

The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears

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Summary

1. The population dynamic and evolutionary effects of harvesting are receiving growing attention among biologists. Cause-specific estimates of mortality are necessary to determine and compare the magnitude and selectivity of hunting and other types of mortalities. In addition to the logistic and financial constraints on longitudinal studies, they are complicated by the fact that nonhunting mortality in managed populations usually consists of a mix of natural and human-caused factors.
2. We used multistate capture–recapture (MCR) models to estimate cause-specific survival of brown bears (*Ursus arctos*) in two subpopulations in Sweden over a 23-year period. In our analysis, we distinguished between legal hunting and other sources of mortality, such as intraspecific predation, accidents, poaching, and damage control removals. We also tested whether a strong increase in harvest quotas after 1997 in one of the subpopulations affected vulnerability to legal hunting.
3. Although only a fraction of mortalities other than legal hunting could be considered natural, this group of causes showed a general pattern of demographic selectivity expected from natural mortality regimes in populations of long-lived species, namely greater vulnerability of young animals. On the other hand, demographic effects on hunting vulnerability were weak and inconsistent. Our findings support the assumption that hunting and other mortalities were additive.
4. As expected, an increase in hunting pressure coincided with a correspondingly large increase in vulnerability to hunting in the affected subpopulation. Because even unbiased harvest can lead to selective pressures on life-history traits, such as size at primiparity, increasing harvest quotas may not only affect population growth directly, but could also alter optimal life-history strategies in brown bears and other carnivores.
5. Legal hunting is the most conveniently assessed and the most easily managed cause of mortality in many wild populations of large mammals. Although legal hunting is the single-most important cause of mortality for brown bears in Sweden, the combined mortality from other causes is of considerable magnitude and additionally shows greater selectivity in terms of sex and age than legal hunting. Therefore, its role in population dynamics and evolution should not be underestimated.

Key-words: carnivore, compensatory mortality, competing risks, M-SURGE, wildlife management

Introduction

In many naturally regulated populations of large mammals, age-specific mortality has been shown to follow a similar U-shaped pattern irrespective of the proximate causes of mortality (Caughley, 1966; Gaillard, Festa-Bianchet &

Yoccoz, 1998; Gaillard *et al.*, 2000). This is not expected to hold for populations that are heavily affected by human exploitation, where prime-aged individuals that otherwise survive well can also be targeted. Indeed, the selective pressures in harvested marine and terrestrial populations have recently raised concern regarding their long-term evolutionary consequences (Coltman *et al.*, 2003; Kuparinen & Merilä, 2007). It is thus not surprising that science dealing

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with the management and conservation of wild populations focuses increasingly on the effects of hunting on population dynamics and evolution.

We further suspect that the spotlight that hunting is receiving, particularly in large mammals, may be motivated partially by the relative ease with which it can be assessed (hunter surveys, tagging systems, etc.) and that it is arguably the most easily influenced by wildlife managers (e.g. through hunting seasons, quotas, and bag limits). Natural mortality is usually more difficult to detect and hence to estimate. Furthermore, natural mortality schemes are often disturbed and at times replaced by human-caused mortalities other than hunting (vehicle accidents, wildlife damage control, poaching, etc.). This makes the otherwise intuitive separation of 'harvest' and 'natural mortality' (Anderson & Burnham, 1976) less useful, even if cause-specific vulnerability estimates are desired. Yet, because survival is determined by the combination of all causes of death, a comprehensive look at survival requires estimates of the magnitude and selectivity of all mortality causes, including those due to proximate causes other than hunting. Additionally, comparing mortality patterns for different age and sex classes can yield insight into deviations from natural mortality patterns and therefore contemporary selection pressures, and may also help determine the degree of compensation in mortality (Otis & White, 2004; Pedersen *et al.*, 2004; Schaub & Lebreton, 2004a; Lebreton, 2005).

Estimating and contrasting cause-specific mortality in long-lived species requires longitudinal studies, which additionally provide opportunities to evaluate how management actions, such as a major change in harvest quotas, may affect vulnerability patterns. The difficulties and costs associated with such studies may explain why they are rare in large mammals. The most well-known longitudinal studies have been performed on ungulate populations, such as red deer (*Cervus elaphus*) on the island of Rum (Clutton-Brock, Guinness & Albon, 1982) and Soay sheep (*Ovis aries*) on the island of St. Kilda, Scotland (Clutton-Brock & Pemberton, 2004). To our knowledge, no study on large carnivores has yet compared harvest and other mortality patterns under contrasting management regimes.

The Scandinavian Brown Bear Research Project has collected an extensive data set with information on 525 marked brown bears (*Ursus arctos*), spanning 23 years of intensive monitoring. Many of the individuals have been followed from the age of 1 to death, which presents a rare opportunity to assess cause-specific vulnerabilities in a large carnivore species. Our first objective was to estimate age- and sex-specific vulnerability to legal hunting in this population and determine if they are comparable to the patterns observed in other harvested bear populations in North America, where there is evidence for selectivity for younger, inexperienced individuals, especially males (Derocher, Stirling & Calvert, 1997; Noyce & Garshelis, 1997; McLellan *et al.*, 1999). In Bischof *et al.* (2008a), we documented differences between males and females in terms of the variables that explained the age of harvested bears, but could not address vulnerability directly, because that analysis was based solely on harvested bears.

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 (Swenson *et al.*, 1997; Swenson & Sandegren, 1999; Swenson, Dahle & Sandegren, 2001; Sahlén *et al.*, 2006). Consequently, our second objective was to compare the magnitude and demographic selectivity of legal hunting mortality with other mortality sources. We use multistate capture–recapture modelling to estimate and compare the magnitude and demographic selectivity of legal hunting with other mortality causes and discuss our findings in the context of carnivore population dynamics and evolution.

Finally, the potential for compensatory mortality is an important consideration for the management of exploited populations. The effect of changes in harvest intensity (i.e. quotas) is dependent on the degree of compensation this causes in other mortality sources, may they be natural or human caused. A dramatic increase in quotas starting in the mid-1990s in one of our two subpopulations enabled us to look for evidence of compensation by monitoring changes in the vulnerability to hunting and other causes of death before and after hunting pressure increased.

Methods

STUDY AREA

Our two study areas were located in northern and south-central Sweden. The northern study area ('north', 67°N, 18°E) encompasses 12 000 km², the other site ('south', 61°N, 18°E) is 11 500 km² in size. These areas are based on genetically distinct subpopulations that match geographical clusters of bears with no or very little interchange of females (Manel *et al.*, 2004). Both study areas occur within the southern, intermediate, and northern boreal vegetation zones (Nordiska insterrådet, 1984; Bernes, 1994). The study areas are described in detail in Zedrosser, Dahle & Swenson (2006).

Protective measures, implemented in Sweden as early as the end of the 19th century, brought the brown bear population back from the brink of extinction (Swenson *et al.*, 1995). In 2005, the population size of brown bears in Sweden was estimated to be between 2350 and 2900 (Kindberg & Swenson, 2006). Hunting brown bears is legal in Sweden, where a fall season results (in recent years) in the harvest of approximately 5% of the estimated population (Bischof *et al.*, 2008a).

