Linking noninvasive genetic sampling and traditional monitoring to aid management of a trans-border carnivore population

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Abstract. Noninvasive genetic sampling has been embraced by wildlife managers and ecologists, especially those charged with monitoring rare and elusive species over large areas. Challenges arise when desired population measures are not directly attainable from genetic data and when monitoring targets trans-border populations. Norwegian management authorities count individual brown bears (*Ursus arctos*) using noninvasive genetic sampling but express management goals in the annual number of bear reproductions (females that produce cubs), a measure that is not directly available from genetic data. We combine noninvasive genetic sampling data with information obtained from a long-term intensive monitoring study in neighboring Sweden to estimate the number of annual reproductions by females detected within Norway. Most female brown bears in Norway occur near the border with neighboring countries (Sweden, Finland, and Russia) and their potential reproduction can therefore only partially be credited to Norway. Our model includes a simulation-based method that corrects census data to account for this. We estimated that 4.3 and 5.7 reproductions can be credited to females detected with noninvasive genetic sampling in Norway in 2008 and 2009, respectively. These numbers fall substantially short of the national target (15 annual reproductions). Ignoring the potential for home ranges to extend beyond Norway's borders leads to an increase in the estimate of the number of reproductions by ~30%. Our study shows that combining noninvasive genetic sampling with information obtained from traditional intensive/invasive monitoring can help answer contemporary management questions in the currency desired by managers and policy makers. Furthermore, combining methodologies and thereby accounting for space use increases the accuracy of the information on which decisions are based. It is important that the information derived from multiple approaches is applicable to the same focal population and that predictions are cross-validated. When monitoring and management are constrained to administrative units, census data should be adjusted by discounting portions of individual space utilization that extend beyond the focal jurisdiction. Our simulation-based approach for making such an adjustment may be useful in other situations where management authorities target portions of trans-border populations.

Key words: artificial boundaries; brown bear; harvest data; microsatellite analysis; Scandinavia; telemetry; Ursus arctos; utilization distribution.

INTRODUCTION

Those charged with the management of terrestrial wildlife populations are typically assigned politically defined jurisdictions, such as national parks, states or provinces, or even entire countries. For large administrative units and for wide-ranging species, monitoring can represent a substantial challenge in terms of both resources and scientific methodology. Many management authorities rely on indirect methods, such as the collection of observation reports (e.g., Kindberg et al. 2009) and harvest data (e.g., Cattadori et al. 1999), as well as noninvasive field methods, including sign

transects (Beier and Cunningham 1996), scent stations (e.g., Diefenbach et al. 1994), camera traps (e.g., Karanth 1995) and noninvasive genetic sampling (NGS, e.g., Bellemain et al. 2005, Kendall et al. 2008). The latter entails the extraction of genetic material from hair, scat, and other sources of DNA, and has been implemented in numerous projects involving many species (review in Waits and Paetkau 2005). Although a powerful and versatile tool, NGS has limitations (e.g., Taberlet et al. 1999, Mills et al. 2000, Luikart et al. 2010). For example, important individual attributes, such as exact age, body condition, or reproductive status, cannot be determined from genetic samples alone (but see Criscuolo et al. 2009), which limits the scope and resolution of investigations based on NGS.

Even large administrative units are finite and, although management authorities typically cannot
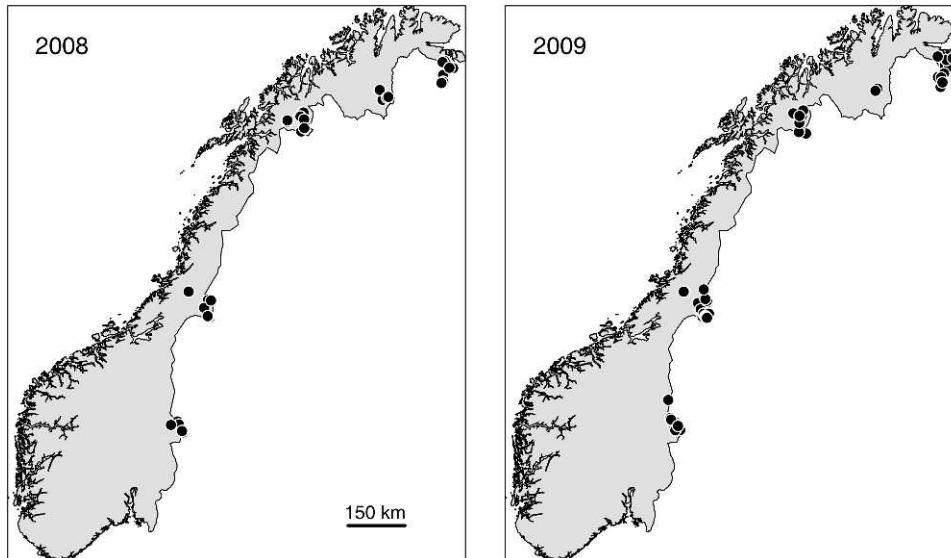
Fig. 1. Central locations of DNA samples collected from individual female brown bears (*Ursus arctos*) in Norway in 2008 ($N =$ 40) and 2009 ($N = 49$).

