Preliminary predictions of the effect of increasing hunting quotas on brown bear population growth in Sweden.

Report 2009-3 from the Scandinavian Brown Bear Research Project to the Swedish Environmental Protection Agency (Naturvårdsverket)

Richard Bischof and Jon E. Swenson, June 2009

Introduction

Brown bear hunting in Sweden is important as a recreational activity, as well as a management tool. Recent studies have shown that a) Swedish hunters show relatively little selectivity, at least with regards to age, b) harvest vulnerability has increased substantially with increasing quotas in the southern study area, and c) mortalities due to causes other than legal hunting also contribute significantly to overall mortality, but affect especially younger individuals (Bischof *et al.*, 2009).

Brown bear harvest quotas have increased quickly in Sweden during the past 10 years. Population growth, which was rapid between 1984 and 1995 (Saether *et al.*, 1998) is now much slower (Kindberg, Swenson & Ericsson, 2009). This begs the question whether current quotas are sustainable or if they will eventually lead to a population decline. The Scandinavian Brown Bear Research Project (SBBRP) has previously estimated that sustainable quotas would be about 7% of the estimated population (Swenson *et al.*, 1994), but stressed that managers should harvest at lower levels when the uncertainty around population size was high (Tufto *et al.*, 1999). However, managers are interested not only in knowing quotas that will allow the population to continue to grow, but also quotas that will decelerate growth or even decrease the population.

As part of a larger study that investigates the demographic effect of protecting females with dependent young, we evaluated the impact of changing hunting quotas on the population growth rate of brown bears in Sweden. We approached this objective by first constructing a population matrix model for the female portion of the population and parameterizing it with vital rates estimated from long-term monitoring using survival analysis. We stress that the results provided are preliminary and subject to a series of limitations, some of which are itemized below. Once finalized, the results should allow managers, given accurate estimates of population size and vital rates in their jurisdiction, to select appropriate quotas to meet their management objectives.

Methods

Field data

Data used for this study were collected during long-term monitoring of brown bears in two study areas in Sweden. Detailed descriptions of the study areas and monitoring are provided in Zedrosser, Dahle & Swenson (2006), Arnemo *et al.* (2006), Dahle & Swenson (2003), and Zedrosser *et al.* (2007). Of particular importance for the present study were radio-monitoring data and the determination of deaths of bears monitored between 1984 and 2007. We distinguished between two main types of deaths, deaths due to legal hunting and deaths due to other causes. The latter included mortalities such as natural (mainly intraspecific kills), damage control and self defense, illegal hunting, and traffic accidents (Bischof *et al.*, 2009). Bears that we lost track of were censored at that time for the analysis.

Survival analysis

We used Cox proportional hazards (CPH) models (Cox, 1972) to evaluate the influence of several potential predictors on cause-specific survival. These variables included age (yearling, subadult, adult), dependency status (in family group vs. independent), study area (north or south), and time period (1984 – 1997 and 1998 - 2007). Following model selection (based on AIC; Burnham & Anderson, 2002), we used the best fitting model for each required constellation (mortality cause and dependency potential) to predict cause-specific mortality risks for each relevant grouping. Survival of cubs of the year (COY) was analyzed in a separate model, because monitoring was not individual-based, but instead consisted of observations of family groups.

In addition to survival, we used CPH models to estimate weaning probabilities and probabilities of loosing an entire litter of COY. We estimated reproductive rates and litter sizes using logistic and linear regression, respectively. Although versions of these parameters have been estimated and published previously (e.g., see Swenson *et al.,* 2001 for litter size), we re-estimated them to suit the time period, interpretation, and analytical resolution desired in this study.

We fit CPH models to the data using the coxph function in the R (R Development Core Team, 2008) “survival” package (Therneau, 1999); survival predictions were made with the cph and survest functions in the “Design” package. We performed model diagnostics following (Fox, 2002) and tested for proportionality of hazards associated with the various covariates retained in the final models using the cox.zph function.

Matrix population model:

We constructed a 10 x 10 population matrix model with 4 age classes (0, 1, 2, 3, 4+), and 2 dependency statuses (independent or in family group, for mothers in relation to the age of the litter). Matrix details will be provided in a designated study description. The stable stage structure and population growth rate (λ) were calculated from the fully parameterized matrix as its right eigenvector and dominant eigenvalue, respectively. We evaluated the relationship between λ and hunting pressure numerically, by reducing or increasing hunting mortality proportionally for all age-stage-groups, in order to leave the risk ratios between groups unchanged.

