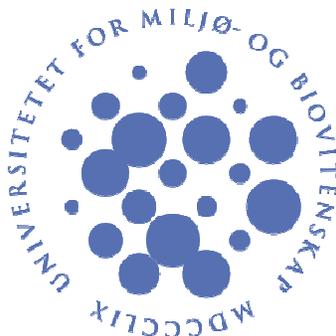# Estimating the number of annual reproductions based on the number of female brown bears documented in Norway in 2008 and 2009

Richard Bischof and Jon E. Swenson

Summary (English)

Norway's brown bear management uses the annual number of female brown bears with cubs-of-the-year for setting population goals and evaluating population status. Because the current goal is a specific number of annual reproductions, rather than lower or upper thresholds, and because its magnitude is small even on a country-wide level (goal: 15 reproducing females per year), accurate estimation is crucial. To accomplish this, we developed a simulation model, parameterized using information from a well-studied bear population in neighboring Sweden. The model's purpose is to calculate the number of annual reproductions based on the number and location of individual female brown bears detected in Norway during genetic mark-recapture monitoring (mainly scat collection in the field). Although Swedish and Norwegian bears (at least in southern and central Norway), can be considered parts of the same population, bears in Norway are at the periphery of the core areas in Scandinavia. We accounted for this in the model, as well as for the fact that home ranges of bears near the Norwegian land borders possibly extend beyond Norway. Adjusting for potential home range extension beyond Norway is an essential component of the model, as it reduces the likelihood of double-counting bears and reproductions over multiple jurisdictions. The model-predicted estimate of the number of reproductions in Norway was 4.29 (95% CI: 1.11-7.96) in 2008 and 5.73 (2.03-9.89) in 2009, based on 40 and 49 individual female bears detected in 2008 and 2009 respectively. These estimates (including their upper 95% CI limits) fall short of their target both on the country and regional level, but we stress that the estimates are based on a minimum number of individual females detected, rather than a total estimate of female bears present in Norway. Model sensitivity to violating key assumptions and cross-validation with a data set that was not used in model parameterization encourage confidence in the predictions. Nonetheless, we discuss several limitations of the model and recommend steps to improve the accuracy of estimation in the future.

Sammendrag (Norwegian)

Bjørnens status og trend i Norge er vurdert basert på antall ynglinger pr år. Siden forvaltningsmålet er uttrykt i et spesifikt antall årlige ynglinger, og ikke nedre og øvrige terskler, og er lavt selv på landsnivå (15 ynglinger pr år) er det viktig for forvaltningen å ha et nøyaktig anslag over antall ynglinger. Derfor har vi utviklet en simuleringsmodell med parametre fra bjørnestammen i Sverige, som det skandinaviske bjørneprosjektet har studert over lang tid. Modellens formål er å estimere antall årlige ynglinger fra binnene som er dokumentert i Norge (både antall og lokalisering) fra årlige innsamlinger av genetiske prøver, vanligvis ekskrementprøver. Bjørnene i Norge finnes i randsonen av bjørnestammene i land med felles grense til Norge. Vi har tatt høyde for dette og for det faktumet at hjemmeområdene til noen binner i Norge ligger delvis utenfor landet. Et viktig aspekt av modellen er derfor å justere for andelen av binnenes hjemmeområder som er utenfor Norge fordi det reduserer dobbeltelling av bjørn og ynglinger. Modellen beregnet 4,29 ynglinger (95% C.I.: 1,11-7,96) i Norge i 2008 og 5,73 (2,03-9,89) i 2009, basert på 40 respektivt 49 dokumenterte individuelle binner. Disse estimatene (og de øvre 95% konfidanseintervallene) er langt under de offisielle målene, både på lands- og regionsnivå, men det er viktig å poengtere at estimatene er basert på antallet binner som ble registrert i Norge og ikke et estimat over antall binner som faktisk finnes i Norge. Vi har testet viktige forutsetninger med data som ikke ble brukt å bygge modellen og resultatene har gitt oss tillit til modellen. Allikevel diskuterer vi modellens begrensninger og anbefaler måter for å øke modellens nøyaktighet i fremtiden.

Contents

1   Introduction

In Norway, national and regional goals for brown bear population management are expressed in the number of annual reproductions, i.e. the number of females that produce cubs in a given year. Whereas in many other jurisdictions management for wildlife is often guided by upper or lower boundaries for some population measure (i.e. a desired maximum or minimum), in Norway, managers target a specific number of reproductions in each Carnivore Management Region, rather than thresholds (Miljøverndepartementet 2005). Hence, the reliable estimation of the number of reproductions is of central importance for brown bear management in Norway today, but until now, there has been no reliable method available to estimate annual reproductions of bears over large areas (Lundvall et al. 2005).

The current country-wide goal for the number of reproductions has been set at 15, distributed over 4 of the 8 Carnivore Management Regions in Norway (Miljøverndepartementet 2005). In the past, the minimum number of reproducing females in Norway was estimated based on observations of females with cubs-of-the-year (COYs) and a key for evaluating the probability that two observations separated in space and time were in fact observations of different family groups (Swenson et al. 2003, Ordiz et al. 2007). The most recent such estimate of between 3.6 - 4.4 females with COYs (annual average between 1998-2002) was obtained in 2002 (Swenson et al. 2003). There are several issues with deriving the minimum number of reproductions from observations of females with dependent cubs, including:

1. A female may have lost her cubs by the time she was observed (-> underestimates the number of reproductions)
2. Two separate family groups may be identified as the same (-> underestimates the number of reproductions)
3. A single family group observed on multiple occasions may be identified as more than one reproducing female (-> overestimates the number of reproductions)
4. Observers may not be able to distinguish COYs from dependent yearlings (-> overestimates the number of reproductions)
5. Observers may confuse a male and female encountered together during the breeding season for a female with cubs (-> overestimates the number of reproductions)

The National Monitoring Program for brown bears in Norway has been conducting sample collections (mainly from scat) in combination with microsatellite analysis with the intent of detecting and identifying individual bears since 2005 (Bjervamoen et al. 2008, Eiken et al. 2007, Wartiainen et al. 2008, Wartiainen et al. 2009). Before 2008, each year's survey focused on different areas, but in 2008, samples were collected in all areas in which bears had been detected previously and the spatial extent of collections was further expanded in 2009. This survey effort and subsequent DNA analysis yielded 40 individual females that were detected in Norway in 2008 (Wartiainen et al. 2009) and 49 females in 2009 (preliminary results, received Apr 2010 from S. Hanssen, Norwegian Directorate for Nature Management). DNA monitoring has also been conducted in Sweden since 2001 (Kindberg et al. 2009b, Aarnes et al. 2009). In January 2010, the Scandinavian Brown Bear Research Project (SBBRP) / Norwegian University of Life Sciences (UMB) was commissioned by the Norwegian Directorate for Nature Management (DN) to develop a model for estimating the annual number of reproductions in Norway based on the number of

unique females identified during genetic captures in 2008 and 2009. The present report details the methods and outcome of this work.

In its simplest form, a model for estimating the number of reproductions in Norway may take the number of individual females identified from DNA and multiply it with the proportion of females observed with COYs in the Swedish bear population. Such an approach has several shortcomings; most importantly that it ignores some potential biases. Among these are:

1. The age structure (i.e. the proportion of breeding-age bears) and reproductive parameters (e.g. inter-litter interval) may differ between the study areas in Sweden and the periphery of the core areas where Norwegian bears are located.
2. Most females detected in Norway are located in close proximity to Norway's land borders (Figure 1), thus their activity areas may fall partially outside of Norway. Ignoring this may lead to estimates of the number of reproductions that are biased high.

