

Harvesting can also affect the expression of certain behaviours in surviving individuals. For example, harvesting is thought to increase the rate of social reorganization in some species, which promotes male turnover and new encounters between individuals, thus leading to an increase of sexually selected infanticide (SSI) [12,13]. SSI occurs when competition between members of one sex for the other sex may make it advantageous for an individual (usually a male) to eliminate offspring of another individual [14]. SSI occurs in a wide array of species, including Rodentia (see [15] for review), non-human primates (e.g. Hanuman langur *Presbytis entellus* [16,17]; but see also [18]) and carnivores [19]. Carnivores are often hunted, with harvest generally focused on males, particularly when they are hunted for trophies [20,21]. In species with SSI, harvesting males can have an indirect negative effect on the population by reducing juvenile survival [4,21].

Although several studies have quantified how behaviour can affect reproductive success and survival [22–24], only a few have linked behaviour to population dynamics [4,25]. The influence of behaviour on population dynamics and its interaction with harvest is difficult to quantify in long-lived wild species, as it requires long-term data on the survival, reproduction and behaviour of individuals as well as on population dynamics [25]. The goal of this study was to assess the direct and indirect effects of hunting through SSI on the dynamics of a brown bear (*U. arctos*) population.

To evaluate the influence of hunting and SSI on population dynamics, we performed prospective and retrospective perturbation analyses for periods with different hunting pressures. Our goals were to determine how demographic rates and population growth vary under low and high hunting pressure and to determine the relative importance of demographic rates, including cub survival, on population growth. We predicted (P1) that hunting would have a direct negative effect on population growth by reducing the survival rates of age classes available for hunting. We also expected (P2) that hunting would have an indirect negative effect on population growth through SSI, owing to lower cub survival. Further, we predicted (P3) that cub survival would have a lower elasticity (i.e. relative influence on population growth) than most other demographic rates, using the prospective analyses [26]. As demographic rates with low elasticity, such as juvenile survival, usually have high variability [26], we predicted (P4) that cub survival would explain a substantial proportion of the variation in population growth using the retrospective analyses. Thus, by evaluating the importance of cub survival, a proxy of SSI, for population growth, we aimed to better understand the effects of behaviour on the population dynamics of a long-lived wild mammal species. We hoped that the results would increase our understanding of both the direct and indirect effects of hunting on population dynamics.

The Scandinavian brown bear offers a unique opportunity to evaluate not only the direct effects of hunting, but also the potential indirect effects that hunting may have on population dynamics through behaviour. SSI is common in Scandinavian brown bears [12,27,28], although its occurrence in North American brown bear populations is controversial [29,30] (but see also [31]). Nevertheless, the species has characteristics that should promote SSI [19]. The long period of maternal care (between 1.5 and 4.5 years) reduces the availability of reproductive females and a female may become receptive only 2–4 days after losing her young during the mating season [32–34]. Therefore, males would

benefit from killing cubs of the year (hereafter referred to as cubs) during the mating season [28,34]. Swenson *et al.* [35] found that 85% of the mortality of cubs occurs during the mating season in Scandinavia, and all confirmed cub mortalities during the mating season were cases of infanticide (14 cubs in 2009–2011) [27]. There is therefore strong evidence of SSI in the Scandinavian brown bear population [28] and it seems to greatly affect cub survival. Moreover, brown bears are hunted in Scandinavia and there is evidence that SSI might increase with hunting pressure [12,35,36]. Indeed, cub survival is lower (from 28% to 42%) when at least one male had been killed in the same area 0.5, and especially 1.5, years earlier [12]. This cub mortality is thought to be caused by SSI, which is promoted by the male turnover created when males die during the hunting season [12,35–37]: when a resident male is killed, he will be replaced by a male who is probably unrelated to cubs present in the area, thus leading to an increase in SSI [12,13].