DATA COLLECTION

Most bears were captured from a helicopter with immobilizing darts during the spring (20 March–10 June) from 1984–2006. Captured bears were measured and weighed, and blood, tissue, and hair samples were collected. Unless they were followed from birth, the first premolar was extracted and sent to Matson's, Inc., Milltown, MT, USA for age estimation using counts of cementum annuli layers (Matson *et al.*, 1993). Bears designated for radiotelemetry ($N = 388$) were equipped with collar-mounted radiotransmitters, radioimplants, or both. All bears, including non-instrumented ones ($N = 137$), were marked individually with tattoos (inside of the upper lip), ear tags, and passive integrated transponder (PIT) tags placed subcutaneously between the shoulder blades. Radio-marked bears were recaptured every 2–3 years to collect new measurements

and to exchange used radiotransmitters for ones with new batteries. Great effort was made to capture all yearlings accompanying radio-marked females. Non-instrumented animals were (re)captured opportunistically based on priorities and available funding. Radio-marked bears were located once every 1–2 weeks during the active period (March–November) and sporadically throughout the denning period with standard triangulation from the ground or from a fixed wing aircraft or helicopter. The radiotelemetry portion of the study has generally focused more on females than males. Arnemo *et al.* (2006), Zedrosser *et al.* (2007), and Dahle & Swenson (2003b) provide additional information about the capture of bears, monitoring, and data collection procedures. Capture, manipulation, marking and monitoring of bears complied with current laws regulating the treatment of animals in Sweden and Norway, where a few bears were captured, and were approved by the appropriate ethical committees in both countries.

Recoveries

The main sources for recoveries of bears (outside of regular monitoring activities of radio-tagged bears) were mandatory hunter reporting, dead bears discovered and reported by members of the public, and bears killed as part of damage control activities. By regulation, successful brown bear hunters in Sweden were required to notify the police on the day of the kill, present their bear carcass to an officially appointed inspector and provide information about harvest methods, the sex of the harvested bear, body mass, and kill location. The Swedish brown bear hunt and reporting of hunter-killed bears are described in Bischof *et al.* (2008a). Between 1984 and 2006, 124 marked bears were shot during legal hunting, accounting for 59.6% of all marked bears recovered dead ($N = 208$). Confirmed mortalities of marked bears due to causes other than legal hunting included the following (in order of prevalence and with the proportion of deaths in parentheses):

1. Natural ($N = 28$, 13.5%, mainly intraspecific kills)
2. Damage control removal and self-defense ($N = 23$, 11.1%)
3. Cause unknown ($N = 15$, 7.2%)
4. Death as a result of capture ($N = 7$, 3.4%)
5. Confirmed illegal hunting ($N = 7$, 3.4%)
6. Accident (including traffic) ($N = 4$, 1.9%)

Although a breakdown into these causes would increase resolution in terms of cause-specific mortalities, in our case data limitations and resulting parameter estimation problems for the various transitions (see below), made such distinction unfeasible. It is worth noting that natural mortality (in the sense of nonhuman-caused mortality) constituted only a small portion (13.5%) of confirmed deaths of marked animals and 1/3 of bears dying due to causes other than legal hunting.

MULTISTATE CAPTURE–RECAPTURE ANALYSIS

Model and parameter description

Modelling of movement was the main motivation for the initial development of multistate capture–recapture (MCR) models (Hestbeck, Nichols & Malecki, 1991; Brownie *et al.*, 1993). Their usefulness for modelling transitions between other types of states, e.g. behavioural and reproductive states (Barbraud & Weimerskirch, 2005; Weladji *et al.*, 2008), has since become apparent, and Lebreton, Almeras & Pradel (1999) showed how multistate models can be used to combine live recaptures and dead recoveries by designating

separate states for alive and newly dead, each state with its respective detection probability. Following Schaub & Pradel (2004b), we extended Burnham's (Burnham, 1993) model (presented as a three-stratum model in Lebreton *et al.*, 1999) for combined analysis of tag recovery and recapture data. Our model (Fig. 1) included an additional cause of mortality and the possibility of return for animals that had left the study area, resulting in four possible states: (1) alive inside the study area, (2) alive outside the study area, (3) newly dead due to legal hunting, and (4) newly dead due to other causes.

State transitions probabilities are defined in the following matrix (row, states of departure; column, states of arrival):

$$T = \begin{bmatrix} (1-h-w)F & (1-h-w)(1-F) & h & w \\ (1-h-w)R & (1-h-w)(1-R) & h & w \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \quad \text{eqn 1}$$

with h being the probability of dying due to legal hunting during the time period t to $t + 1$, w the probability of dying due to causes other than legal hunting during the same time period, and $1 - h - w$ the probability of surviving. F , a fidelity term, represents the probability of remaining within the study area, and R is the probability of returning to the study area for animals that are outside. The mortality parameters associated with the transition to states 3 and 4 are true mortalities, whereas the parameters in the other two states are only local survival. Detection probabilities differ depending on the cause of mortality among animals newly dead, but the model assumes that dead animals are detected with equal probability inside and outside the study area, as does Burnham's model (Burnham, 1993). Equal detection probability inside and outside our study areas is a reasonable assumption given that animals killed by legal hunting were all detected by definition, and bears that died due to other causes were either detected because they were followed by radiotelemetry, or incidentally encountered. The weakest part of the assumption is equal detection of instrumented bears dead due to causes other than legal hunting, regardless of

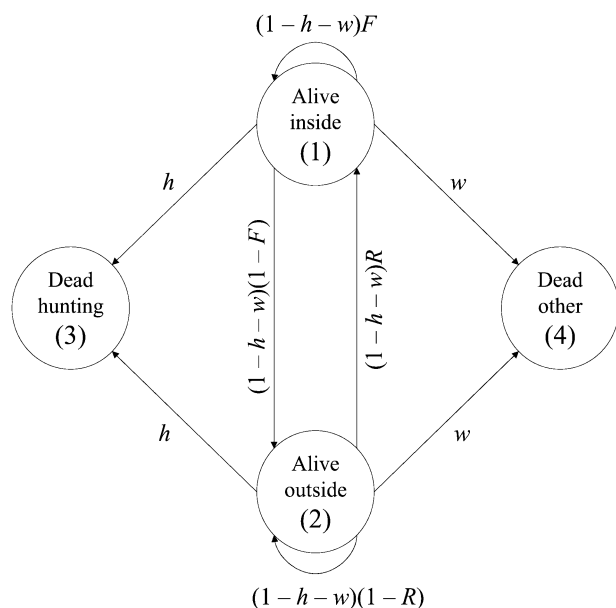


Fig. 1. Fate diagram illustrating MCR model state transitions of marked brown bears in Sweden. Bears can die due to two competing risks (legal hunting and all other mortality causes) or stay alive. Bears alive inside or outside the study area may remain in their current location or move out of or into the study area, respectively.

location in- or outside the study area. This potential lack of realism is necessitated by the need for parameter identifiability (Gimenez, Choquet & Lebreton, 2003; Hunter & Caswell, 2009).