To assess uncertainty in survival and reproductive parameter estimates and their impact on matrix predictions, we first created 100 re-sampled versions of the dataset. We then refit each regression model - CPH, linear, and logistic, depending on the parameter - and arrived at 100 alternative sets of parameters. We constructed confidence limits around estimates of λ by calculating the dominant eigenvalue of the matrix for each re-sampled version of the parameter set and determining the 0.975th and 0.025th quantile of the distribution of alternative λ. All analyses and simulations were performed in R 2.8.1 (R Development Core Team, 2007) and matrix calculations were performed using the demogR package in R (Jones, 2007).

Preliminary results

Vital rates

Nearly all mortality of female bears 1 year old and older due to causes other than legal hunting occurred during the mating and hunting seasons, with greater overall risk during the mating season (Apr – Jul). Most COY mortality also occurred during the mating season. Legal hunting mortality, by definition occurred only during the hunting season (Aug – Oct). Mortalities during the post hunting season (Nov – Mar) were negligible. Preliminary estimates of vital rates that emerged from regression modeling are summarized in Table 1.

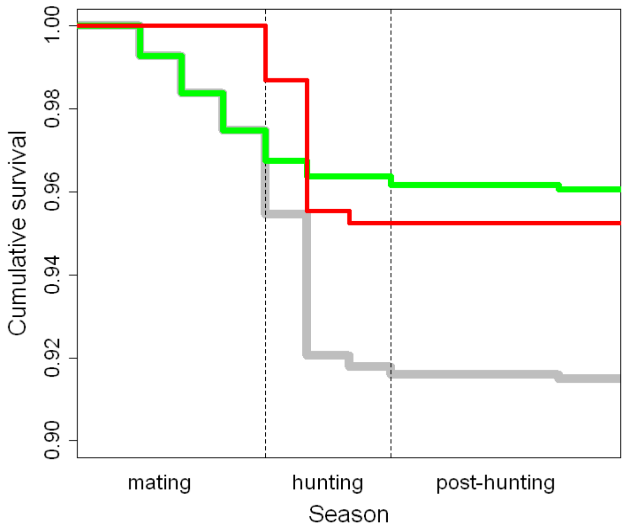

Fig. 1. Average cumulative survival for radiomarked brown bears in Sweden, associated with total risk (gray), legal hunting (red), and non-hunting risk (green).

Table 1. Vital rate estimates for brown bears in two study areas in Sweden between 1998-2007 (with 95% confidence interval limits). Small letters “i” and “d” indicate whether the animal is independent or part of a family group, respectively. Non-hunting mortality estimates are for the mating period only. The parameter “reproduction”, refers to the probability that a female emerged from the winter den with a litter of cubs if she could have mated during the previous year’s mating season. All vital rates, except for COY survival, are female-specific.

		North			South		
	Parameter	LCI	**estimate**	UCI	LCI	**estimate**	UCI
Recruitment	Reproduction	45.1%	**52.7%**	60.5%	85.3%	**88.9%**	93.7%
	Litter size	2.4	**2.6**	2.7%	2.2	**2.4**	2.5
	Litter loss	5.5%	**11.6%**	21.6%	15.0%	**23.6%**	30.3%
	Weaning	29.7%	**44.1%**	55.5%	71.2%	**80.2%**	86.8%
Non-hunting mortality	COY (d)	8.7%	**16.2%**	24.0%	15.2%	**21.9%**	30.9%
	COY (i)	-	**100.0%**	-	-	**100.0%**	-
	Yearling (i)	9.7%	**14.7%**	21.6%	9.7%	**14.7%**	21.6%
	Yearling (d)	2.5%	**6.0%**	10.5%	2.5%	**6.0%**	10.5%
	Adult	0.3%	**1.2%**	3.0%	2.5%	**4.6%**	7.1%
Legal hunting	independent	0.7%	**2.2%**	4.5%	9.2%	**11.8%**	15.3%
	dependent	-	**0.0%**	-	-	**0.0%**	-

Hunting pressure and population growth:

Projection matrices parameterized with vital rates from the northern and southern study areas showed similar predicted changes in λ with changing harvest rates. Average estimated harvest mortality within the period 1998-2007 was 1.2% in the northern and 6.7% in the southern study area. However, extrapolating harvest risk relative to the increase in the size of the annual harvest (assuming a constant population), leads to predictions of current harvest risk of 13.1% in the southern study area. Predicted growth rates for a range of hunting pressures are shown in Figure 2.