ignore jurisdictional boundaries, wildlife routinely does. This is especially the case for highly mobile species like large carnivores, and when borders are artificial. Transborder populations present challenges to natural resource management, which would benefit from coordinated monitoring and management between the jurisdictions that share a population (Grant and Quinn 2007, Bull et al. 2009). Although sometimes monitoring and management transcend administrative borders (e.g., Nichols et al. 2007), political and economic realities usually do not facilitate such an inclusive approach (e.g., Bull et al. 2009). In most cases, each jurisdiction monitors and manages its own part of a shared population.

The brown bear (*Ursus arctos*) in Scandinavia exemplifies the challenges associated with managing trans-border populations within national jurisdictions. After brown bears were extirpated from nearly all of Scandinavia, protective measures implemented in Sweden led to a partial recovery of the species (Swenson et al. 1995). This recovery was driven mainly by a growing bear population in Sweden, which continues to expand westward into Norway (Swenson et al. 1998). The result is a single population divided into three subpopulations centered on female concentration areas (core areas [Manel et al. 2004]), a division that does not correspond to international boundaries. Because of a shared bear population, Swedish and Norwegian bear management are necessarily intertwined. Notwithstanding, Norway and Sweden differ substantially in their management policies and management goals with respect to bears, stemming largely from a difference in livestock (mainly domestic sheep) husbandry practices and associated depredation risk (Swenson and Andrén 2005). Norwegian management aims to keep population sizes low for all large carnivores, including brown bears

(Miljøverndepartementet 2005), whereas in Sweden there are an estimated 3300 bears today (Kindberg et al. 2011).

Traditionally, brown bear monitoring in Norway consisted of counting observations of females with cubs of the year (cubs [Swenson et al. 2003, Ordiz et al. 2007]). Although a common method for monitoring bear populations (see Knight and Eberhardt 1984, Palomero et al. 1997, Schwartz et al. 2002, Ordiz et al. 2007), observation-based monitoring of females with cubs has received little trust from decision makers in Norway; in fact, an uncritical application of this method led to a gross overestimation of population size in the 1980s (Kolstad et al. 1986, see also Swenson et al. 1995).