Schaub & Pradel (2004) demonstrated the use of multistate models to assess the relative importance of different sources of mortality. Our approach is similar to theirs, however, whereas they estimated the probability of death being caused by a certain source of mortality conditional on having died during the interval, we estimated the cause-specific probability of dying conditional on being alive at the beginning of the interval.

We constrained the capture probability (p) for state 3 to equal 1, recognizing that all legally shot bears had to be reported to the management authorities in Sweden. Consequently, we only estimated capture probabilities in states 1, 2 and 4. Being able to constrain capture probability in state 3 supplied a significant benefit, by allowing for the separate estimation of the capture probability in state 4 and transition probabilities from the live states to state 4. As Lebreton *et al.* (1999) pointed out, in cases where recoveries are obtained from specific causes of death (with associated cause-specific mortality m_{cause}), hence $m_{\text{cause}} \neq 1 - s$ (s , survival), the detection probability cannot be identified separately from a specific type of mortality. For this reason, the pair of parameters (s, p) is often replaced by $[s, (1 - s)p]$. In our case, constraining the capture probability in state 3 to 1 made p identifiable.

To construct capture histories, we pooled captures and live resightings for each individual during the spring capture season (20 March–10 June), using a capture interval of 1 year. We used an extended period (3.5 months) as a single occasion, because the biases associated with parameters derived from pooled estimates are minimal if mortality during the capture interval does not exceed about 50% (Hargrove & Borland, 1994). Animals encountered alive and inside the study area during the capture season were assigned to state 1, live animals outside the study area were assigned to state 2. Animals killed by legal hunting during the hunting season preceding capture occasion $i + 1$ (regardless of whether or not they were shot inside or outside the study area) were assigned to state 3 at occasion $i + 1$, and animals discovered as having died for reasons other than legal hunting between the end of capture occasion i and the end of capture occasion $i + 1$ were assigned to state 4 at occasion $i + 1$. We assigned animals encountered in the 'newly dead' states (3 and 4) between capture occasions i and $i + 1$ to occasion $i + 1$, instead of the previous occasion (as is carried out in combined tag recovery and live recapture data; Barker, White & McDougall, 2005), because we were estimating survival indirectly as a transition probability from occasion i to occasion $i + 1$. Whereas direct survival estimates at occasion i are interpreted as having survived from occasion i to occasion $i + 1$, transition probabilities at occasion i are interpreted as having made a transition during the interval between $i - 1$ to i . Animals not encountered alive at occasion $i + 1$ and not discovered dead between the end of occasion i and the end of occasion $i + 1$ received a 0 in the capture history at occasion $i + 1$. Capture histories were constructed for 464 individuals.

Model selection and parameter estimation

We used the program M-SURGE (Choquet *et al.*, 2004; Choquet *et al.*, 2006) for model fitting and parameter estimation. We assessed the effects of the following variables in the multistate modelling framework:

1. Sex (male, female; symbol: s) – for transition and capture
2. Age class (yearlings = 1y, subadults = 2–4y, adults = 5y +; symbol: a) – for transition and capture

3. Subpopulation (north, south; symbol: p) – for transition and capture
4. Radiocollar (yes, no; symbol: r) – for capture
5. Harvest intensity (low, high; symbol: i) – for transition

The symbols for explanatory variables defined above were used in the M-SURGE notation presented later and are not italicized to avoid confusion with variables used earlier in the text. We implemented and compared several candidate MCR models, with the most complex model including all of the above variables and biologically meaningful/interpretable interactions between them (full model, Table 1). No tests are currently available to test the goodness-of-fit (GOF) of multistate models to data consisting of a combination of recaptures and recoveries. Nevertheless, because most of the information about cause-specific mortality came from dead recoveries, we carried out a GOF test using only the recovery data (Brownie *et al.*, 1985), and the fit was found to be satisfactory ($\chi^2_{53} = 65.23$, $P = 0.12$). Because data demands are high for multistate models and the number of parameters increases quickly with increasing number of states and groups (Lebreton & Pradel, 2002), we did not consider the fully time-dependent model, but instead used time periods we believed to be relevant for survival, i.e. two time periods representing a change in harvest intensity due to a 3.4-fold increase in average annual quotas in the south, beginning with the 1998 hunting season (from 11.4 bears in 1984–97 to 38.6 bears after 1997). Similarly, age was defined as a categorical variable with cuts roughly identified based on splines in a preliminary Cox proportional hazards regression model (Lunn & McNeil, 1995).

We estimated capture probabilities separately for instrumented and non-instrumented bears, as bears equipped with radio transmitters can be expected to have much greater recapture probabilities than bears without (e.g. Amstrup, McDonald & Stirling, 2001). Because convergence on local minima is a concern in multistate models (Choquet *et al.* 2006), we either re-ran models at least three times with random starting values for unconstrained parameters, or (when available) re-ran models with starting values from a well-defined simpler model (Choquet *et al.* 2006). As mentioned above, identifiability is a crucial issue in multistate models combining dead recoveries and live recaptures (Gimenez *et al.*, 2003), both in terms of model selection and interpretation of parameter estimates. We relied on M-SURGE which implements up-to-date algorithms to check for parameter identifiability (Choquet *et al.*, 2004). Model selection was based on Akaike's information criterion values corrected for small sample sizes (AIC_c; Burnham & Anderson, 2002).

Results

Sex, age, subpopulation, and harvest intensity were retained as variables predicting survival in the best MCR models (Table 1). Demographic effects were relatively mild, with a trend towards greater vulnerability of male bears to legal hunting, at least in the north. The best-performing models indicated no differences in vulnerability between age categories, except that cause-specific risk to hunting was estimated to be 0 for yearlings in the north. However, due to a small sample size and a lack of mortalities in that age category in our sample, standard error could not be estimated for the parameter. During the period with increased harvest quotas (1998–2006) in the south, the average cause-specific risk of dying due to legal hunting was 2.8 times higher than during the preceding low-pressure period (Fig. 2, Table 2). Harvest intensity had no significant effect on vulnerability in the north, where there was no corresponding increase in harvest quotas.

Table 1. Model ranking and fit parameters^a with respect to the focal transitions (mortality parameters h and w) for Swedish brown bears. Parameters were estimated using multistate capture–recapture (MCR) modelling in M-SURGE. Shown are the most complex model considered and representative candidate models, including three top models that differ only slightly in AIC_c value ($w_i = AIC_c$ weights). Regression terms are shown for transition probabilities of the MCR model. Following M-SURGE notation, interactions are signified by a period between the interacting factors. The last two columns indicate the model for immediate comparison ('comp.') and the term(s) targeted ('effect'). Model terms for capture probabilities and conditional movement in and out of the study areas are shown separately in Table 3.