Furthermore, an assessment of the uncertainty around such an estimate may not be straight-forward, because the stochastic processes that yield the multiplier are not conveyed by it.
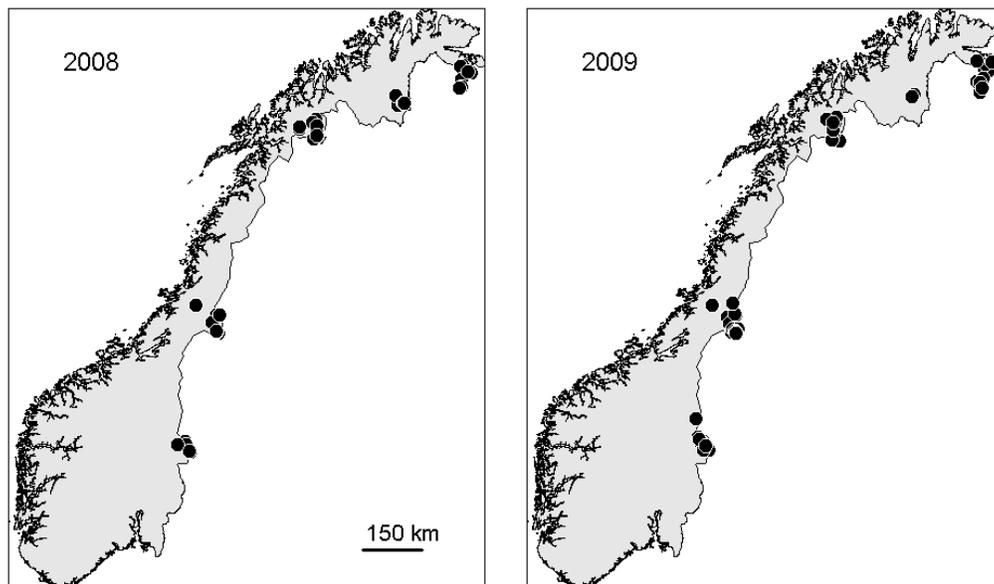
Figure 1. Central locations of DNA samples collected from individual female brown bears in Norway in 2008 and 2009.

There is additional information that encourages consideration of point 2. Forty-two individuals were identified in both the Norwegian (collected between 2005-2009, and the Swedish (collected between 2001 – 2009) DNA monitoring data sets (Aarnes et al. 2009), highlighting the cross-border activity by bears. Similarly, at least 12 female bears monitored by the SBBRP have had relocations (VHF and GPS) within a year (total: 56 bear-years between 1990 and 2009) in both Sweden and Norway, indicative of home ranges shared by both countries (SBBRP, unpublished data). Precedence for accounting for cross-border activities in large carnivores is also provided in the Norwegian management guidelines for wolves (*Canis lupus*). These state that reproductions are only to be counted as belonging to the management area designated for reproducing wolves if over 50% of a reproducing pack's territory falls within that area (Miljøverndepartementet 2005).

With the aforementioned considerations in mind, we developed a stochastic and spatially explicit model to estimate the annual number of reproductions attributable to Norway. For the construction of the model and its parameterization, we relied heavily on long-term datasets from a population of individually monitored brown bears in neighboring Sweden, as well as data on brown bears harvested (Bischof et al. 2008, Bischof et al. 2009). Using these data is appropriate, as the population in Sweden has been and continues to be the main source of bears encountered in Norway (Swenson et al. 1995, Swenson et al. 1998, Sagor et al. 1997). A particular emphasis of this study is not only to provide an estimate of the number of reproductions, but to quantify the uncertainty around that estimate. To evaluate the reliability of model predictions, we test several submodels with a cross-validation data set that had not been used during the estimation of model parameters.

2   Methods

2.1   Model description

2.1.1   Process

The model derives estimates of the number of reproductions and associated estimates of uncertainty through simulations using an individual-based approach. The DNA monitoring data - mean location of each female bear detected in Norway in a given year - serve as the basis for these simulations. Each individual simulation run consists of the following steps (see also Figure 2):

1. Age assignment: Each individual female bear detected in Norway during the focal year is assigned an age, which has been randomly drawn from the COY-augmented age distribution in Sweden, derived partially from hunter-killed bears (Section 2.2.3).
2. Reproduction: Each individual is then assigned an age- and region-specific reproductive probability, determined using the logistic regression model predicting the probability of reproducing for brown bears monitored by the SBBRP in Sweden (Section 2.2.2). Actual reproduction is decided through a random binomial event, where p (the probability of success) is equal to an individual's designated probability of reproducing.
3. Home range assignment: Individuals designated as reproducing are assigned utilization density (UD) grids selected randomly from a set of 95% annual kernel home ranges from monitored bears that exhibit representative characteristic (outside the core area, with dependent COYs, Section 2.2.4). The center location of DNA samples of a Norwegian female is associated with one of the grid points of the assigned kernel density grid through weighed random sampling based on each grid point's relative intensity of utilization (i.e. a more intensely utilized grid point in the assigned UD grid is more likely to fall on a DNA center location). The grid is then rotated around that pivot point at a random angle.
4. Determination of the home range proportion that falls within Norway: All grid point utilization intensities associated with a given UD grid (based on a 95% kernel home range) are scaled to add up to 1. The proportion of each simulated home range attributable to Norway is calculated as the sum of the scaled weights of grid cells in a home range that fall within Norway (Section 2.2.4). Simulated grid cells that fall in water outside the Norwegian shoreline are not omitted, as such edges represent real barriers to bear movement.

5. <u>Determination of the annual number of reproductions:</u> The sum of all home range proportions that fall within Norway (by females designated as reproducing), is interpreted as the number of reproductions that can be attributed to Norway. Estimations are performed on a national level and separately for each Carnivore Management Region.
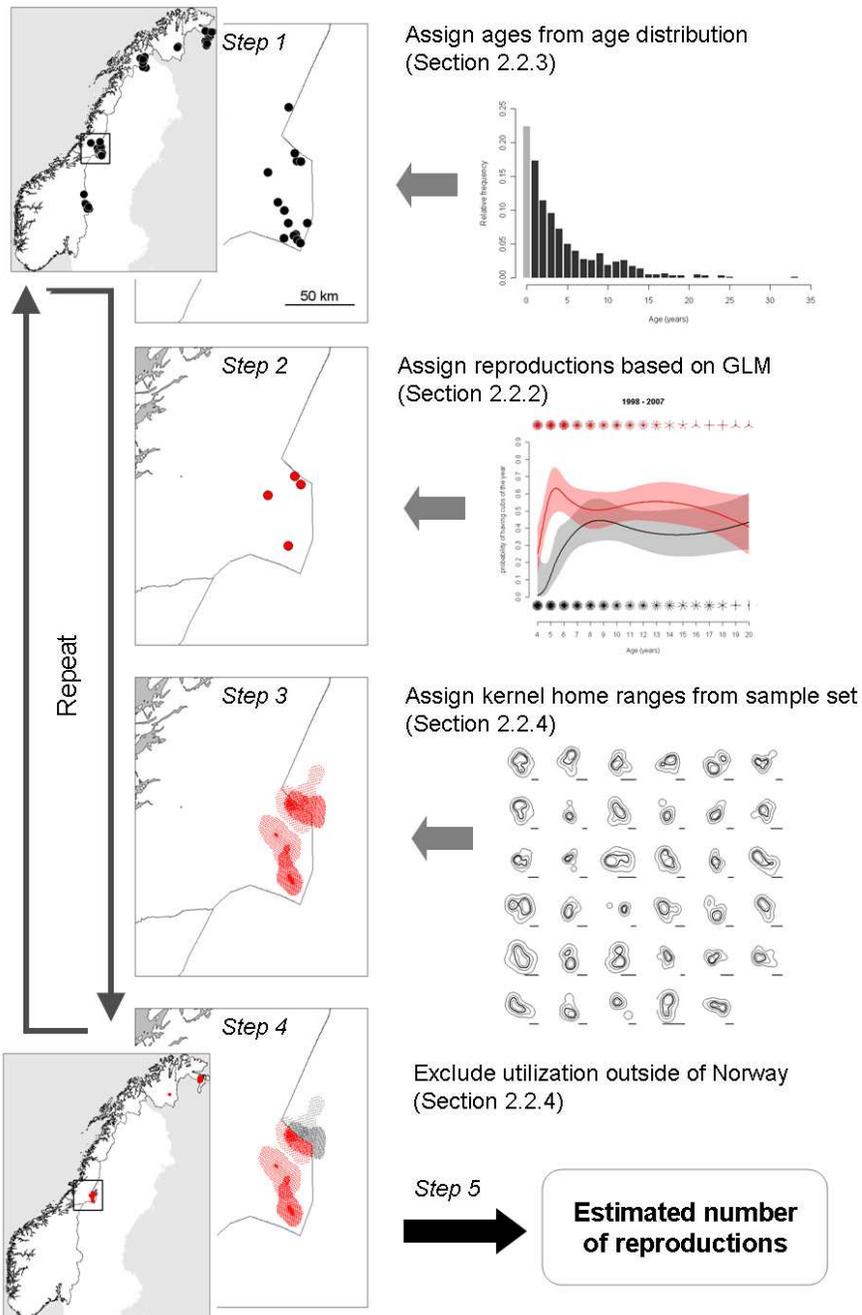
Figure 2. Simplified schematic of a model cycle (read from top down) and associated information input. Assignments of ages and kernel home ranges are made randomly. Detailed explanations and higher resolution individual figures illustrating the source information can be found in section 2.2 of this report.