In 2005, NGS was added to the brown bear monitoring program in Norway, and since 2008, the National Monitoring Program has been conducting annual sample collections (mainly from scats) throughout most of the species' range in Norway, in combination with microsatellite analysis to detect and identify individual bears (Wartiainen et al. 2009a, 2010). Although NGS data lend themselves to abundance estimation through capture–mark–recapture (CMR) methods (Lukacs and Burnham 2005), Norwegian management authorities rely on counts of individuals identified, i.e., a minimum number of bears. Interestingly, despite a switch from counting observations of females with dependent cubs to counting bears in general using NGS, the Norwegian government continues to express management goals in the annual number of reproductions (number of females that produce cubs), which is not directly attainable from NGS data. Complicating matters, female bears detected with NGS in Norway are concentrated along the border with Sweden (Figs. 1 and 2), and some home ranges are shared by the two countries (Scandinavian Brown Bear
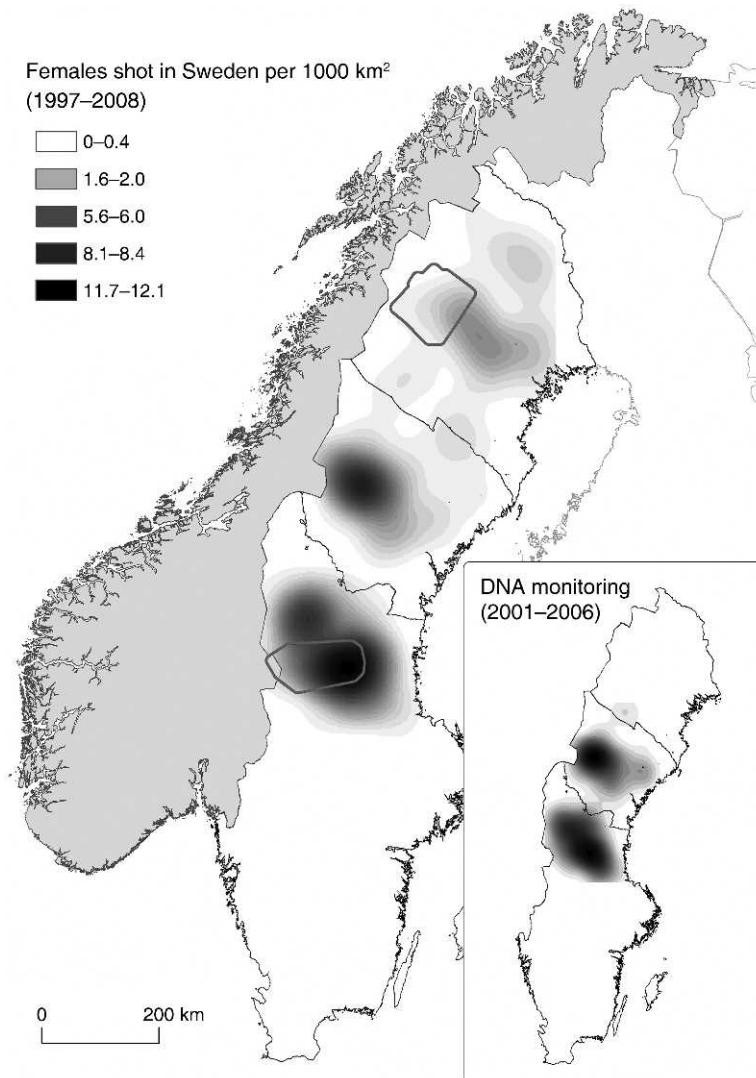
Fig. 2. The large map shows Norway (gray area) and the kernel density of female brown bears killed by hunters in three regions (southern, central, and northern) in Sweden from 1997 to 2008. Thick gray boundaries mark the two areas in which long-term monitoring of brown bears has been conducted since 1984. The smaller map shows the kernel density of female bears detected during DNA monitoring between 2001 and 2006 in Sweden. Darker shaded areas indicate higher kernel densities. DNA monitoring data were not yet available for the northern region in Sweden, but DNA-detected density patterns (i.e., clearly discernible core areas) in the southern and central regions are similar to density patterns of hunter-killed bears.

Research Project, *unpublished data*). Ignoring this fact may lead to double-counting bears over jurisdictions, and hence overestimating the number of female bears (and consequently reproductions) in Norway. 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 >50% of a reproducing pack's territory falls within that area (Miljøverndepartementet 2005). Wolf management is much more contentious than bear management, so wolf packs are monitored intensively, and kill permits can be issued more easily for wolf packs

defined as occurring outside the management area. According to the present agreement, trans-border packs are counted in the Swedish estimate, and not in the Norwegian estimate.

With this backdrop, policy makers and managers posed the following question: What is the estimated number of reproductions attributable to the individual female brown bears detected using NGS in Norway? This article describes our approach to addressing this question and serves as an example of how to:

1) combine information from noninvasive genetic sampling and traditional research methods to attain estimates of a population measure, e.g., the number of reproductions, that is not directly available from NGS, and

2) incorporate knowledge about space use to determine the proportion of this population measure that can be credited to a focal jurisdiction.

To accomplish this, we developed a simulation model parameterized with empirical information available for brown bears in neighboring Sweden. Although ours is a specific example, the issues addressed and approach taken should be of interest to others charged with the study and management of wide-ranging and transborder populations.

METHODS

General approach

The main objective of this study was to estimate the annual number of brown bear reproductions in Norway that can be credited to female bears detected through NGS in 2008 and 2009. To meet this objective, we constructed a simulation model that links NGS data on uniquely identified females in Norway with information obtained during a 25-year monitoring study of brown bears in neighboring Sweden. For practical purposes, the number of reproductions is defined as the number of females that emerge with cubs from the winter den (April–May). With this definition in the Norwegian regulations, the reproductive event is counted even if all the cubs of a litter perish in the spring shortly after emerging from the den.