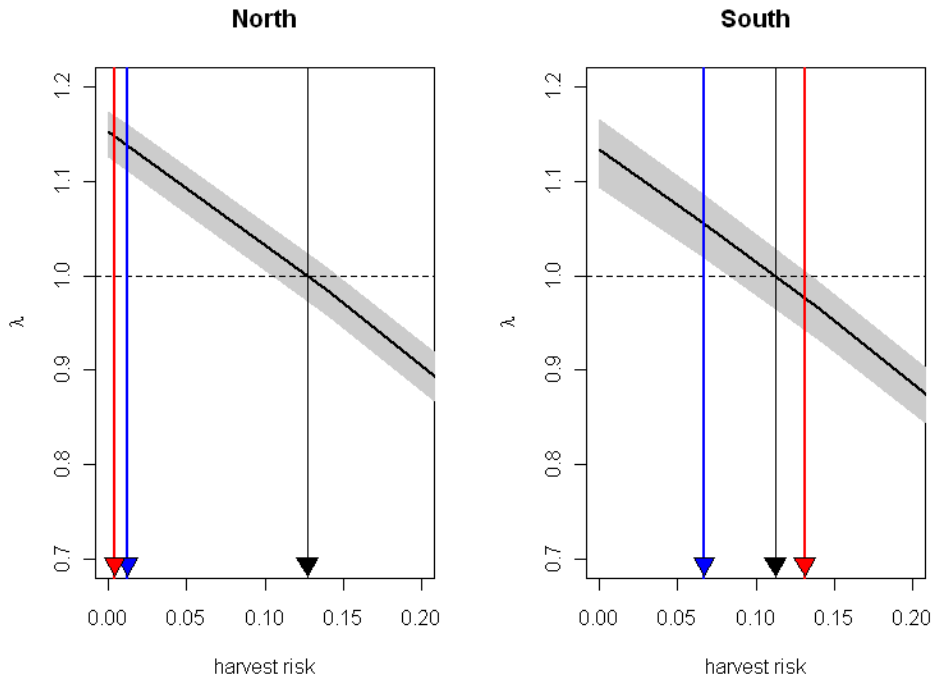

Fig. 2. Model-predicted population growth rates (thick solid black line) in the northern and southern study areas in relation to average harvest risk experienced by female bears. Harvest risk is the projected risk for the entire female population (including dependent and independent females of all age classes), based on the stable-stage distribution predicted by the population matrix. The gray area represents the 95% confidence band around the λ estimate. The arrows point at hunting risk estimates associated with 1) a stable population (black), 2) the average risk experienced during 1998-2007 within the study areas (blue), and 3) the extrapolated risk estimate based on the number of female bears killed in 2008 within the study areas (red).

Discussion

Population growth rates of 1 were predicted to occur on average with harvest risks at 11.2% of the population in the southern study area (95% CI: **8.2%** - 13.5%) and 12.7% (95% CI: **10.4%** - 14.5%) of the population in the northern study area. We recommend that the lower 95% confidence interval limits are considered as thresholds for harvest sustainability rather than the mean estimate, unless population reduction is desired. The thresholds presented here are somewhat higher than earlier estimates of maximum sustainable yield in Swedish brown bears (Swenson *et al.*, 1994).

Extrapolations indicate that current harvest risk for females in the southern study area is at the upper end of the 95% confidence interval around maximum sustainable harvest. The number of bears harvested within the southern study area in 2008 was about twice as high as the average harvest between 1998 and 2007, and the harvest within the entire southern subpopulation (Dalarna, Gävleborg, Härjedalen) increased even more, about 2.5 times during the same period. This suggests that current harvest levels in the southern study area are likely unsustainable, and may lead to a population decline. Although legal harvest pressure within the northern study area at this time is sustainable, harvest risk for bears within that study area is not representative of the hunting mortality experienced by bears within the entire northern subpopulation. As Saether *et al.* (1998) reported, large portions of the northern study area are closed to hunting during the hunting season, yielding substantially lower legal hunting mortality risk inside compared with outside the study area. Furthermore, whereas harvest pressure has remained relatively low within the study area in the north, harvest in the northern subpopulation (Norrbotten and northern Västerbotten) in 2008 was 1.7 times greater than the average harvest during 1998-2007.

