Estimating the total population size of brown bears in an area based on the number of annual reproductions.

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Introduction

Sweden and Norway express political goals for brown bear population size as annual reproductions. Using annual reproductions is useful for managers, because this is a concrete number that is easier to document than the actual total number of bears, and is biologically relevant because it concentrates on reproduction. The number of reproducing adult female bears is a very important parameter when evaluating the long-term viability of a bear population. Nevertheless, there is great interest among managers and the public to translate the number of annual reproductions into the actual total number of bears. A calculation made several years ago, based on general data from both study areas of the Scandinavian Brown Bear Research Project (SBBRP), in northern and central Sweden, suggested that the annual number of reproductions (litters in early spring) could be multiplied by about 10 to obtain an estimate of the total number of bears within a reproductive "core area".

The Swedish Environmental Protection Agency has requested the SBBRP to carry out a more thorough study to evaluate the feasibility of calculating the total number of bears by extrapolating from the number of annual reproductions. The "extrapolation factor" refers to a number that one multiplies times the number of reproductions to obtain a total population estimate. It is important to point out that this is not necessarily as straightforward as it may seem at first. The primary reason is that bear populations can experience different rates of cub-of-the-year mortality and different litter intervals. Thus, the extrapolation factor for an annual reproduction will increase during the season as the mortality of cubs continues. On the other hand, this extrapolation factor might be higher and more stable throughout the year in a population with low cub mortality, because there will be a longer period between the litters born to females, but little loss during a given year. If the litter mortality rate is high, females will give birth more often. Female bears tend to keep their young longer in the north. This would increase the extrapolation factor in the north relative to the south.

Due to this very complicated situation, we have modeled population data to determine extrapolation factors. We used demographic data from two periods, 1984-1995, when the legal hunting mortality was generally low, and 1984-2004, which included periods of lower and higher hunting mortality. In addition, we analyzed the data separately for two subpopulations, the south (northern Dalarna and western Hälsingland), which has experienced high rates of cub mortality, and the north (in and around Sarek National Park in Norrbotten), where the cub mortality rates have been low. We also estimated the extrapolation factor of an annual litter at three times during a given year; right after denning, after the breeding season in mid-summer, and just prior to entering the den in the autumn. This should provide a good indication of the range of extrapolation factors. All calculations are based on litters of young-of-the-year.

Methods

The methods and parameters of the population model are presented in the attached appendix. The modeling is based on actual data from our radio marked bears. The model output "average proportion of bears with a litter" (p) was used to calculate the extrapolation factor, which was simply the inverse of this proportion (1/p). The average proportion of bears with a litter included all bears, including males and cubs of the year, so 1 could be divided by p to estimate the total number of bears.

Results

The results of the modeling effort showed clearly that it is very difficult to use any single extrapolation factor to accurately estimate the total number of bears from the number of reproductions. The extrapolation factors for annual reproductions varied from 6.4 to 17.3 (Table 1). The factors vary by study period, study area, and time of the year. This is very clearly illustrated in Fig. 1.

The primary reason for the variation seems to be variation in the rate of litter loss and litter interval, although the age of first birth has changed with increasing bear densities. These factors also affect the extrapolation factors. The extrapolation factors immediately after den emergence are lowest where the cub litter losses are highest (p highest, 1/p lowest). This is because the females that loose their cubs have young again the next year, resulting in shorter litter intervals and a high proportion of the adult females having cubs of the year in the early spring. The extrapolation factors were the highest in the northern subpopulation in both study periods. This is because the rate of litter loss was lower and the litter interval was longer there. In the south, where cub mortality has always been higher than in the north, the extrapolation factors are lower.

The extrapolation factors also change during the year. This is because cub mortality is occurring throughout the year. In areas with lower cub mortality (the upper lines in the figure), the lines are less steep, because fewer cubs die. Where the cub mortality is higher, the lines are very steep and the extrapolation factors increase very rapidly during the year. Although the extrapolation factors from the northern and southern study areas are clearly separated for the early spring period, they overlap during the late autumn period (Fig. 1).

Discussion

The SBBRP first reported that managers could use an approximate extrapolation factor of about 10 bears, based on all available data and the situation in the early spring. This seems to have been a reasonable estimate, because the average of the four extrapolation factors from early spring (Table 1) is 9.0.

However, our modeling showed that the extrapolation factor is not stable. It is affected by litter interval, age of first birth, and particularly by cub mortality rate. Thus, there is variation in extrapolation factors between study areas, variation between study periods within the same study area, and an even greater variation within a given year. The extrapolation factors we have calculated are valid within reproduction cores areas. At the periphery of the bear's range, the sex ratio is very different from that in the reproduction core areas, so the factors we have calculated will not apply. Young males dominate in peripheral areas, so the extrapolation factors would be much higher there. However, we expect that these extrapolation factors would vary so greatly within different potions of the peripheral areas that we do not recommend using them at all.