2.1.2   Simulations

A full simulation consists of repeated implementation of the steps outlined in Section 2.1.1. Each simulation run yields a value for the number of reproductions (country-wide and separately for each management unit), and the resulting vector of values from all simulation runs provides an estimate of the distribution of the estimated number of reproductions attributable to Norway in a given year. The mean of this distribution represents the expected number of reproductions and the 0.025 and 0.975 quantiles of the distribution constitute the lower and upper 95% confidence limits, respectively.

2.2   Parameter estimates and assumptions

Information about contemporary age structure, vital rates, and home ranges of bears in Norway is not available. However, a long-term study conducted by the SBBRP in neighboring Sweden provides the necessary data for a population that represents part of the same metapopulation that most bears in Norway belong to (aside from those farthest north). Detailed information about study areas and data collection can be found in Zedrosser et al. (2007), Dahle and Swenson (2003), and Bischof et al. (2009).

We used 4 main sources of data for this study:

► Individual-based data from female brown bears monitored by the SBBRP from 1984-2008. In addition to birth years and mortalities, these data contain spatial information (VHF relocations) and reproductive histories.
► Harvest data (1981-2008) compiled by the Swedish Veterinary Institute, containing information about age, kill location, kill date/time and hunting method.
► DNA capture data from Sweden (2001-2008) with information about each unique individual identified by DNA and associated sample locations and date.
► DNA capture data from Norway (2005-2009) with information about each unique individual identified by DNA and associated sample locations and date.

Because of potential changes associated with a growing bear population and to ensure temporal proximity between the parameters derived from the empirical data and the population for which predictions are to be made, we limited most analyses to using empirical data collected after 1997. This was justified by preliminary findings that suggested that both average home range size and the probability of a breeding-age female having COYs have declined during the study period.

We made use of the aforementioned data to estimate model parameters, test model assumptions, and finally to validate the model, while considering that bears in Norway are at the fringe of or outside what is considered core areas in Scandinavia (areas of high female bear concentration; Swenson et al. 1998, Manel et al. 2004). Detailed descriptions of parameters and model assumptions are presented below.

2.2.1   Location relative to the core areas

Bears in Sweden are spatially configured into three core areas, which are at the center of genetically distinct subpopulations with no or very little interchange of females (Manel et al. 2004). Bears in Norway are at the periphery of these core areas, hence one is justified to question whether research findings in the study areas (which are within the core areas) apply to Norway. For this reason, we tested for the effect that the location of a bear relative to the core area within a given region has on relevant parameters, such as its age, probability of having COYs, and home range size.

Brown bear harvest data have been used repeatedly in the past to delineate core areas (Swenson et al. 1998, Waits et al. 2000) although harvesting is governed not only by bear densities, but also by differential harvest effort, which in turn is partially determined through regional quotas. Nonetheless, on a large scale the distribution of shot bears follows the assumed spatial distribution of bear densities closely (Kindberg et al. 2009a). We used harvest data to derive an index of proximity to a core area within each of the 3 bear regions in Sweden (Figure 3) by calculating a kernel density estimate of female bears shot between 1997 and 2008. Because of the aforementioned bias in harvest effort, harvest data likely only follow the actual density distribution of bears on a coarse scale, therefore we used a large search radius for kernel estimation (70km).
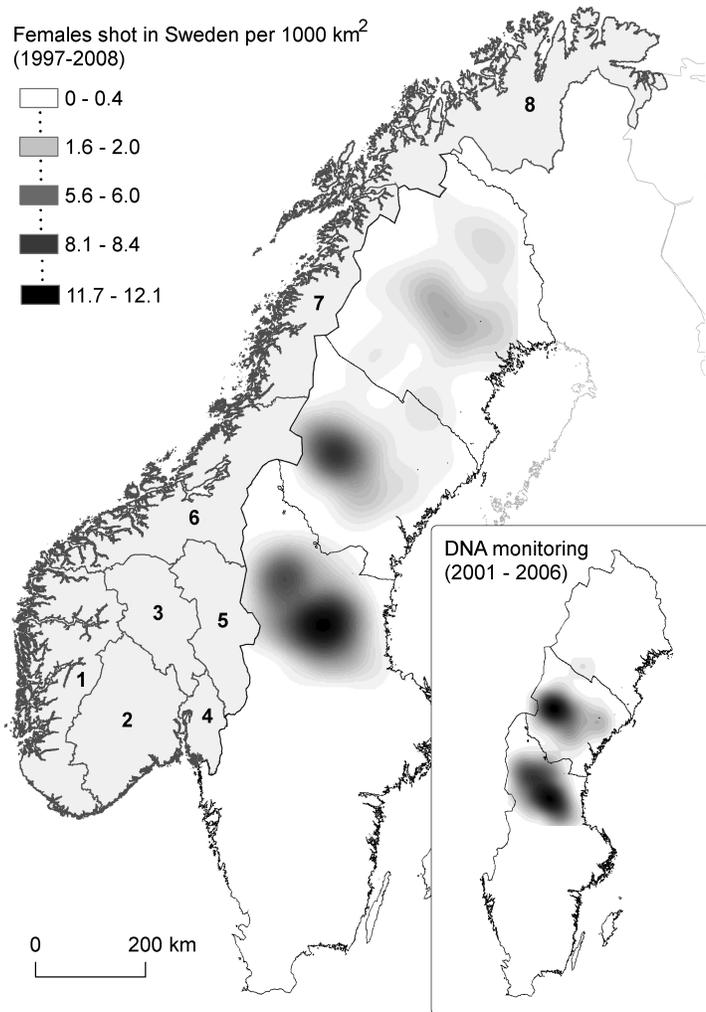
Figure 3. The large map shows the 8 Carnivore Management Regions in Norway (numbered) and the kernel density of female brown bears killed by hunters in 3 regions[*] (southern, central, and northern) in Sweden between 1997–2008. The smaller map shows the density patterns of female bears detected during DNA monitoring between 2001 and 2006 in Sweden. Darker shaded areas indicate higher kernel densities. DNA monitoring data are not yet available for the northern region, but DNA detection density patterns (i.e. clearly discernable core areas) in the southern and central regions are similar to density patterns of hunter-killed bears.

We visually compared the resulting density distribution with previous delineations of the core areas (Swenson et al. 1998, Manel et al. 2007) and with the kernel density distribution of DNA captures in Sweden (only available for the southern and central subpopulations, Figure 3). Highly corresponding patterns suggested that the use of female harvest densities was appropriate to determine a location's position relative to the core area, at least within each region. During subsequent use of density as a predictor in regression models, we always included both the main effect of density and the interaction between density and region, to

---

[*] Note that the bear regions in Sweden, as used here, do not correspond to the official carnivore management regions in Sweden.

ensure that any density effects estimate was always interpreted within the context of its region.

2.2.2   Probability of reproducing

We used logistic regression to estimate the probability that a breeding age female (≥4y) in our study areas in Sweden emerges from the winter den with COYs in a given year. The most complex model considered included age, year, region (north, south), and density of shot bears modified by region (as described in Section 2.2.1). Preliminary analysis indicated that the effect of age was non-linear, therefore we modeled age using natural splines. Because individual females were observed in multiple years, we also considered using a mixed-effects model by including individual identifiers as a random effect. However, accounting for between-individual variation through inclusion of the random effect did not improve the model (Likelihood ratio test: $X^2 \sim 0$, df = 1, p ~ 1), so we ultimately only modeled fixed effects. We used the Akaike Information Criterion (AIC, Burnham and Anderson 2002 to distinguish between models in terms of the balance between parsimony and model fit. The final model included age and region. The higher frequency and earlier age of reproduction in the southern study area (Figure 4) are consistent with previous findings by the SBBRP (Swenson et al. 2001, Zedrosser et al. 2009).
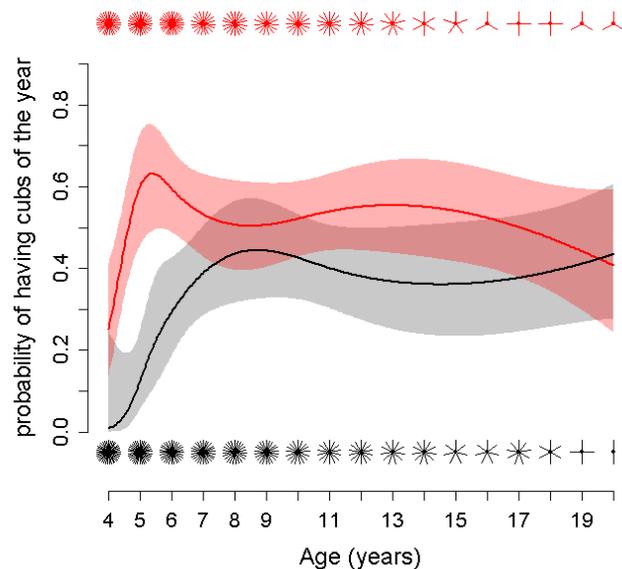
Figure 4. GLM-predicted age-dependent probability (and associated 95% CI bands) of adult female brown bears producing cubs-of-the-year in two subpopulations in Sweden (red: south, black: north). Sample sizes are shown as sunflower plots (red: south, black: north), where each leaf represents a single bear-year.