Sources of data

Information about contemporary age structure, vital rates, and home ranges of bears in Norway was not available. However, a long-term study conducted in neighboring Sweden provided the necessary data for a population that represents part of the same metapopulation that most bears in Norway belong to (with the exception of those farthest north, which are associated with populations in Finland and Russia).

The following three data sets were available for this study:

1) Individual-based data from female brown bears monitored by the Scandinavian Brown Bear Research Project (SBBRP) from 1984 to 2008 (1240 bear-years, 263 individuals) in two study areas in Sweden (Fig. 2). In addition to birth years and mortalities, these data contain spatial information (VHF relocations) and reproductive histories. Details are in Zedrosser et al. (2007) and Dahle and Swenson (2003).

2) Harvest data (1982–2008) compiled by the Swedish Veterinary Institute, containing information about age, kill location/date and hunting method (583 female bears). Details in Bischof et al. (2008) and Bischof et al. (2009).

3) DNA capture data from Norway in 2008 (147 captures of 40 individual females) and 2009 (223 captures of 49 females) with information about each unique individual identified by DNA and associated sample locations and dates. Details are in Aarnes et al. (2009) and Wartiainen et al. (2009b, 2010).

Model description

Process.—The model derived estimates of the number of reproductions and associated uncertainty through simulations using an individual-based approach. Center locations of female bears (mean coordinates of fecal DNA capture locations) detected in Norway in a given year served as the basis for these simulations. Each individual simulation run consisted of the following steps (see also Fig. 3):

1. *Age assignment.*—Each individual female bear detected in Norway during the focal year was assigned an age, randomly drawn from an empirical age distribution of bears in Sweden.

2. *Reproduction.*—Each individual female was then assigned an age- and region-specific reproductive probability (p, see Fig. 2 for the location of Swedish bear regions), determined using a logistic regression model predicting the probability of reproducing for individual brown bears monitored in Sweden. Actual reproduction was decided through a random binomial event based on p.

3. *Home range assignment.*—Individuals designated as reproducing were assigned utilization distribution (UD) grids selected randomly from a set of 95% annual kernel home ranges from monitored bears that exhibited representative characteristics (outside the core area, with dependent cubs). The center location of DNA samples of a Norwegian female was 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 was more likely to fall on a DNA center location). The grid was 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) were scaled to add up to 1. The proportion of each simulated utilization distribution in Norway was calculated as the sum of the scaled weights of grid cells in a home range that fell within Norway.

5. *Determination of the annual number of reproductions.*—The sum of all home range proportions that fell within Norway (by females designated as reproducing), was interpreted as the number of reproductions in Norway during the focal year, based on female brown bears detected in the country.

Simulations.—A full simulation consisted of repeated implementation of the steps outlined above. Each simulation run yielded a value for the number of reproductions. 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.