Recommendations

Based on our modeling, we caution managers about using extrapolation factors to calculate the total number of bears in an area based on the number of annual reproductions. The main reason for our caution is that we do not know how much the cub-of-the-year mortality varies within Scandinavia. Therefore we do not know which factor to recommend for any given area. If it is deemed important enough that managers wish to use an extrapolation factor to estimate the total population size from the number of annual reproductions, we recommend the following: 1) calculations should only be made for large areas, such as all of Sweden, or perhaps an entire subpopulation. 2) If extrapolation factors are to be used over all of Sweden, we recommend using the mean value we found, i.e. 9 or 10 as a factor. If they are to be used within and adjacent to our study areas, the appropriate factors that are reported here can be used, i.e. about 7 in the south and about 11 in the north. 3) It would be advisable to calculate the total population size based on two relevant extrapolation factors, to give a range in the calculated total population size. 4) Extrapolation factors cannot be used in peripheral areas, such as Norway. 5) Extrapolation factors should <u>only</u> be used on annual reproductions that are based on litters present in early spring before the mating season. Much of the cub mortality occurs during the mating season.

Table 1. Extrapolation factors used to calculate the total number of brown bears that correspond to one reproduction, depending on the study period, study area, and season of the year in Scandinavia.

Study Period	1984-2004		1984-1995	
Area	Southern	Northern	Southern	Northern
Using litters with young of the year				
after emerging from the den	6.4	11.5	7.6	10.5
after the mating season	7.9	12.3	9.5	10.8
before entering the den	12.1	17.3	14.7	13.1

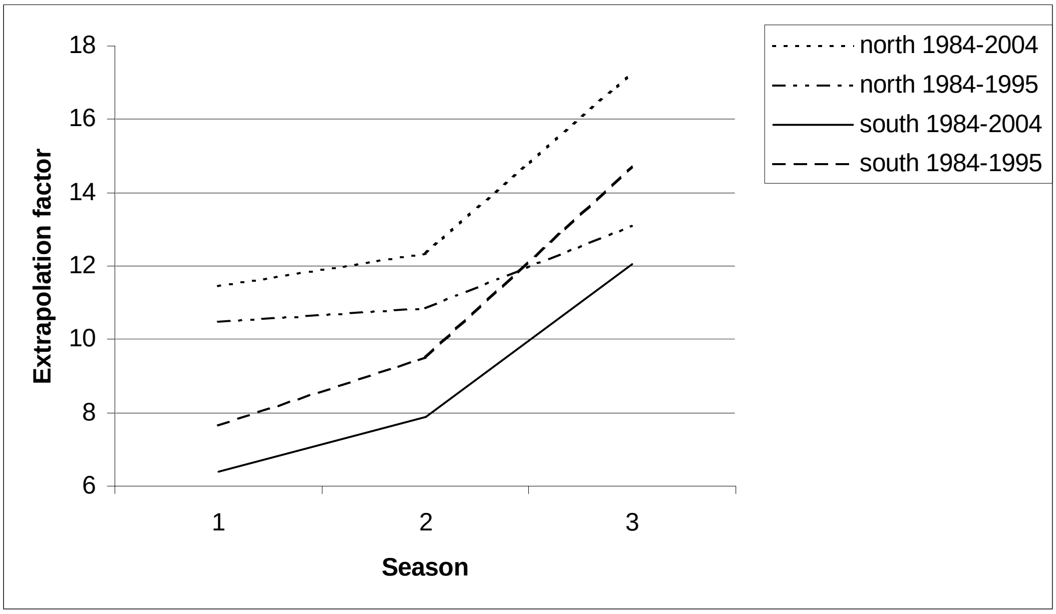

Fig. 1. Extrapolation factors (from Table 1) used to calculate the total number of brown bears that correspond to one reproduction, depending on the study period, study area, and season of the year in Scandinavia. Seasons are: 1) early spring after denning, 2) midsummer after the mating season, and 3) late autumn prior to denning.

Model used for estimating the proportion of female bears with young of the year

We used an individual based simulation model to estimate the proportion of all bears with young of the year (*p*) in the population at three times of the year: (1) after emerging from the den, (2) after the mating season and (3) before entering the den again. The model rules were based on the yearly cycle of bears. Parameter values associated with each rule for time period 1984 – 2004 were estimated separately for the two study areas directly from the data collected by the project (Katajisto et al. unpublished, Table A1). We also used parameter values from Sæther et al. (1997) for comparison (Table A1).