| Mortality (h and w in Transition, Ψ) | | Model performance | | | | |
|---|---------------------------------------|-------------------|----------|----------------|--------|-----------------------|
| Legal hunting | Other | NP | Deviance | ΔAIC_c | w_i | Comp. Effect |
| Full model: | | | | | | |
| a + s + p + i + a.s + p.s + p.a + p.i | a + s + p + i + a.s + p.s + p.a + p.i | 52 | 3164.7 | 15.5 | 0.0002 | |
| Other candidate models: | | | | | | |
| 1 a + s + p + i + p.a + p.i + p.s | a + s + a.s | 41 | 3176.4 | 0 | 0.3804 | |
| 2 a + s + p + i + p.a + p.i | a + s + a.s | 40 | 3180.4 | 1.6 | 0.1709 | 1 p.s. on hunting |
| 3 a + s + p + i + p.a + p.i | a + s + p + a.s | 41 | 3178.4 | 2 | 0.1400 | 2 p on other |
| 4 a + s + p + i + p.a + p.i | a + s + p + a.s + p.s | 42 | 3176.9 | 2.9 | 0.0892 | 2 p.s. on other |
| 5 a + s + p + i + p.a + p.i + a.s | a + s + a.s | 42 | 3177 | 3 | 0.0849 | 2 a.s. on hunting |
| 6 a + s + p + i + p.a + p.i | a + s + p + a.s + p.a | 43 | 3175.6 | 4 | 0.0515 | 2 p.a. on other |
| 7 a + s + p + i + p.a + p.i | a + s + p + i + a.s + p.i | 43 | 3176.6 | 5 | 0.0312 | 3 i + p.i. on other |
| 8 s + p + i + p.i + p.s | a + s + a.s | 37 | 3191.3 | 5.3 | 0.0269 | 1 a + p.a. on hunting |
| 9 a + s + p + i + p.i + p.s | a + s + a.s | 39 | 3187.5 | 6.3 | 0.0163 | 1 p.a. on hunting |
| 10 a + s + p + i + p.a | a + s + a.s | 39 | 3189.1 | 7.9 | 0.0073 | 2 p.i. on hunting |
| 11 a + s + p + p.a | a + s + a.s | 38 | 3196.8 | 13.2 | 0.0005 | 10 i on hunting |
| 12 a + s + p + i + p.a + p.i | a + s + a.s | 39 | 3194.5 | 13.3 | 0.0005 | 2 s on hunting |
| 13 a + s + p + i + p.a + p.i | a + s | 38 | 3199.5 | 15.9 | 0.0001 | 2 a.s. on other |

^aSymbol interpretation: age (a), sex (s), subpopulation (p), harvest pressure (i).

Table 2. Estimates of cause-specific mortality for brown bears monitored in Sweden between 1984 and 2006. Parameter estimates are from the best-fitting candidate multistate model, with the following effects on mortality transition probability in M-SURGE notation: $\Psi_{\text{from}(12)\text{to}(3)(\text{intensity subpop}+\text{subpop age}+\text{subpop sex})+\text{from}(12)\text{to}(4)(\text{sex age})+\text{others}}$. The age categories are defined as follows: yearlings = 1y, subadults = 2–4y, adults = 5y+. The vulnerability of yearling brown bears to legal hunting in the north was estimated to be 0 (not shown here), but no confidence interval could be constructed due to the small sample size and lack of hunting mortalities in that group. Nonetheless, legal hunting mortality for yearling bears in the north can be expected to be relatively small, for reasons outlined in the main text. The top-performing model for mortalities other than legal hunting did not distinguish between subpopulations and periods of harvest intensity.

| Cause | Subpop. | Age category | Sex | Harvest intensity | Estimate | 95% ICI | 95% uCI | SE | |
|---------|-------------|--------------|----------|-------------------|----------|---------|---------|-------|-------|
| Hunting | North | Subadult | f | low | 0.036 | 0.014 | 0.089 | 0.017 | |
| | | | f | high | 0.023 | 0.009 | 0.058 | 0.011 | |
| | | | m | low | 0.103 | 0.052 | 0.193 | 0.035 | |
| | | | m | high | 0.068 | 0.033 | 0.136 | 0.025 | |
| | | | f | low | 0.019 | 0.007 | 0.051 | 0.010 | |
| | | f | high | 0.012 | 0.005 | 0.031 | 0.006 | | |
| | | m | low | 0.067 | 0.027 | 0.154 | 0.030 | | |
| | | m | high | 0.043 | 0.018 | 0.100 | 0.019 | | |
| | | South | Yearling | f | low | 0.019 | 0.008 | 0.045 | 0.008 |
| | | | | f | high | 0.054 | 0.028 | 0.103 | 0.018 |
| | m | | | low | 0.034 | 0.015 | 0.073 | 0.013 | |
| | m | | | high | 0.092 | 0.051 | 0.163 | 0.028 | |
| | f | | | low | 0.021 | 0.010 | 0.043 | 0.008 | |
| | f | | high | 0.058 | 0.034 | 0.097 | 0.016 | | |
| | m | | low | 0.023 | 0.011 | 0.045 | 0.008 | | |
| | m | | high | 0.063 | 0.038 | 0.102 | 0.016 | | |
| | Adult | | f | low | 0.031 | 0.017 | 0.057 | 0.010 | |
| | | | f | high | 0.086 | 0.058 | 0.126 | 0.017 | |
| | | m | low | 0.040 | 0.023 | 0.071 | 0.012 | | |
| | | m | high | 0.109 | 0.075 | 0.157 | 0.021 | | |
| m | | high/low | 0.177 | 0.121 | 0.251 | 0.033 | | | |
| Other | North/south | Yearling | m | | 0.086 | 0.039 | 0.179 | 0.034 | |
| | | | f | | 0.060 | 0.036 | 0.099 | 0.016 | |
| | | Subadult | m | | 0.183 | 0.134 | 0.244 | 0.028 | |
| | f | | | 0.066 | 0.047 | 0.092 | 0.012 | | |
| | m | | | 0.107 | 0.076 | 0.148 | 0.018 | | |