2. Methods

(a) Study area and population

The study area was located in southcentral Sweden (61° N, 15° E), mostly in the counties of Dalarna and Gävleborg. It is composed of 13 000 km² of rolling landscape (from 200 to 1000 m) with intensively managed boreal forest dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) [38]. The Scandinavian population is one of the most productive brown bear populations in the world [39], with an early mean age at first reproduction (4.71 years [36]) and short interlitter intervals (1.6 years [35]). Density of bears in the study area increased over our study period (1990–2011), although not evenly nor constantly [40,41]. Demographic consequences of this increase are unknown, but they are unlikely to affect subadult and adult survival [42]. Indeed, hunting is the main cause of mortality for bears aged 1 year and older, and 84.4% of deaths of marked bears in our study area were caused by humans from 1990 to 2011. Most natural mortalities are intraspecific predation and affect mostly yearlings and subadults [43]. Another study has also suggested that the population did not seem to be food limited [40]. Therefore, hunting is the main driver of the population and fluctuations in harvest rates explain 83% of the population trend [44].

(b) Data collection

(i) Captures and monitoring

Females without young and females accompanied by yearlings were immobilized with a dart gun from a helicopter. Captures were carried out after den emergence from mid-April to early May. Females with cubs were not captured for animal welfare reasons. All females were marked individually with tattoos (inside the upper lip), and passive integrated transponder (PIT) tags under anaesthesia. Females were fitted with radiotransmitters, radio-implants (Telonics, model IMP/40/L HC), or both. Females were originally fitted with VHF radiotransmitters (Telonics, model 500). However, since 2003, most (gradually from 6% to 90%) females captured or recaptured were fitted with GPS–GMS transmitters (GPS Plus, Vectronic Aerospace GmbH). A vestigial premolar tooth was collected from all females not captured as a yearling to estimate age based on the cementum annuli in the root (Mattson's Inc., Milltown, MT). For further information about capture and handling of bears, see Arnemo *et al.* [45] and Zedrosser *et al.* [46].

Females fitted with VHF radiotransmitters were located once a week during the non-denning period using standard triangulation

methods [47]. Females fitted with GPS radiotransmitters were located at least once every 30 min during the active period. To ascertain timing of cub loss, females with cubs were observed from a helicopter three times per year: at den emergence (early May), after the breeding season (mid-July) and in autumn before den entrance (late September to early October). Most cub loss (80.9%) occurred during the breeding season (mid-May to mid-July). Litter size was defined as the number of cubs observed with the mother at the first sighting following den emergence.

(ii) Hunting

Bears were hunted across the entire study area. Hunting started in late August or early September and lasted until either 15 October or when the quota within the designated area had been reached, whichever came first. Hunters could kill any solitary bear, regardless of sex and age. The only protected segment of the population was family groups (i.e. females and their dependent offspring of any age) [48].

After harvesting a bear, hunters were required to report the kill and present the carcass to an official inspector on the same day. Hunters were required to give information about hunting method, sex of the bear, body weight and the location of the harvest. In addition, hunters provided a premolar tooth for age determination. The sex ratio of individuals harvested was 45% female and 55% male. The Swedish bear hunt and reporting of hunter-killed bears are further described by Bischof *et al.* [48].

(c) Statistical analyses

(i) Subperiods of consistent hunting pressure

As demographic models are better performed on relatively long periods of time, we tested the effect of hunting on the population by comparing the population dynamics in periods of different hunting pressure. We calculated the yearly hunting pressure in our study area as the number of marked bears that had been killed legally divided by the number of marked bears available for hunting (i.e. the number of marked bears known to be alive at the start of the hunting season, excluding family groups). We tested whether there were periods with statistically different hunting pressure over the study period by dividing the study period into 2–5 subperiods and calculating the Calinski–Harabasz (CH) index for all possible chronological combinations of subperiods. The CH index is computed as $[\text{trace } B/(k-1)]/[\text{trace } W/(n-k)]$, where n and k are the total number of items and the number of clusters in the solution, respectively. The B and W terms are the between- and within-cluster sum of squares and cross product matrices, and the trace is the sum of the main diagonal of the matrices [49,50]. Higher values of the CH index represent higher between-cluster variance relative to within-cluster variance. We compared the CH index for the most probable chronological groups and determined the most likely number of subperiods. The maximum hierarchy level was used to indicate the correct number of partitions in the data, which maximized between-cluster variance and minimized within-cluster variance.

