of the population is fully representative of the entire population, a number of individual, spatial, and temporal covariates were included in the analysis to account for and minimize biases. Note that our analysis accounted for imperfect detection through the use of capture-recapture methodology.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

The data were obtained during an observational study. No experiments were conducted (e.g. no treatment groups). However:
 1) Capture and data collection (primarily telemetry) was conducted following strict protocols and standard wildlife capture and telemetry procedures.
 2) Parameter estimation was conducted in a comprehensive Bayesian framework where coefficient estimation were based purely on the data, without manipulation/modulation by observers.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted
- A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

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7. Software

Describe the software used to analyze the data in this study.

R
JAGS

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). [Nature Methods guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

N/A

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

N/A

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

N/A

b. Describe the method of cell line authentication used.

N/A

c. Report whether the cell lines were tested for mycoplasma contamination.

N/A

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

N/A

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

Use of animals in our study included:

- 1) capture and marking of live brown bears (*Ursus arctos*)
- 2) monitoring of marked live brown bears using VHF/GPS telemetry
- 3) recording information (location, date, cause of death) on dead bears (hunting and natural mortality)

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 nämnden i Uppsala).

Policy information about [studies involving human research participants](#)

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

N/A

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