2.2.3   Age distribution

Previous investigations have indicated that, overall, bear hunting in Sweden shows no strong age-specific bias (Bischof et al. 2009). COYs are the exception, as

they still accompany their mother during the hunting season and are therefore protected from legal hunting in Sweden. Consequently, the age distribution of harvested bears can be assumed to closely resemble the actual age distribution of the population in Sweden for bears 1y old and older. However, it is possible that the female age distribution exhibits spatial patterns related to region or position relative to the core areas, as has been previously documented for male bears by Swenson et al. (1998). To test this, we conducted a linear regression with log-transformed age as the continuous response and density and region as the independent variables. Neither region nor density had a significant effect on age (Model: $R^2 < 1\%$, $F_{5, 442} = 0.795$, p=0.554). This, together with earlier findings reported in Swenson et al. (1998), provided justification for using a single age distribution for female bears, regardless of region or location relative to core areas.

The age distribution of hunted bears is incomplete however, as COYs are excluded from legal hunting. To augment the age distribution with COYs, we estimated their number by using the age distribution of breeding-age females (≥ 4 years), their age- and region-specific probability of producing COYs (Section 2.2.2), and an estimate of litter size. The latter we obtained through a linear regression analysis, which indicated that litter size was greater for females ≥ 7 than females < 7 years old ($\beta = 0.632$, SE = 0.112, p < 0.001) and, as a trend, lower in the southern study area than in the north ($\beta = -0.17$, SE = 0.096, p = 0.073). With this information, we could calculate the number of female cubs (assuming a 1:1 sex ratio at birth) of the year as:

$$N_{COY} = \frac{\sum_r \sum_a N_{a,r} p_{a,r} l_{a,r}}{2} ,$$

where $N_{a,r}$ is the number of individuals of a given age and in a given region, $p_{a,r}$ is the age and region-specific probability of producing COYs, and $l_{a,r}$ is the age and region specific litter size.

This approach resulted in an age distribution (Figure 5) where 22.5% of the female population consists of COYs, which corresponds reasonably well with previous predictions of the proportion of COYs (122 COYs / 619 total ~ 20%, Swenson et al. 1994). We used this as the source distribution that ages were sampled from for stochastic age assignment to female Norwegian bears in step 1 of each simulation (Section 2.1.1).
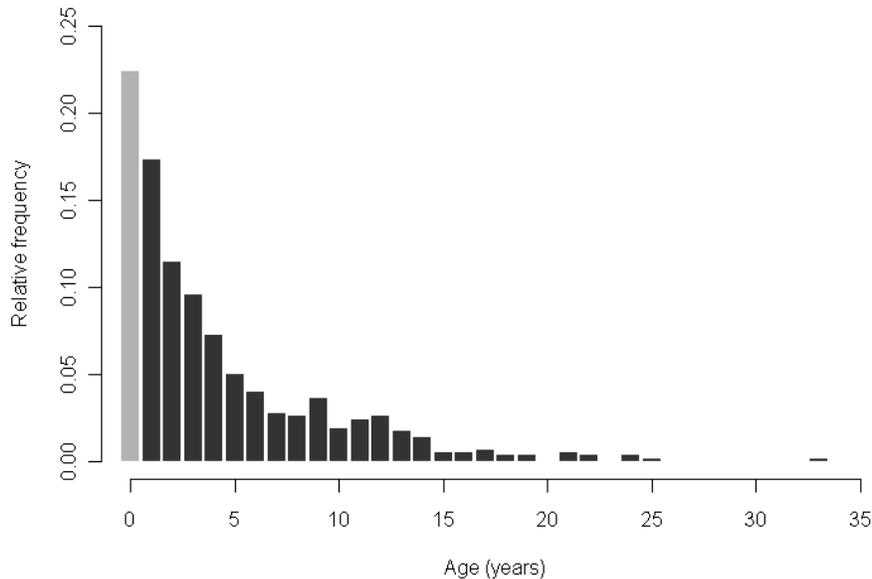
Figure 5. Age distribution of female bears killed by hunters in Sweden between 1998 and 2008 (dark bars). The age distribution was augmented with cubs-of-the year (light gray bar, see main text for information about the augmentation procedure), because cubs-of-the-year accompany their mother during the hunting season and are consequently protected from legal hunting.

2.2.4 Home range size

We calculated kernel home ranges for VHF monitored females with relocations in at least 6 separate weeks between week 18 (May) and week 40 (Sep). To reduce autocorrelation, we only used one relocation per 4-day period for each bear in a given year. Because of an insufficient sample size and lower reliability of VHF data from the northern subpopulation, we only included data from bears monitored in the southern subpopulation in this analysis.

To identify potential predictors for home range size, we used mixed-effects linear regression, with the 95% kernel home range size as the response, density, age, year, and the association with COYs as fixed effects and individual ID as the random effect. We found no evidence of overdispersion (Pearson X^2 = 23.6, df = 217, p ~ 1), therefore we were justified in using AIC for selecting among different candidate models (Bolker et al. 2009). The final model showed a decrease in home range size with higher density (i.e. closer proximity to a core area) and smaller home ranges for females that had emerged from the winter den with COYs in a given year (Figure 6). These findings are consistent with those obtained during a previous analysis of a smaller set of monitoring data for brown bears in Sweden (Dahle and Swenson 2003). Additionally, we found that home range sizes decreased over the course of the study period, presumably due to an increase in bear densities.
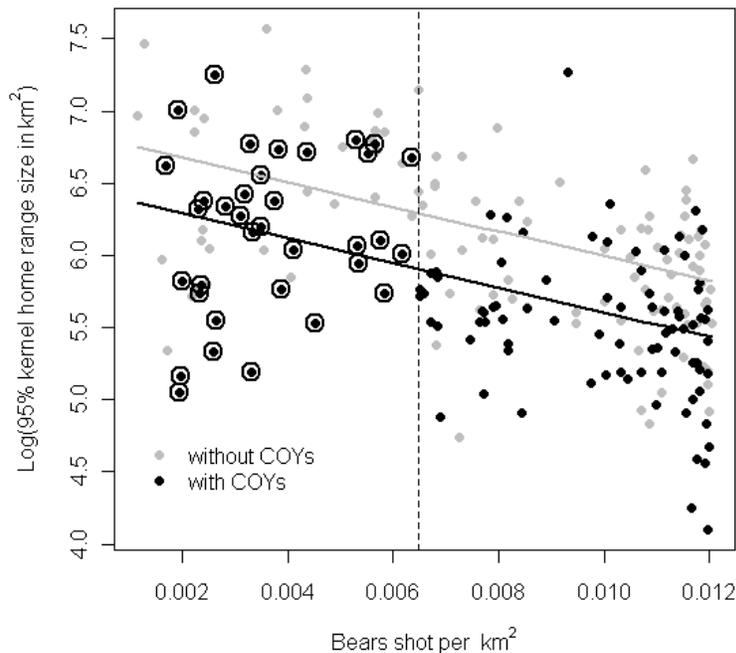
Figure 6. 95% kernel home range size (log transformed) dependent on the density of adult (≥4y) female brown bears monitored in Sweden between 1998 and 2007. Points represent the data (annual home ranges) and the solid lines the regression slopes predicted with a linear mixed effects regression model (gray for bear-years without cubs-of-the-year and black for bear-years with cubs-of-the-year). The regression lines shown here are based on predictions for year 2002, the average year of samples in the data set used during model fitting. Additional circles indicate annual home ranges that were selected for use during simulations in the simulation model for estimation of the number of reproductions in Norway. The regression was based on 223 annual home ranges from 60 individuals.

Based on the results of the regression analysis, we decided to draw home ranges for simulations by randomly selecting one annual home range from each of the 35 bears with home ranges within the lower 30%[1] of the distribution of the density index (to the left of the vertical dashed line in Figure 6). We chose to use actual home ranges during simulations, rather than circular buffers with a radius calculated from model-predicted home range size, based on the following rationale:

1. Circular home ranges with a certain radius *r* will, if the central location of the relocations associated with a bear is at a distance ≥ *r* from the border, never extend beyond the focal area's boundary. However, real-life home ranges (with the same area size as the circular buffer) have irregular shapes (Figure 7) and may extend outside the focal area, even if the average distance from the home range center is less than the closest distance of the center to the boundary.