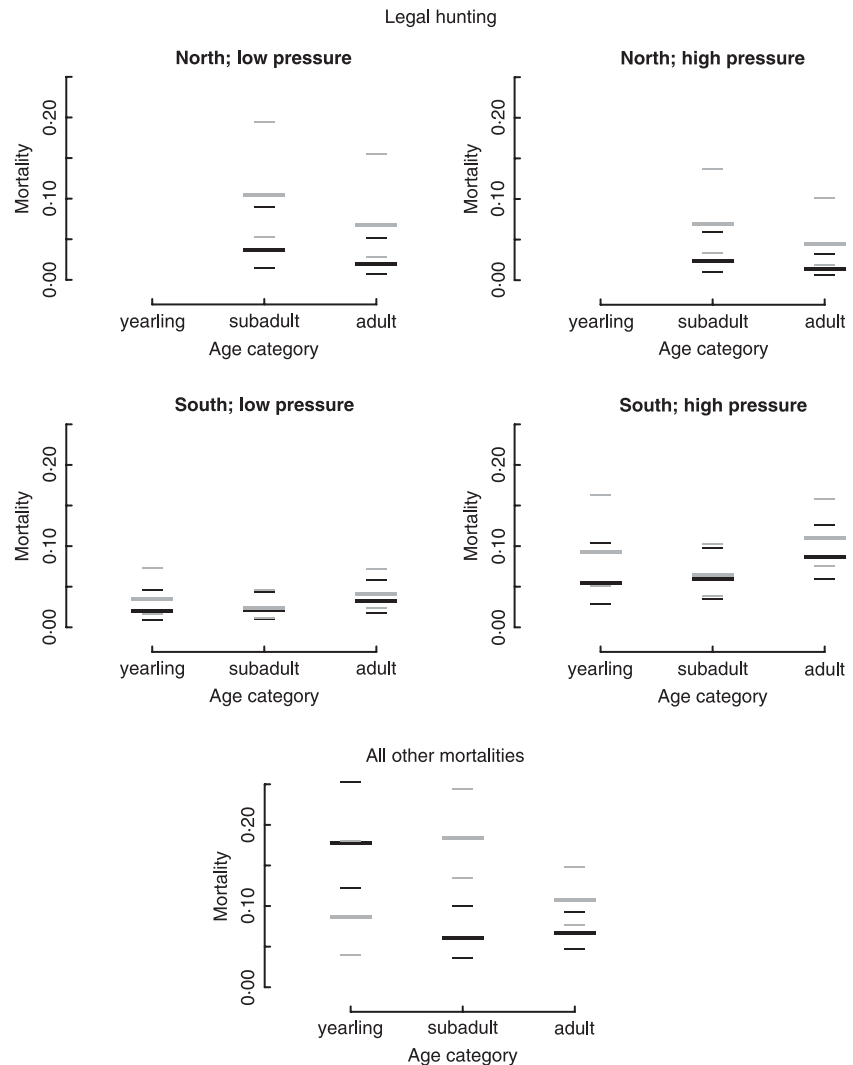


Fig. 2. Estimates of cause-specific mortality (thick bars) and 95% CI boundaries (thin bars) for female (black) and male (grey) brown bears monitored in Sweden between 1984 and 2006. Parameter estimates are from the best-fitting candidate multistate model, with the following effects on mortality transition probability in M-SURGE notation: $\Psi_{\text{from}(12)\text{to}3(\text{intensity subpop}+\text{subpop age}+\text{subpop sex})+\text{from}(12)\text{to}(4)(\text{sex age})+\text{others}}$. The vulnerability of yearling brown bears to legal hunting in the north was estimated to be 0 (not shown here), but no confidence interval could be constructed due to the small sample size and lack of hunting mortalities in that group. Nonetheless, legal hunting mortality for yearling bears in the north can be expected to be relatively small, for reasons outlined in the main text. The graph for mortalities other than legal hunting does not distinguish between subpopulations and periods of harvest intensity because these terms were not included in the top-performing multistate capture–recapture model.

The general pattern for vulnerability to causes other than legal hunting was one of greater risk for young individuals, particularly males (Fig. 2, Table 2). Subadult males and yearling females were most vulnerable. Subadult male bears were more vulnerable than subadult females and adults of both sexes, whereas among females, yearlings were the most vulnerable. Depending on population and age/sex group, individuals were between 1.6 and 9.1 times more vulnerable to the combination of other mortalities than to legal hunting. However, during the period of high harvest quotas, legal hunting mortality estimates in the south, with the exception of subadult males and yearling females, were similar to the mortality estimates associated with other causes (Fig. 2, Table 2).

In addition to the top model, two other candidate models received plausible support based on AIC_c (ΔAIC_c 0–2; Burnham & Anderson 2002); one included an effect of subpopulation on mortality due to causes other than legal hunting (slightly lower in the south), and the other did not include a subpopulation:sex interaction on legal hunting mortality. Aside from these differences, all top-performing candidate models showed similar results in terms of structure and effect sizes.

Recapture probability estimates (Fig. 3) were at or near 1 for instrumented bears alive inside the study area but were substantially lower for bears alive outside the study area. Recapture probabilities for live bears without radiotransmitters were at or near 0, regardless of location. The probability of detecting a newly dead bear due to mortality causes other than legal hunting was higher for instrumented bears than bears without transmitters and higher for animals in the south than the north (with yearling bears having the highest detection probability among the three age categories). The top-performing candidate models did not make a distinction between the sexes in terms of capture probability, regardless of the state (Table 3).

Discussion

Assessing the magnitude and selectivity of cause-specific mortality in managed populations is crucial for understanding their population dynamics and the evolutionary forces acting upon them. Legal hunting, in addition to being the most convenient to assess, is also the most easily managed component of mortality in many wild populations. Although it is the single-most

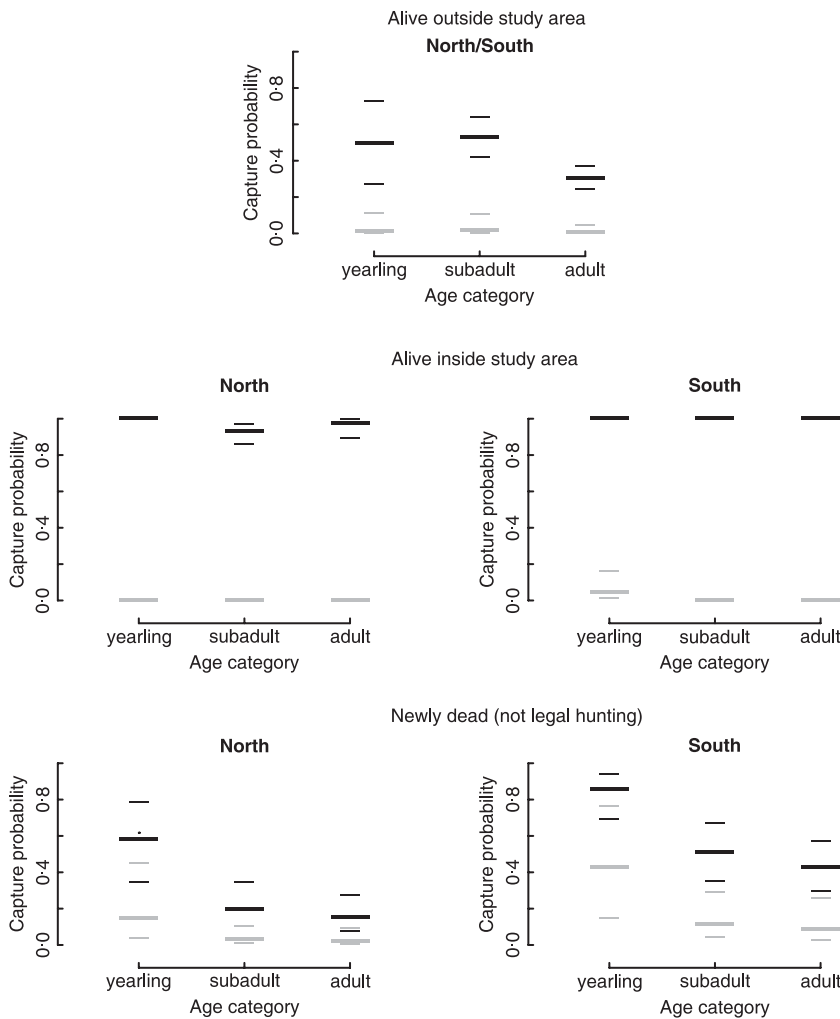


Fig. 3. Recapture probability estimates (large horizontal bars) for brown bears in Sweden with 95% CI boundaries from the top MCR model for states 1 (alive inside the study area), 2 (alive outside the study area), and 4 (newly dead due to causes other than legal hunting). Recapture probability for animals newly dead due to legal hunting was set to 1 (because of the reporting requirement of legally harvested bears) and is not shown. Black and grey bars represent estimates for instrumented and non-instrumented bears, respectively. Parameters without standard error boundaries indicate that all individuals in that group either had 0% or 100% recapture probability. The recapture probability component of the MCR model in M-SURGE notation is: $P_{to(1,4)(age+radio+pop)+to(2)(age+radio)+others}$

| Probability | State | Full model | Top ranking model (see table 1) |
|-------------|-------------------------------|-----------------|---------------------------------|
| capture | alive inside | a + s + p + r | a + p + r |
| | alive outside | a + s + p + r | a + r |
| | newly dead: legal hunting | 1 | 1 |
| | newly dead: other | a + s + p + r | a + p + r |
| transition | alive inside -> alive outside | a + s + p + a.s | a + s |
| | alive outside -> alive inside | a + s + p + a.s | a + s + p + a.s |

*Symbol interpretation: age (a), sex (s), subpopulation (p), radio-marked (r).