Conclusions:

1. Based on vital rate estimates from this analysis and assuming population sex ratios that are not male biased, the Swedish bear population may sustain harvests under around 8% and 10% of females in the southern and northern subpopulations, respectively. This assumes that family groups are correctly identified as such and that they remain protected.
2. Current harvest quotas are likely above sustainable levels, at least in the southern study area.
3. Quota increases should follow the obtainment of population estimates, because responses to over-harvesting may lag behind quotas. Large and frequent changes in quotas paired with infrequent population estimates can lead to undesired results and make adaptive management difficult.

Limitations

There are a number of limitations associated with the analytical approach and parameter estimation, the most important ones being:

1. The assumption of non-informative censoring may be violated, especially in the northern subpopulation, because of suspected poaching (and thus “disappearance” of bears from the sample). As a result, mortality estimates associated with causes other than legal hunting may be biased low, therefore biasing the estimated rate of sustainable harvest high.
2. Only females were considered in the model.
3. Predictions are based on parameters estimated in the study areas and should not be extrapolated beyond the associated subpopulations.
4. No density dependence was considered; consequently non-hunting survival estimates may be biased high.

Future:

The completion of this project will at a minimum require 1) finalization of parameter estimation and matrix modeling, 2) model validation with available information about population dynamics of Swedish brown bears, 3) an evaluation of model sensitivity to violations of assumptions, and possibly 4) incorporation of population and harvest estimates at a smaller spatial scale (län).

Literature

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.

Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A., & Gimenez, O. (2009) The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology*, 78, 656-665.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach* Springer, New York, USA.

Cox, D.R. (1972) Regression models and life tables (with discussion). *Journal of the Royal Statistical Society, Series B*, 34, 187-220.

Dahle, B. & Swenson, J.E. (2003) 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.

Fox, J. (2002). Cox proportional-hazards regression for survival data (Appendix). In *An R and S-Plus companion to applied regression*, pp. 18. Sage Publications, Thousand Oaks, CA, USA.

Jones, J.H. (2007) demogR: A package for the construction and analysis of age-structured demographic models in R. *Journal of Statistical Software*, 22, 28pp.

Kindberg, J., Swenson, J.E., & Ericsson, G. (2009). Björnstammens storlek i Sverige 2008 – länsvisa uppskattningar och trender. Rapport 20092 från det Skandinaviska björnprojektet.

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, ISBN 3-900051-07-0, URL http://www.R-project.org, Vienna, Austria.

Saether, B.-E., Engen, S., Swenson, J.E., Bakke, O., & Sandegren, F. (1998) Assessing the Viability of Scandinavian Brown Bear, Ursus arctos, Populations: The Effects of Uncertain Parameter Estimates. *Oikos*, 83, 403-416.

Swenson, J.E., Sandegren, F., Bjarvall, A., Soderberg, A., Wabakken, P., & Franzen, R. (1994) Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation*, 70, 9-17.

Swenson, J.E., Sandegren, F., Brunberg, S., & Segerstrom, P. (2001) Factors associated with loss of brown bear cubs in Sweden. *Ursus*, 12, 69-80.

Therneau, T.M. (1999). A package for survival routines in S. Technical Report. http://www.mayo.edu/hsr/people/therneau/survival.ps, Mayo

Clinic, Department of Health Sciences, Sect. of Biostatistics, Rochester, MN, USA.

Tufto, J., Saether, B.-E., Engen, S., Swenson, J.E., & Sandegren, F. (1999) Harvesting Strategies for Conserving Minimum Viable Populations Based on World Conservation Union Criteria: Brown Bears in Norway. *Proceedings: Biological Sciences*, 266, 961-967.

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., Sæbø, S., & Swenson, J.E. (2007) Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour*, 74, 369-376.