2. Home ranges represented by a simple buffer do not account for the fact that the probability of encountering an animal in a given location generally

---

[1] This threshold was picked to balance the desire for a large sample size of home ranges to be used during simulations and the need to use home ranges associated with sites at the periphery of the core bear areas.

decreases from the center towards the edges of the home range. Therefore, "flat" home ranges, where each location is weighed the same, may bias the estimated proportion of an animal's activity that falls outside the focal area. In contrast, weighing each part of a home range according to the UD density provides a way to compare the intensity of utilization that falls within and outside the focal region (Figure 8).
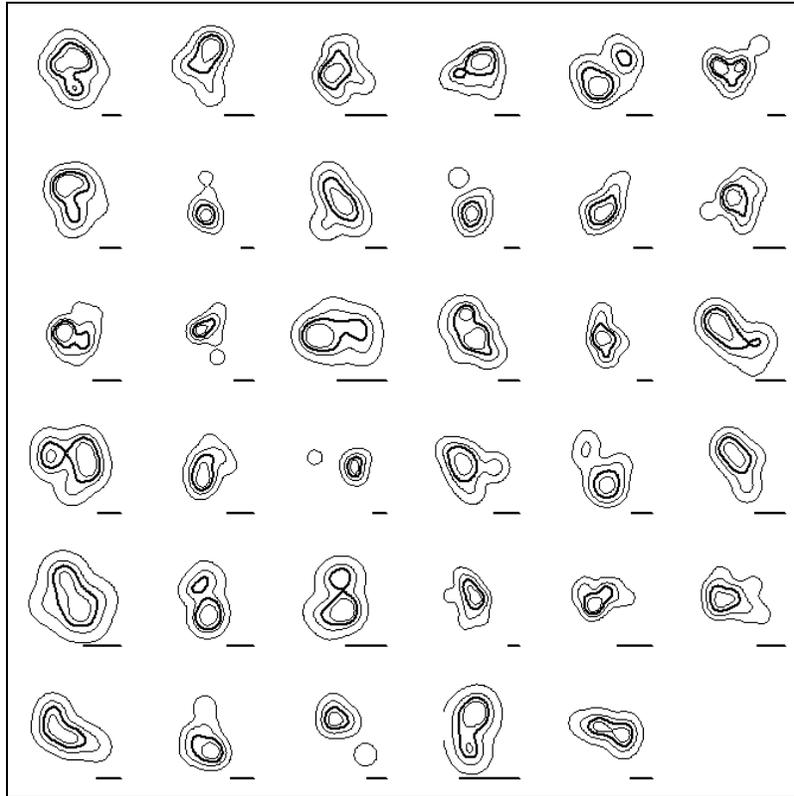
Figure 7. Sample kernel home ranges (35 bear-years from 16 different female bears with cubs-of-the-year) used for simulating home ranges for female brown bears detected in Norway. Contour lines represent 25%, 50% (thicker), 75%, and 95% kernel density volumes, from the center of each home range outwards. A straight 10 km size reference is provided below each home range.
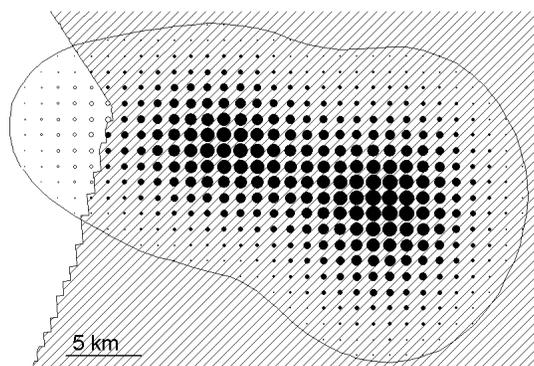
Figure 8. Example of how the proportion of a home range within a focal polygon (shaded area) is determined. Each grid point of a utilization distribution (UD) density grid within the

annual 95% kernel home range (outlined around the cloud of grid points) of an individual is weighed according to the UD density at its location (indicated by the relative size of each circle), i.e. the relative probability of encountering the individual at that point vs. another point on the grid. The UD densities are scaled to add up to 1, hence the proportional utilization intensity within the focal polygon is equal to the sum of the scaled utilization densities of all points contained within the focal polygon (black circles).

The same approach for home range allocation was also used when determining the proportion of each home range that falls within a given Norwegian Carnivore Management Region. As a result, potential reproductions by bears with encounters in multiple management units were proportionally allocated according to the intensity of simulated utilization within each management unit, rather than counting reproductions by the same bear multiple times (once in each of the management units that shared occurrences).

2.3   Implementation and computing

Most statistical analyses and modeling were conducted using the statistical programming environment R (R-Development-Core-Team 2008) and various functions contained in the following packages:

- ► *lme4* (Bates et al. 2008) to fit generalized linear mixed-effects models
- ► *adehabitat* (Calenge 2006, Calenge 2007) to estimate kernel home ranges
- ► *PBSmapping* (Schnute et al. 2008) for importing and displaying shapefiles
- ► *sp* (Pebesma and Bivand 2005), for polygon and identity operations

We used ArcGIS 9 and the Spatial Analyst extension for Kernel density estimation of shot bears and the Hawth's Tools extension for associating density estimates with point locations.

3   Results

3.1   Model-predicted number of reproductions

Based on the 40 individual females detected during the DNA collection in Norway in 2008, the model-predicted number of reproductions was 4.29 (95% CI: 1.11 to 7.96, Figure 9). In 2009, we estimated 5.73 reproductions (95% CI: 2.03 to 9.89, Figure 9), associated with the 49 individual females detected through DNA collection. In both years, only Carnivore Management Regions 5, 6, and 8 contributed annual reproductions to the estimated total (Table 1). When no adjustment was made for the possibility that home ranges of females near the border fall partially outside of Norway, the number of estimated reproductions increased (2008: mean=5.6, 95% CI 2 - 10; 2009: mean=7.5, 95% CI 3 - 13;).
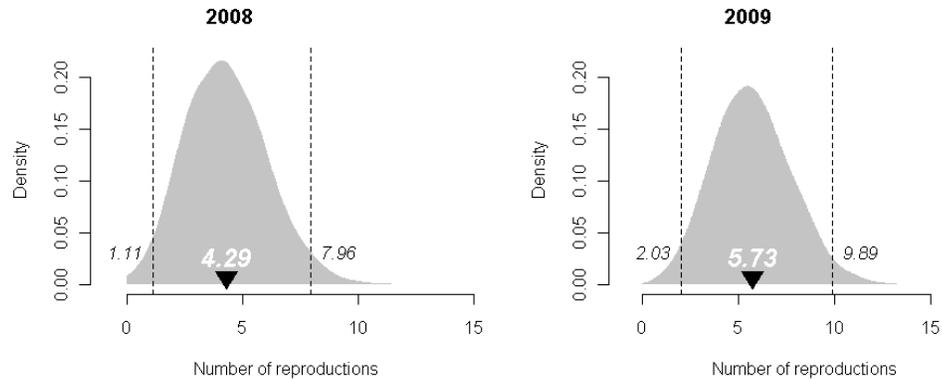
Figure 9. Distribution of model-predicted number of annual reproductions of brown bears in Norway based on the number and location of individual females detected in 2008 and 2009. Black triangles mark the mean of each distribution (i.e. the expected number of annual reproductions) and the hashed vertical lines indicate the lower and upper 95% confidence limits of the distribution. Corresponding values for the mean (white) and 95% CI limits are shown in italics. These results are based on 5000 simulation runs for each of the two years.

Table 1 The estimated number of annual brown bear reproduction and management goal for each Norwegian Carnivore Management Region (see Figure 3). Estimates (together with their 95% CI limits) were generated by a simulation model based on 40 individual female bears detected in Norway during DNA monitoring in 2008 and 49 female bears detected in 2009. See Figure 3 for a map of the management regions. No samples containing bear DNA (male or female) were collected in regions marked with a "*".