Table 3. Comparison of model terms^a and interactions with respect to state-specific capture probabilities and conditional movement in and out of the study areas in the full MCR model and those used in the best performing overall models (see also Table 1). Because of the reporting requirement of legally harvested bears, capture probability for animals newly dead due to legal hunting was set to 1.

important cause of mortality for bears in Sweden (Sahlén *et al.*, 2006), we found that the combined mortality from other causes is as great, and for several demographic groups greater than legal hunting. In addition to being of considerable magnitude, mortalities other than legal hunting also show greater demographic selectivity than legal hunting. Interestingly, although only a fraction of the 'other' mortality category was natural mortality, these nonharvest mortalities still showed a general pattern of demographic selectivity that we would expect from a natural mortality regime in long-lived species, namely greater vulnerability of young animals. We

cannot say whether this comparison also holds quantitatively, as no similar brown bear population has been studied under purely natural conditions. Nonetheless, it is clear that this combination of natural and human-caused mortalities is an equally important contributor to this brown bear population's dynamics and potentially evolution as is hunting. The low selectivity of harvesting mortality, on the other hand, contrasts clearly with results obtained in marine ecosystems (Olsen *et al.*, 2004) and trophy hunting cultures (Coltman *et al.*, 2003) with a very strict size-selective harvesting regime. Therefore, one should not underestimate the role of hunting

traditions and management regimes for harvesting as a selective force.

Demographically selective harvesting is receiving growing attention from ecologists and evolutionary biologists, as it has the potential to affect population dynamics (Langvatn & Loison, 1999; Mysterud, Coulson & Stenseth, 2002; Milner, Nilsen & Reassen, 2006) and evolutionary processes (Coltman *et al.*, 2003; Garel *et al.*, 2007; Proaktor, Coulson & Milner-Gulland, 2007). Males have generally been found to be more vulnerable to hunting than females, with young males being the most vulnerable age/sex class, both in bears (Derocher *et al.*, 1997; Noyce & Garshelis, 1997; McLellan *et al.*, 1999) and in other large mammals, such as cervids (e.g. Langvatn & Loison, 1999). Such selectivity may arise due to direct management actions (e.g. selective quotas), active choice by the hunter (e.g. trophy hunting), or differential vulnerability caused by differences in individual characteristics (e.g. behaviour, morphology). We found an overall pattern of weak demographic selectivity of legal hunting, with a trend towards greater male vulnerability, at least in the north. Although only a trend, a difference in vulnerability between the sexes (at least among adults) could in part be due to the legal protection that females receive in Sweden during the time they are with dependent young. Another contributing factor may be passive selectivity as a result of behavioural differences between male and female bears, rather than active hunter selectivity (see also Bischof *et al.*, 2008a). With respect to the first argument, lower cub-of-the-year mortality (Swenson *et al.*, 2001) and higher average age at weaning (Dahle & Swenson, 2003a) in the north means that females spend a greater proportion of their time with dependent young than in the south, which could explain the trend towards a gender effect on legal hunting mortality in the north, but not in the south.

With the exception of yearling bears in the north, we found no clear indication of age-specific vulnerability to legal hunting among Swedish brown bears. The vulnerability of yearling bears to legal hunting in the north was estimated to be 0, but no confidence interval could be constructed due to the small sample size and lack of hunting mortalities in that group. Nonetheless, legal hunting mortality for yearling bears in the north can be expected to be relatively small, mainly for two reasons: (i) because in the north 46% of litters are weaned at 2.5, thus a smaller proportion of yearlings are available for legal harvest than in the south, where almost all litters are weaned at age 1.5 (Dahle & Swenson 2003a) and (ii) about one-third of the northern study area is made up of national parks, where bears are protected by law and most yearlings born in those areas have not yet dispersed to be available to hunters on the periphery of the protected areas (Støen *et al.*, 2006). Several studies on bears have found age-specific vulnerabilities to hunting (e.g., brown bears: McLellan & Shackleton, 1988; Bunnell & Tait, 1985; black bears, *Ursus americanus*: Noyce & Garshelis, 1997; Czetwertynski, Boyce & Schmiegelow, 2007; polar bears, *Ursus maritimus*: Derocher *et al.*, 1997). The lack of consistent and pronounced age effects on vulnerability to legal hunting in our study is therefore somewhat surprising.

Analysis of the composition of the harvest revealed relatively little demographic bias between hunting methods in the Swedish harvest (Bischof *et al.*, 2008a), and we suggested that differences in the hunting system (no bag limit, few guided hunts, quota-limited season, etc.) are partially responsible for the limited effect of sex and age on relative vulnerability, compared with North American bear populations. It is worth stressing again that a quota-limited harvest without individual bag limits provides little incentive for a hunter to pass up a shot at a legal brown bear. We note that active hunter selectivity may increase in the future should the brown bear population continue to grow, thus increasing encounter probabilities and therefore harvesting opportunities for hunters. An increase in active selectivity, although not necessarily desirable, is more likely to be brought on by a change in the hunting system, for example, a shift from the current quota-limited hunt to one with a single bear tag assigned to individual hunters.

Although biased harvest can cause demographic and evolutionary side effects, so can unbiased harvest. In an ungulate population model, Proaktor *et al.* (2007) noted that harvest pressure played a greater role in the selection for lighter weight at first reproduction than the degree of harvest selectivity. An increase in overall mortality can lead to a discounting of future reproduction, which may eventually result in the benefits of earlier reproduction outweighing its cost, such as lower offspring survival (Bischof, Mysterud & Swenson, 2008b). Thus, an elevated total mortality of Swedish brown bears as a consequence of growing harvest quotas may not only directly reduce the population growth rate in the long run, but cause additional indirect effects if a reduced age (and body mass) at primiparity is favoured.