(ii) Demographic parameters

We modelled only the female component of the population, because in brown bears, as in most large mammals, it is the number of reproductive females that limits reproduction [51,52]. To ascertain which age classes best represented the life stages in the population, we tested different age-class models and selected the one that best described the survival pattern. Model selection was based on Akaike's information criterion corrected for small sample sizes (AICc) [53].

The recapture probability of females alive in the study area was estimated to be 100% [43]. Therefore, survival and reproductive output of the females were assessed from repeated observations

of the individuals. Based on these data, we calculated the mean survival and fecundity for each age class over the study period and for each subperiod. Fecundity rates represent the probability that a female produces a cub the following year ($\text{fecundity}_{t \rightarrow t+1} = \text{survival}_{t \rightarrow t+1} \times \text{reproduction}_{t \rightarrow t+1}$). The demographic rates were calculated from all of the survival and reproduction information available from the females followed during 1990–2011. We lost contact with some females (about 14%) without known mortality. A sensitivity analysis revealed that whether or not we included individuals with truncated life histories did not affect demographic rates (see the electronic supplementary material, table S1). Therefore, we included individuals with unknown mortality for the period they were followed. Demographic rates were used to construct pre-breeding quasi-Leslie matrices describing the transition probabilities between or within age classes from one year to the next [54]. One matrix was built for the entire study period, and other matrices were built on subsets of the data corresponding to each hunting pressure subperiod (1990–2005 and 2006–2011; see Results). Because cubs were not captured, their sex was therefore unknown. All cubs were used for cub survival and fecundity estimations. We assumed that there was no difference in survival between male and female cubs, which has been suggested in our population [55]. Fecundity rates were adjusted using a secondary sex ratio of 50:50 [56].

(iii) Prospective analysis

Prospective analyses predict the change in the asymptotic growth rate that would result from a change in a demographic rate and are independent of past variation in demographic rates [57]. We calculated the asymptotic growth rate of the population (λ , the exponential growth rate at the stable age distribution) for the entire study period and for each hunting pressure subperiod. We calculated elasticities of the population growth rate independently from each matrix for each demographic rate. Elasticities of the population growth are the proportional change in λ resulting from a proportional change in a demographic rate (r_i), $\Delta \log \lambda / \Delta \log r_i$ [54]. Prospective analyses were performed with the 'popbio' package in R [58]; the confidence intervals of λ were calculated with the 'boot.transitions' function.

(iv) Retrospective analysis

Retrospective analyses compare the contributions of past changes in demographic rates with the variation in λ and are not indicative of future changes [57]. We estimated the association between variation in a demographic rate r_i and variation in λ by: $s_i^2 \times v_i$, where s_i is the sensitivity of the population growth rate to a demographic rate r_i , and v_i is the variance of r_i [59]. These associations are presented as contributions to variation in λ , when rescaled as percentages. We did not include covariations of demographic rates in the analysis, owing to low annual sample size. Calculations and statistics were performed using R v. 3.0.0 [60].

3. Results

(a) Subperiods of consistent hunting pressure

Based on the highest CH index, the most likely number of subperiods with different levels of hunting pressure was two (see the electronic supplementary material, table S2). The two subperiods that minimized intragroup variation and maximized intergroup variation were 1990–2005, with low hunting pressure (0.073 ± 0.014 , mean \pm s.e.; figure 1), and 2006–2011, with high hunting pressure (0.199 ± 0.018 ; figure 1). Consequently, we retained these two periods in our subsequent analyses. The sex ratio of bears harvested changed slightly between the two hunting pressure subperiods (48%