Year	Management region	Number of females detected	Goal	LCI	Mean	UCI
2008	Region 1*	0	**0**	-	**-**	-
	Region 2*	0	**0**	-	**-**	-
	Region 3*	0	**0**	-	**-**	-
	Region 4*	0	**0**	-	**-**	-
	Region 5	6	**3**	0	**0.78**	2.46
	Region 6	8	**4**	0	**1.05**	2.93
	Region 7	0	**2**	-	**-**	-
	Region 8	26	**6**	0	**2.45**	5.51
2009	Region 1*	0	**0**	-	**-**	-
	Region 2*	0	**0**	-	**-**	-
	Region 3	0	**0**	-	**-**	-
	Region 4*	0	**0**	-	**-**	-
	Region 5	10	**3**	0	**1.39**	3.48
	Region 6	16	**4**	0	**2.32**	5.14
	Region 7	0	**2**	-	**-**	-
	Region 8	23	**6**	0	**2.03**	4.75

3.2   Convergence

To determine the minimum number of runs required for consistent estimates, we tested for convergence in predictions by running the model through 20 cycles at each of the following settings for the number of simulation runs: 50, 100, 250, 500, 1000, 2500, and 5000. Standard deviation in the mean estimates changed little after about 1000 - 2500 runs (Figure 10), so ~2000 is the minimum number of runs we recommend for other users of the model. We note that the 2009 data (49 females) were used for the convergence test – a substantial change in the annual number of females detected may possibly alter the convergence pattern.
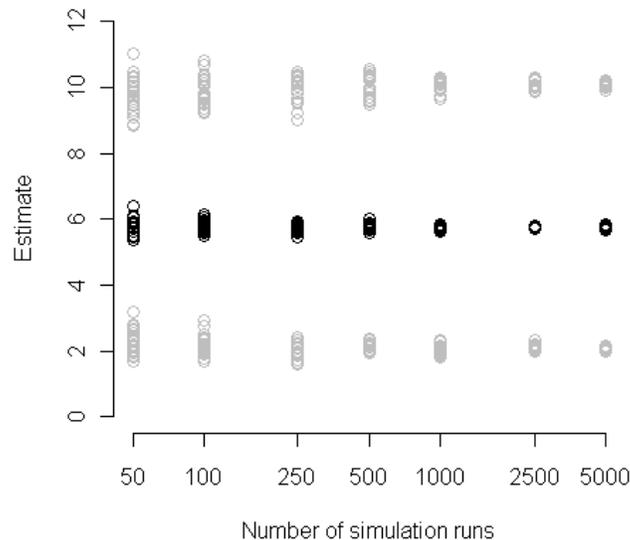
Figure 10. Effect of the number of simulations (on a log-scale, 20 repeats of each set of runs) on consistency in the estimated mean number of brown bear reproductions in Norway (black circles) and associated upper and lower CI limits (gray circles). Scatter decreases with increasing number of simulations. Results are based on the 2009 data of individual females identified in Norway.

3.3   Model validation

At the onset of this project, we set aside 91 bear-years of data (annual data from 16 monitored bears). Intended for cross-validation, these data were not used during model parameterization. The remaining data were used as the training data (866 bear-years from 252 bears), i.e. for the estimation of required parameters. The cross-validation data were randomly selected from all relocation sets with centers within a 75km buffer around the Swedish/Norwegian border, because we intended the validation data to be as similar as possible to expected (albeit unknown) data from bears detected in Norway.

With the validation data, we conducted tests to answer the following questions:

1. How does the distribution of 95% kernel home range size estimate for the cross-validation data set compare with that of the set of home ranges used for simulations in the model?
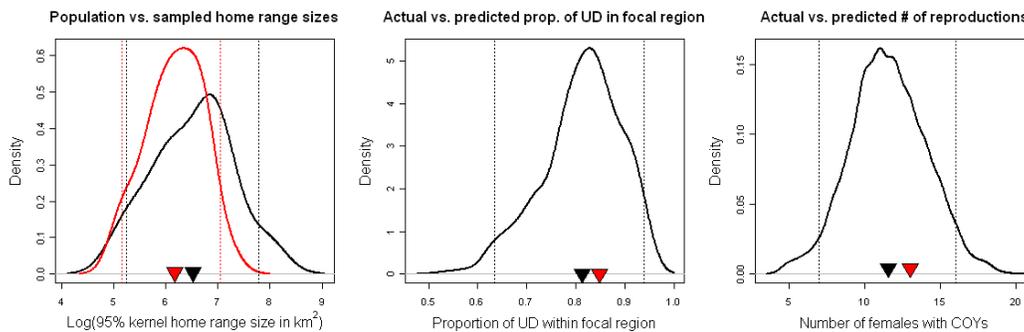
Result: The distributions of the 95% kernel home range sizes of the cross-validation set (N=91) and the simulation set (N=35) show substantial overlap. No significant difference between their means was detected (t = 1.49, df = 16.62, p-value = 0.155, Figure 11).

2. How does the actual proportion of UDs attributable to the southern bear region in Sweden (for reproducing females) compare with the model-simulated proportion for the same region?
   Result: The predicted proportion of annual UDs for cross-validation females that falls within the southern bear region in Sweden (81.3%) corresponded closely with the proportion predicted through using the home range simulation submodel of the model (84.8%, Figure 11).

3. How does the actual number of reproductions in the cross-validation dataset compare with the predicted number of reproductions using the logistic regression model described in Section 2.2.2?
   Result: The number of observed reproductions (11.6 reproductions for 91 bear-years) and the number of reproductions (13) predicted using the logistic regression model (applied to the known age structure) were comparable (Figure 11).

Figure 11. Cross-validation results: left panel - a comparison of the distribution of log-transformed 95% kernel home range sizes of the cross-validation data set (red line, mean: red triangle) and the home range sample used during simulations (black line, mean: black triangle); middle panel - the distribution of the model-predicted proportion of utilization distributions within a focal area (southern bear region in Sweden) and the value of the actual proportion of utilization by cross-validation bears-years within the same area (red triangle); right panel – distribution of the GLM-predicted number of reproductions (black line, mean: black triangle) and the number of actual reproductions during cross-validation bear-years (red triangle). 95% confidence limits for the distributions are marked by dashed vertical lines.

3.4   Sensitivity analysis

3.4.1   Relative COY detection probability

For the default parameter set (Section 2.2), we assumed that the age distribution of bears detected with scat surveys (for genetic mark-recapture) was identical to the true age distribution of the population. However, it is conceivable that some age classes are less likely to be detected than others. Specifically, feces of COYs may have a lower detection probability than the scat of older bears. If that were the case, using the COY-augmented age distribution (Section 2.2.3) would result in an underestimation of the proportion of breeding-age females and consequently the

annual number of reproductions. To explore the effects of violating the assumption of equal detection probability of COYs, we ran the model with several different version of the original age source sample, simulating relative detection probabilities of COYS of 0, 0.25, 0.5, 0.75, and 1 (default). We found that the model was relatively robust to changes in the detection probability of COYs (relative to other age classes); even in the unlikely event that COYs were completely missed during genetic capture occasions (resulting in an older age structure of detected bears), the estimated number of reproductions increases by less than 30% (Figure 12).

3.4.2   Home range size

For the simulation of home range configuration and home range extension beyond Norway's boundaries, we used 35 kernel home ranges from 16 bears with COYs monitored in Sweden (Figure 7). This approach was based on the assumption that the sample of 35 home ranges is representative of home ranges for females with COYs in Norway. However, if actual home ranges in Norway are smaller than those in the sample, their extension beyond Norway's borders is overestimated and hence the number of reproductions attributable to Norway is underestimated. Conversely, if actual home ranges are larger, they may extend even further outside of Norway and consequently using the sample home range set in the model would overestimate the annual number of reproductions. We explored the effect of violations of this assumption, by re-running the model with smaller and larger versions of the 35 sample home ranges. We found that as home range sizes increased, the predicted number of reproductions did decline as predicted (Figure 12). For example, if home ranges of females with COYs in Norway are assumed to be 1.5 times larger than those in the original simulation set, the estimated number of annual reproductions attributable to Norway would decrease by about 15%.