Our results confirm that the increase in harvest pressure coincided with elevated vulnerability to hunting for individuals in the affected subpopulation. Whereas a positive effect of hunting pressure on vulnerability is intuitive, the quantitative effect of increased harvest pressure and how this may affect the level of compensation has rarely been evaluated. We found that the 3–4-fold increase in average annual quotas in the south was comparable to the estimated 2.8-fold increase in average vulnerability to hunting over the same time periods. The change in harvest pressure in conjunction with the availability of cause-specific mortality estimates presented an opportunity to evaluate the assumption of additivity in mortalities implemented in the matrix of transition probabilities (equation 1). This assumption was motivated by the precautionary principle and the following considerations: (i) hunting mortality occurs over a relatively short time frame (1–2 months), (ii) it takes place after much of the other mortalities have already been experienced (see below), and (iii) as Lebreton (2005) suggested, strong compensation can rarely be expected as a consequence of density dependence or heterogeneity in survival, and should be less likely in long-lived species than short-lived ones. The assumption of additivity was supported by the finding that vulnerability to natural mortality did not change as a result of increasing harvest pressure in the south. In the case of complete or partial compensation, we would have expected a depressing

effect of increasing harvest intensity on the risk due to mortalities other than legal hunting. Nonetheless, overall population densities increased during the study period, so we concede that some caution is advised when interpreting changes in risk between periods of high and low harvest pressure.

Sex and age effects were most pronounced for mortality causes other than legal hunting and showed patterns of greater vulnerability of young animals and greater vulnerability of males than females, at least among subadults. These effects are similar to findings from brown bear populations in North America (McLellan *et al.*, 1999; Haroldson, Schwartz & White, 2006), with the exception that in our study population female yearlings were the most vulnerable female age class to mortality causes other than legal hunting, rivaling the vulnerability of male subadults. As mentioned earlier, the relatively high vulnerability of subadult males can be explained by increased mobility and dispersal behaviour of males, as well as their propensity to be less cautious (Blanchard & Knight, 1991; McLellan *et al.*, 1999). The causes of elevated vulnerability of yearling females, compared with the other two female age classes and even adult males, are less clear. Swenson *et al.* (2001) reported mortality rates due to intraspecific predation for female yearlings in Sweden that were several times higher than that of male yearlings, but the reason for this sex bias is unknown and warrants further investigation.

In addition to the differences in magnitude and selectivity, legal hunting and other mortalities also differ in the timing during the biological year. Whereas legal hunting is concentrated in a relatively short time period in late summer and early fall, the combined other mortalities are spread over the entire out-of-den period, albeit unevenly. The strong temporal focus of hunting mortality, compared with other mortalities, is likely to have consequences in terms of selectivity, for example if there is seasonal variation in the manifestation of life-history strategies (e.g. if some individuals were to wean their young after, rather than before the hunting season). This issue goes beyond the scope of our current analysis, but should be explored in future empirical and theoretical work.

An obvious information gap that remains for our study population is an assessment of the spatial and temporal patterns of harvest effort. Bischof *et al.* (2008a) explored and described harvest patterns and the demography of the harvest in the Swedish brown bear population. In the present study, we examined individual vulnerability to cause-specific risks in the same population, over roughly the same time frame. Estimates of cause-specific risk, harvest patterns, and harvest effort should be considered an essential information triage that can give ecologists and managers a comprehensive picture of the implications of harvest and other mortalities for wild populations.

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References

- Amstrup, S.C., McDonald, T.L. & Stirling, I. (2001) Polar bears in the Beaufort Sea: A 30-year mark-recapture case history. *Journal of Agricultural, Biological, and Environmental Statistics*, **6**, 221–234.
- Anderson, D.R. & Burnham, K.P. (1976) Population ecology of the mallard: VI. The effect of exploitation on survival. *US Fish and Wildlife Service Resource*, **128**, 1–66.
- Arnemo, J.M., Ahlqvist, P., Andersen, R., Berntsen, F., Ericsson, G., Odden, J., Brunberg, S., Segerström, P., & Swenson, J.E. (2006) Risk of capture-related mortality in large free-ranging mammals: experiences from Scandinavia. *Wildlife Biology*, **12**, 109–113.
- Barbraud, C. & Weimerskirch, H. (2005) Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology*, **86**, 682–692.
- Barker, R.J., White, G.C. & McDougall, M. (2005) Movement of paradise shelduck between molt sites: A joint multistate-dead recovery mark-recapture model. *Journal of Wildlife Management*, **69**, 1194–1201.
- Bernes, C. (1994) *Biologisk Mångfald i Sverige; En Landstudie* Naturvårdsverket Förlag, Solna, Sweden.
- Bischof, R., Fujita, R., Zedrosser, A., Söderberg, A. & Swenson, J.E. (2008a) Hunting patterns, the ban on baiting, and harvest demographics of brown bears in Sweden. *Journal of Wildlife Management*, **72**, 79–88.
- Bischof, R., Mysterud, A. & Swenson, J.E. (2008b) Should hunting mortality mimic the patterns of natural mortality? *Biology Letters*, **4**, 307–310.
- Blanchard, B.M. & Knight, R.R. (1991) Movements of Yellowstone grizzly bears. *Biological Conservation*, **58**, 41–67.
- Brownie, C., Anderson, D.R., Burnham, K.P. & Robson, D.S. (1985) *Statistical Inference from Band-Recovery Models – a Handbook*. Resource Publication 156, 2 edn. U.S. Fish and Wildlife Service, Washington, DC.
- Brownie, C., Hines, J.E., Nichols, J.D., Pollock, K.H. & Hestbeck, J.B. (1993) Capture-recapture studies for multiple strata including non-markovian transitions. *Biometrics*, **49**, 1173–1187.
- Bunnell, F.L. & Tait, D.E.N. (1985) Mortality rates of North American bears. *Arctic*, **38**, 316–323.
- Burnham, K.P. (1993) A theory for combined analysis of ring recovery and recapture data. *Marked Individuals in the Study of Bird Populations* (eds J.D. Lebreton & P.M. North), pp. 199–213. Birkhäuser, Basel, Switzerland.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* Springer, New York.
- Caughley, G. (1966) Mortality patterns in mammals. *Ecology*, **47**, 906–918.
- Choquet, R., Reboulet, A.M., Pradel, R. & O. Gimenez, J.D.L. (2004) M-SURGE: New software specifically designed for multistate capture–recapture models. *Animal Biodiversity and Conservation*, **27**, 207–215.
- Choquet, R., Reboulet, A.-M., Pradel, R., Gimenez, O. & Lebreton, J.-D. (2006) *M-SURGE 1-8 User's Manual* (Multistate SURvival Generalized Estimation). CEFE, Montpellier, France.
- Clutton-Brock, T. & Pemberton, J. (2004) *Soay Sheep: Dynamics and Selection in an Island Population*. Cambridge University Press, Cambridge, UK.
- Clutton-Brock, T.H., Guinness, F.E., & Albon, S.D. (1982) *Red deer: Behaviour and Ecology of two Sexes*. Edinburgh University Press, Edinburgh, UK.
- Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003) Undesirable evolutionary consequences of trophy hunting. *Nature*, **426**, 655–658.
- Czetwertynski, S.M., Boyce, M.S. & Schmiegelow, F.K. (2007) Effects of hunting on demographic parameters of American black bears. *Ursus*, **18**, 1–18.
- Dahle, B. & Swenson, J.E. (2003a) Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring. *Behavioral Ecology and Sociobiology*, **54**, 352–358.
- Dahle, B. & Swenson, J.E. (2003b) Home ranges in adult Scandinavian brown bears (*Ursus arctos*): Effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, **260**, 329–335.
- Derocher, A.E., Stirling, I. & Calvert, W. (1997) Male-biased harvesting of polar bears in western Hudson Bay. *Journal of Wildlife Management*, **61**, 1075–1082.
- Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 58–63.

- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review in Ecology, Evolution, and Systematics*, **31**, 367–393.
- Garel, M., Cugnasse, J.-M., Maillard, D., Gaillard, J.-M., Hewison, A.J.M. & Dubray, D. (2007) Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecological Applications*, **17**, 1607–1618.
- Gimenez, O., Choquet, R. & Lebreton, J.-D. (2003). Parameter redundancy in multistate capture-recapture models. *Biometrical Journal*, **45**, 704–722.
- Hargrove, J.W. & Borland, C.H. (1994) Pooled population parameter estimates from mark-recapture data. *Biometrics*, **50**, 1129–1141.
- Haroldson, M.A., Schwartz, C.C. & White, G.C. (2006) Survival of independent grizzly bears in the Greater Yellowstone ecosystem, 1983–2001. *Temporal, Spatial, and Environmental Influences on the Demographics of Grizzly Bears in the Greater Yellowstone Ecosystem* (eds M.A. Haroldson, C.C. Schwartz, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody & C. Servheen), pp. 33–42. Wildlife Monographs 161.
- Hestbeck, J.B., Nichols, J.D. & Malecki, R.A. (1991) Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology*, **72**, 523–533.
- Hunter, C.M. & Caswell, H. (2009) Rank and redundancy of multistate mark-recapture models for seabird populations with unobservable states. *Modeling Demographic Processes in Marked Populations* (eds D.L. Thomson, E.G. Cooch & M.J. Conroy), Vol. 3, pp. 797–825. Springer Series: Environmental and Ecological Statistics, New York.
- Kindberg, J. & Swenson, J.E. (2006) Populationsberäkning av björnstammen i Sverige. Report of the Scandinavian Bear Project to the Swedish Environmental Protection Agency, Stockholm, Sweden.
- Kuparinen, A. & Merilä, J. (2007) Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution*, **22**, 652–659.
- Langvatn, R. & Loison, A. (1999) Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildlife Biology*, **5**, 213–223.
- Lebreton, J.-D. (2005) Dynamical and statistical models for exploited populations. *Australian and New Zealand Journal of Statistics*, **47**, 49–63.
- Lebreton, J.-D. & Pradel, R. (2002) Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics*, **29**, 353–369.
- Lebreton, J.-D., Almeras, T. & Pradel, R. (1999) Competing events, mixtures of information and multistratum recapture models. *Bird Study*, **46** (suppl.), 39–46.
- Lunn, M. & McNeil, D. (1995) Applying cox regression to competing risks. *Biometrics*, **51**, 524–532.
- Manel, S., Bellemain, E., Swenson, J.E. & Francois, O. (2004) Assumed and inferred spatial structure of populations: the Scandinavian brown bear revisited. *Molecular Ecology*, **13**, 1327–1331.
- Matson, G.M., Van Daele, L., Goodwin, E., Aumiller, A., Reynolds, H.V. & Hristenko, H. (1993) *A laboratory manual for cementum age determination of Alaskan brown bear first premolar teeth*. Matson's Laboratory, Milltown, Montana, USA.
- McLellan, B.N. & Shackleton, D.M. (1988) A comparison of grizzly bear harvest data from Montana and southeastern British Columbia. *Wildlife Society Bulletin*, **16**, 371–375.
- McLellan, B.N., Hovey, F.W., Mace, R.D., Woods, J.G., Carney, D.W., Gibeau, M.L., Wakkinen, W.L. & Kasworm, W.F. (1999) Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *Journal of Wildlife Management*, **63**, 911–920.
- Milner, J.M., Nilsen, E.B. & Reassen, H.P. (2006) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, **21**, 36–47.
- Mysterud, A., Coulson, T. & Stenseth, N.C. (2002) The role of males in the dynamics of ungulate populations. *Journal of Animal Ecology*, **71**, 907–915.
- Nordiska inisterrådet (1984) *Naturgeografisk regionindelning av Norden*. Nordisk ministerrådet Berlings, Arlöv, Sweden.
- Noyce, K.V. & Garshelis, D.L. (1997) Influence of natural food abundance on black bear harvests in Minnesota. *Journal of Wildlife Management*, **61**, 1067–1074.
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. & Dieckmann, U. (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, **428**, 932–935.
- Otis, D.L. & White, G.C. (2004) Evaluation of ultrastructure and random effects band recovery models for estimating relationships between survival and harvest rates in exploited populations. *Animal Biodiversity and Conservation*, **27**, 157–173.
- Pedersen, H.C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R.A., Svendsen, W. & Yoccoz, N.G. (2004) Weak compensation of harvest despite strong density-dependent growth in willow ptarmigan. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 381–385.
- Proaktor, G., Coulson, T. & Milner-Gulland, E.J. (2007) Evolutionary responses to harvesting in ungulates. *Journal of Animal Ecology*, **76**, 669–678.
- Sahlén, V., Swenson, J., Brunberg, S. & Kindberg, J. (2006) *Björnen i Sverige*. A report from the Scandinavian Bear Project to the Swedish White Paper on Predator Management, Stockholm, Sweden.
- Schaub, M. & Lebreton, J.D. (2004) Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. *Animal Biodiversity and Conservation*, **27**, 73–85.
- Schaub, M. & Pradel, R. (2004) Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology*, **85**, 930–938.
- Støen, O.G., Zedrosser, A., Sæbo, S. & Swenson, J.E. (2006) Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia*, **148**, 356–364.
- Swenson, J.E. & Sandegren, F. (1999) Mistänkt illegal björnjakt i Sverige. *Bilagor till Sammanhållen rovdjurspolitik; Slutbetänkande av Rovdjursutredningen*. Statens offentliga utredningar 1999:146, Stockholm, Sweden.
- Swenson, J.E., Wabakken, P., Sandegren, F., Bjaervall, A., Franzen, R. & Soederberg, A. (1995) The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology*, **1**, 11–25.
- Swenson, J.E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. & Wabakken, P. (1997) Infanticide caused by hunting of male bears. *Nature*, **386**, 450–451.
- Swenson, J.E., Dahle, B. & Sandegren, F. (2001) Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus*, **12**, 81–92.
- Swenson, J.E., Sandegren, F., Brunberg, S. & Segerstrom, P. (2001) Factors associated with loss of brown bear cubs in Sweden. *Ursus*, **12**, 69–80.
- Weladji, R.B., Loison, A., Gaillard, J.-M., Holand, Ø., Mysterud, A., Yoccoz, N.G., Nieminen, M. & Stenseth, N.C. (2008) Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia*, **156**, 237–247.
- Zedrosser, A., Dahle, B. & Swenson, J.E. (2006) Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy*, **87**, 510–518.
- Zedrosser, A., Støen, O.-G., Sæbo, S. & Swenson, J.E. (2007) Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour*, **74**, 369–376.

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