Because the current growth rates of the populations are positive and we have limited information about the carrying capacity and the relation of density and vital rates in the population, simulations over long time periods may lead into unrealistic results. Therefore, we restricted our simulations to 50 years and calculated average *p* over the time period. First ten years were excluded from the analysis to minimize the effect of initial population settings. We ran 50 simulation replicates with each parameter value set. The resulted average age distributions followed those typical for harvested populations and were identical for females and males. Consequently, *1/p* can be used as an extrapolation factor over the entire population or subpopulation.

The individual based simulation model follows the fate of individual bears through the following steps (related parameters in parenthesis):

1. Individuals are born
   a. female gives birth only if she has successfully mated the previous year (*f*, step 4)
   b. number of cubs per litter follows the probability distribution that is separate for first and subsequent reproductions (l_1, l_2, l_3, l_4, fl_1, fl_2, fl_3, fl_4)
   c. number of cubs per litter for females older than 20 follows the distribution for first reproduction to mimic reproductive senescence (fl_1, fl_2, fl_3, fl_4)
   d. females over 30 years (seniors) do not reproduce anymore
2. Yearlings and older cubs separate from their mother
   a. based on probabilities of separating for a litter of different age (s_1, s_2)
   b. cubs always separate as 3-year-olds at the latest
3. Losing a litter with cubs-of-the-year
   a. probabilities separately for first and subsequent litters (d_f, d_o)
4. Mating
   a. only females not accompanied by a litter can mate (see steps 2 and 3)
   b. probability for successful mating (*f*, if successful, leads into birth in step 1)
   c. probabilities to start reproduction as 4, 5 or 6 year old (r_4, r_5, r_6)
   d. number of breeding females restricted to 2000 (based on estimated area of suitable habitat)
5. Final mortality and aging
   a. probabilities to lose a litter after mating season (*a*)
   b. individual mortality rates depending on sex and age (m_0, mf_1, mf_j, mf_a, mm_1, mm_j, mm_a)
   c. if female with cubs-of-the-year dies, cubs also die
   d. individuals surviving become one year older

Table 1A. Model parameters and their values that were used in the simulation.

Study period		1984 - 2004		1984 - 1995	
Study area		Southern	Northern	Southern	Northern
l_1	probability of litter size 1	0.11	0.11	0.13	0.14
l_2	probability of litter size 2	0.36	0.36	0.42	0.45
l_3	probability of litter size 3	0.47	0.47	0.42	0.32
l_4	probability of litter size 4	0.06	0.06	0.03	0.09
fl_1	probability of litter size 1 at first reproduction	0.19	0.19	0.13	0.14
fl_2	probability of litter size 2 at first reproduction	0.61	0.61	0.42	0.45
fl_3	probability of litter size 3 at first reproduction	0.19	0.19	0.42	0.32
fl_4	probability of litter size 4 at first reproduction	0.01	0.01	0.03	0.09
s_1	probability of separating yearlings	0.9	0.5	0.9	0.5
s_2	probability of separating 2-year-old litter	0.95	0.9	0.95	0.9
d_f	probability of losing first litter during mating season	0.36	0.18	0.5	0.045
d_o	probability of losing second or subsequent litter during mating season	0.22	0.06	0.2	0. 045
f	probability of successful mating	0.91	0.9	0.91	0.91
r_4	probability of start reproducing as 4 yr old	0.45	0.06	0.50	0.0
r_5	probability of start reproducing as 5 yr old	0.41	0.63	0.25	0.71
r_6	probability of start reproducing as 6 yr old	0.14	0.31	0.25	0.29
a	probability of losing a litter after mating season	0.18	0.18	0.2	0. 045
m_0	mortality of individual cubs-of-the-year after litter loss	0.1	0.086	0.1	0.02
mf_1	mortality of female yearlings	0.171	0.057	0.15	0.11
mf_j	mortality of female juveniles (2-3 years old)	0.042	0.024	0	0.1
mf_a	mortality of adult females (4 years or older)	0.070	0.019	0.04	0.05
mm_1	mortality of male yearlings	0.05	0.037	0.05	0.15
mm_j	mortality of male juveniles (2-3 years old)	0.078	0.108	0.25	0.3
mm_a	mortality of adult males (4 years or older)	0.078	0.086	0.07	0.075

References

Sæther, B. E., Engen, S., Swenson, J. E., Bakke, Ø. and Sandegren, F. 1997. Levedyktighetsanalyser av skandinavisk brunbjørn. NINA fagrapport 25, Trondheim, pp. 41.