3.4.3   Probability of reproducing

The age- and location-specific probability of producing COYs is implemented during simulations through the logistic regression model, which has been fit to data from female bears monitored in Sweden (Section 2.2.2). This is based on the probability of observing a given female with COYs at least once during the year. Because observations on nearly all bears begin in the spring, this is equivalent to the probability of observing a female with COYs shortly after den emergence. Nonetheless, it is possible that some reproductions are missed, for example if a female loses her litter sometime between den emergence and the first observation by the SBBRP in that year. We tested the effect that changing the probability of being observed with COYs had on the model-estimated number of reproductions. This was accomplished by running sets of simulations where the probability of reproducing (based on the original fitted GLM, Section 2.2.2) is multiplied by a factor of 0.75 (i.e. a probability of reproducing that is 75% of the one predicted from the SBBRP's data), 1 (default), 1.25 and 1.5 (i.e. the probability of reproducing is 1.5 times higher than predicted by the SBBRP). As expected, increasing the probability of reproducing leads to higher estimates of annual reproductions. For example, a 25% increase in the probability of producing COYs will increase the estimated number of reproductions by a similar proportion (Figure 12). However, even a 25% increase seems unrealistically high, as it would require that current monitoring methods by the SBBRP in Sweden miss that a female has emerged from the den with COYs 25% of the time, even though she is observed (either by failing to observe a litter of COYs

that is present or because the female lost her litter before the first observation in a given year was made[2]).
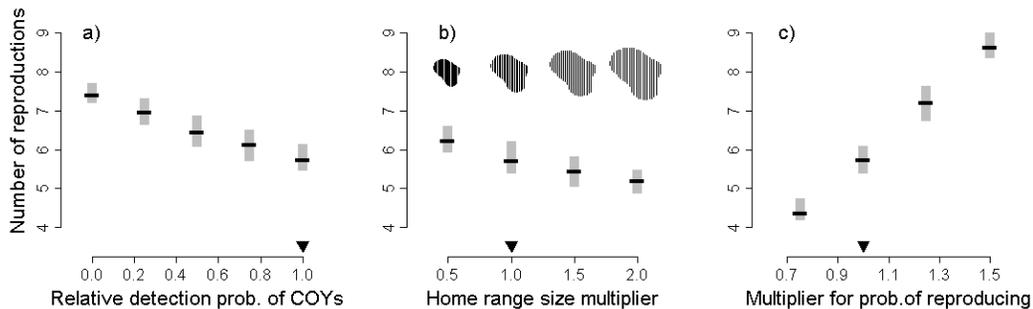
Figure 12. Sensitivity of the model-predicted number of annual brown bear reproductions attributable to Norway in 2009 a) to changes in the probability of detecting brown bear cubs-of-the-year (COYs) relative to other ages with DNA monitoring, b) to changes in the size of the set of 35 home ranges used during simulations (an example home range is shown above each value set to help visualize differences in relative size), and c) to changes in the probability of reproducing (applying a multiplier to age- and region-specific probabilities of reproducing from the GLM described in Section 2.2.2). The default value for each parameter is indicated with a black triangle. Twenty simulations with 100 cycles each were run for each parameter value. Black horizontal bars indicate the mean of the predicted number of reproductions and gray vertical bars represent the 95% CI around the mean prediction.

4   Discussion

4.1   General comments on the findings

Based on the 49 individual female brown bears identified in Norway in 2009, we estimate that 5.73 reproductions occurred in and are attributable to those females in Norway, with an upper 95% CI limit of 9.89 reproductions during that year. In 2008, fewer females were detected, and the estimated number of reproductions is correspondingly lower at 4.29. These estimates take into account the possibility that females, specifically those near the border with Norway's neighbor countries, do not spend their entire time within Norway and consequently their potential reproductions are only partially attributable to Norway. This adjustment is a crucial component of the estimation procedure and reduces the risk of double-counting over multiple jurisdictions. The consequences are not benign, as highlighted by the difference between predictions that incorporate the spatial adjustment vs. those that do not (4.29 vs. 5.6 in 2008; 5.73 vs. 7.5 in 2009) and is bound to remain relevant as long as most female bears detected in Norway remain in proximity to the country's land borders. In addition to the spatial adjustment, we have accounted for certain bias-causing heterogeneities in key parameters, such as reproductive frequency and home-range size. We stress that the estimates provided in this report are based on unique female bears identified in Norway, which is a minimum number of individuals present during a given year.

---

[2] The SBBRPs monitoring methods are likely to detect almost all instances of den emergence with COYs by monitored females bears, even if the litter ist lost before the first observation of the female; females that could have been reproducing, but are not observed with COYs in the spring, are captured and checked for physical signs that they have been nursing young.

The total estimate of the number of reproductions attributable to female brown bears detected in Norway during 2009 is only 38% of the country-wide management goal (15). The goals (nationwide and for each management unit separately) remain beyond the upper 95% CI limit, regardless of whether or not adjustments are made for home ranges that could fall partially outside of Norway.

Looking at earlier estimates, the total number of females observed annually with COYs within the 5 areas with bear reproductions in Norway reported in Swenson et al. 2003 ranged from 3 – 5 per year during 1998-2002 (after adjusting for potential observations of females with yearlings instead of COYs). These are comparable to our estimate of 5.6 (in 2008) and 7.5 (in 2009) bears (if home range extension beyond Norway is ignored, as they were for the estimates reported in Swenson et al. 2003), but we caution that all estimates, including the ones we generated, are based on a minimum number of observations and are thus may be biased low.

Swenson and Katajisto (2005) suggested that an extrapolation factor of 9 or 10 be used to multiply the number of reproductions in order to calculate the total number of bears throughout Sweden. These authors recommended against applying the Swedish extrapolation factor to estimate the total number of bears in Norway. Nonetheless, it is tempting to compare the ratio (6.5) of detected females (49 in 2009) to the estimated number of unadjusted reproductions from the model (7.5) with the mean extrapolation factors reported by Swenson and Katajisto (2005, between 4.5 – 5 females per annual reproduction, if only females are considered). The somewhat higher ratio of bears per female with COYs (or conversely, the lower average rate of reproduction) may have various causes. One potential reason is the difference in how the age structure was derived in the two projects, namely through the use of a COY-augmented age structure in the present project and through population dynamic modeling in Swenson and Katajisto (2005). Nonetheless, the average extrapolation factor in the present study can be expected to be higher than the average reported in Swenson and Katajisto (2005), because we associated attributes (such as lower reproductive rate) with many of the bears detected in Norway based on their proximity to the northern subpopulation in Sweden, which is less productive than the southern one.

4.2   Model limitations

Like any model, ours is a simplification of a complex real-life system. This simplification facilitates comprehension and permits a certain degree of generalization when making predictions. On the other hand, lack of acute realism and a restricting set of assumptions mean that model predictions have to be interpreted cautiously. Results of the cross-validation of important submodels in our model encouraged confidence in its predictions, but there are several assumptions that are based on limited data or conjecture, which the user of the model should be aware of when interpreting its predictions.

Habitat: Although the model is spatially explicit, it does not consider specific habitat features or differences therein along latitudinal or longitudinal gradients. The most relevant spatial features considered were proximity to Norwegian land borders and location relative to the southern vs. the northern core area in Sweden. Through the location relative to the main core areas in Sweden (through the use of harvest density as a proxy), habitat differences were indirectly addressed during model parameterization. Furthermore, the regression model for home range size in the southern subpopulation exhibited very good model fit, with only harvest density, year, and reproductive status as the predictors.

Russia and Finland: The model has been parameterized using available information from an intensely monitored population in Sweden. This is appropriate, as many of the bears in Norway originate in Sweden; in fact bears in southern and central Norway and Sweden should be considered part of the same population (Swenson et al. 1998). However, Russia and Finland are additional sources for brown bears in northern Norway (Carnivore Management Region 8), which may affect assumptions about age structure, vital rates, and home range sizes. We recommend that, as information about these other source populations becomes available (and if it differs from that of the Swedish population), it be incorporated into the present model to increase its predictive accuracy.

Male bears: Because the ultimate goal was to estimate the number of females that produce COYs in a given year, we ignored males in this model. However males do play a role in population dynamics (Mysterud et al. 2002), and their density and age distribution may impact properties of the female population (such as home ranges and vital rates) and consequently the number of reproductions. Specifically in Scandinavia, where infanticide is an important contributor to juvenile bear mortality (Swenson et al. 1997), the impact of males may change across the landscape and according to the location relative to the core areas. Differences in spatial and social relationships between bears in Norway vs. those surveyed in and around the core areas in Sweden could mean differences in vital rates, for example through alterations in the incidence of infanticide.

Age structure: In our opinion, the weakest assumption of the model is the one about the age structure. We assumed that the age structure of female bears detected during DNA monitoring represents the true underlying age structure of female bears in Norway. Furthermore, we assumed that this age structure is similar to the age structure of bears killed by hunters in Sweden, after augmenting with COYs. Although we have no evidence to the contrary, we also have little evidence that would strongly support these assumptions. The two pieces of evidence that provide some justification are 1) the lack of an obvious effect of region or location relative to the core area on age (Section 2.2.3), and 2) the lack of strong age-specific vulnerability to hunting by bears in Sweden, with the exception of COYs (Bischof et al. 2009). Similarly, Kojola and Heikkinen (2006) detected no difference in the age of brown bears harvested Finland along a north-south or east-west gradient. Although these findings and the results of the sensitivity analysis are encouraging, we recommend that future investigations determine the age-specific capture probability for brown bears in genetic mark recapture studies as conducted in Sweden and Norway.

4.3   Further recommendations

For the time being, the estimated number of female bears in Norway is a minimum number, identified as genetically unique individuals detected in the country. Consequently, estimates of the number of reproductions may be biased low. Similarly, previous estimates of the number of reproductions based on observations of females with COYs were also minimum estimates. In the future, capture-mark-recapture methods could be used to estimate the total number of females in the areas surveyed, by accounting for capture probabilities that are < 1. An estimated total number of females could yield an estimated total number of reproductions instead of an estimated number of reproductions attributable only to females detected. Furthermore, recaptures of the same individuals in multiple years allows for establishing minimum ages (i.e. an individual detected in 2007 and 2009 cannot be

younger than 2 years. This information, if incorporated into the model, may help reduce stochasticity during simulations and hence narrow the confidence band around the estimate.

As has been noted repeatedly (Swenson et al. 1998, Swenson et al. 1995, Swenson 1995), many bears in Norway are dependent on, and in fact are part of the bear population that has its core in Sweden. For this reason, Swedish and Norwegian bear management are necessarily intertwined, with Norway being influenced to a greater degree by Swedish management than vice versa. Both countries' estimates of the number of bears present would become more accurate if surveys (DNA collections) could be synchronized in time and target the entire Scandinavian brown bear range. Synchronized surveys would result in data suitable for comprehensive analysis using multi-state capture-mark-recapture analysis, for example with different countries or their management units as separate states (e.g. see Brownie et al. 1993). Given the current situation, such an analysis would only be possible sporadically; Norway now surveys annually, whereas Sweden is conducting surveys on a 5-year basis in some jurisdictions and so far has not surveyed its entire bear range.

5   Literature cited

Aarnes, S. G., E. Bellemain, H. G. Eiken, and I. Wartiainen. 2009. Interlaboratory comparison of genetic profiles of brown bears from Sweden (Laboratoire d'Ecologie Alpine) and Norway (Bioforsk Svanhovd). Bioforsk Report Vol. 4 No. 133. Bioforsk.

Bates, D., M. Maechler, and B. Dai. 2008. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-28. http://lme4.r-forge.r-project.org/.

Bischof, R., R. Fujita, A. Zedrosser, A. Söderberg, and J. E. Swenson. 2008. Hunting patterns, the ban on baiting, and harvest demographics of brown bears in Sweden. Journal of Wildlife Management 72:79-88.

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

Bjervamoen, S. G., H. G. Eiken, M. Smith, H. Brøseth, P. Aspholm, E. Maartmann, P. Wabakken, P. M. Knappskog, and I. Wartiainen. 2008. Populasjonsovervåkning av brunbjørn 2005-2008: rapport for Sør-Norge, 2007. Bioforsk.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127-135.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-markovian transitions. Biometrics 49:1173-1187.

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

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519.

_____. 2007. Exploring habitat selection by wildlife with adehabitat. Journal of Statistical Software 22:1-19.

Dahle, B., and J. E. Swenson. 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.

Eiken, H. G., S. G. Bjervamoen, M. Smith, H. Brøseth, S. Wikan, L. Jensen, P. M. Knappskog, T. A. Bjørn, L. Ollila, and P. Aspholm. 2007. Populasjonsovervåkning av brunbjørn 2005-2008: rapport for Sør-Trøndelag, Nord-Trøndelag, Nordland, Troms og Finnmark 2006. Bioforsk.

Kindberg, J., G. Ericsson, and J. E. Swenson. 2009a. Monitoring rare or elusive large mammals using effort-corrected voluntary observers. Biological Conservation 142:159-165.

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

Kojola, I., and S. Heikkinen. 2006. The structure of the expanded brown bear population at the edge of the Finnish range. Annales Zoologici Fennici 43:258-262.

Lundvall, A., H. Andrén, H. Lindén, J. E. Swenson, and B.-E. Sæther. 2005. Utvärdering av Norges nationella övervakningsprogram för stora rovdyr. Direktorat for naturforvaltning. Report 2005-7.

Manel, S., E. Bellemain, J. E. Swenson, and O. Francois. 2004. Assumed and inferred spatial structure of populations: The Scandinavian brown bear revisited. Molecular Ecology 13:1327-1331.

Manel, S., F. Berthoud, E. Bellemain, M. Gaudeul, G. Luikart, J. E. Swenson, L. P. Waits, and P. Taberlet. 2007. A new individual-based spatial approach for identifying genetic discontinuities in natural populations. Molecular Ecology 16:2031-2043.

Miljøverndepartementet. 2005. Forskrift om fovaltning av rovvilt. http://www.lovdata.no/for/sf/md/xd-20050318-0242.html.

Mysterud, A., T. Coulson, and N. C. Stenseth. 2002. The role of males in the dynamics of ungulate populations. Journal of Animal Ecology 71:907-915.

Ordiz, A. s., C. Rodríguez, J. Naves, A. Fernández, D. Huber, P. Kaczensky, A. Mertens, Y. Mertzanis, A. Mustoni, S. Palazón, P. Y. Quenette, G. Rauer, and J. E. Swenson. 2007. Distance-based criteria to identify minimum number of brown bear females with cubs in Europe. Ursus 18:158-167.

Pebesma, E. J., and R. S. Bivand. 2005. Classes and methods for spatial data in R. R News 5.

R Development Core Team. 2008. R: A language and environment for statistical computing. in R Foundation for Statistical Computing,Vienna, Austria.

Sagor, J. T., J. E. Swenson, and E. Roskaft. 1997. Compatibility of brown bear Ursus arctos and free-ranging sheep in Norway. Biological Conservation 81:91-95.

Schnute, J. T., N. Boers, R. Haigh, and A. Couture-Beil. 2008. PBSmapping: PBS Mapping 2.59. R package version 2.59. CRAN,http://cran.r-project.org/web/packages/PBSmapping/PBSmapping.pdf.

Swenson, J. E., B. Dahle, J. M. Arnemo, S. Brunberg, H. Hustad, E. Nerheim, F. Sandegren, K. H. Solberg, and A. Söderberg. 2003. Utredninger i forbindelse med ny rovviltmelding: Status og forvaltning av brunbjørnen i Norge. Norsk Institutt for Naturforvaltning.

Swenson, J. E., F. Sandegren, A. Bjärvall, and P. Wabakken. 1995. Living with success: research needs for an expanding brown bear population. Ursus 10:17-23.

Swenson, J. E., and J. Katajisto. 2005. Estimating the total population size of brown bears in an area based on the number of annual reproductions. Report No. 2005-1 from the Scandinavian Brown Bear Research Project. Prepared for the Swedish Environmental Protection Agency, Stockholm.

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

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

Swenson, J. E., F. Sandegren, and A. Söderberg. 1998. Geographic expansion of an increasing brown bear population. evidence for presaturation dispersal. Journal of Animal Ecology 67.

Swenson, J. E., F. Sandegren, A. Söderberg, A. Bjärvall, R. Franzén, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. Nature 386:450-451.

Swenson, J. E., P. Wabakken, F. Sandegren, A. Bjärvall, R. Franzén, and A. Soederberg. 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.

Waits, L., P. Taberlet, J. E. Swenson, F. Sandegren, and R. Franzen. 2000. Nuclear DNA microsatellite analysis of genetic diversity and gene flow in the Scandinavian brown bear (*Ursus arctos*). Molecular Ecology 9:421-431.

Wartiainen, I., C. Tobiassen, S. G. Bjervamoen, M. E. Smith, S. Wikan, and H. G. Eiken. 2008. DNA analyse av sporprøver fra brunbjørn, Øst-Finnmark 2007. Bioforsk.

Wartiainen, I., C. Tobiassen, H. Brøseth, S. G. Bjervamoen, H. Geir, and H. G. Eiken. 2009. Populasjonsovervåkning av brunbjørn 2005-2008: DNA analyse av prøver samlet i Norge i 2008. Bioforsk Report Vol. 4 Nr. 58. Bioforsk Jord og miljø.

Zedrosser, A., B. Dahle, O.-G. Stoen, and J. E. Swenson. 2009. The effects of primiparity on reproductive performance in the brown bear. Oecologia 160:847-854.

Zedrosser, A., O.-G. Støen, S. Sæbø, and J. E. Swenson. 2007. Should I stay or should I go? Natal dispersal in the brown bear. Animal Behaviour 74:369-376.