Parameter estimates and assumptions

Visual inspection of the various time series and preliminary analysis revealed substantial changes in
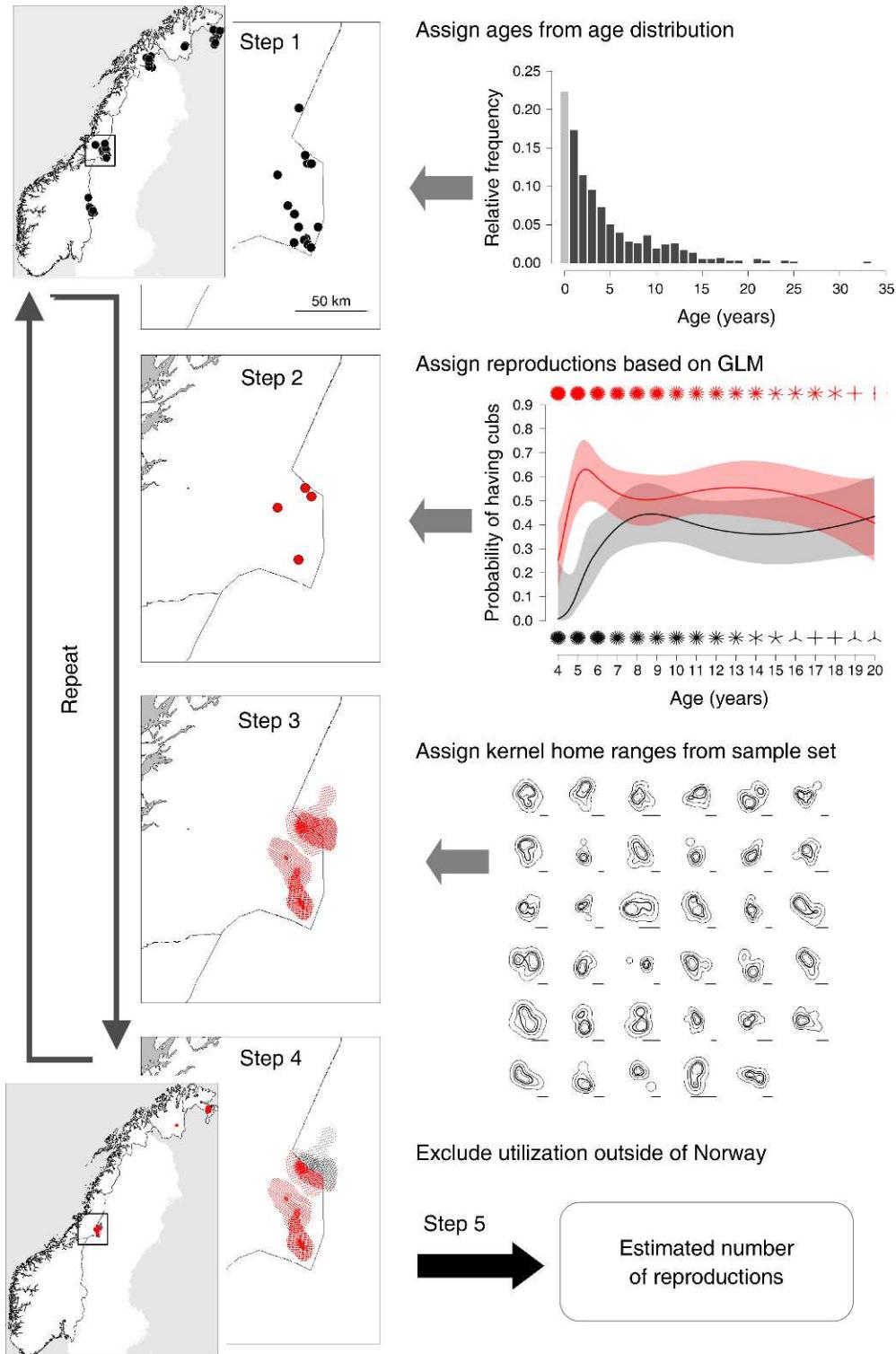
Fig. 3. Simplified schematic of a model cycle (read from top down) and associated information input. Assignments of ages and home ranges are made randomly. Detailed explanations and enlarged versions of the graphs illustrating the source information can be found in the *Methods* section, Figs. 4–8, and Appendix A.

monitoring effort and harvest pressure over time, as well as several population attributes (density index, harvest mortality; see also Bischof et al. 2008). Preliminary findings also suggested that both average home range size and the probability of a breeding-age female having cubs have declined during the study period. Because of these changes (for the most part associated with a growing bear population) and to ensure temporal proximity between the parameters derived from empirical data and the population for which predictions were to be made, we limited most analyses to data collected after 1996/1997.

Detailed descriptions of parameters and model assumptions are presented below. We include results from parameter estimation here, rather than in the next section, as they are prerequisite to implementing the main model.

Location relative to the core areas.—Brown bears in Sweden are concentrated in 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 core areas in neighboring countries; hence one is justified to question whether research findings in the study areas (which are within the core areas) apply to Norway. Therefore, we tested for the effect that a bear's location, relative to the core area within a given region, has on relevant parameters, such as its age, probability of having cubs, and home range size.

Brown bear harvest data have been used to delineate core areas in Sweden (Swenson et al. 1998, Waits et al. 2000). Spatial patterns in harvest are determined not only by bear densities, but also by differential harvest effort, which in turn is partially determined through regional quotas. Nonetheless, on a coarse scale the distribution of shot bears follows the assumed spatial distribution of bear densities closely (Fig. 2; see also Kindberg et al. 2009). We used harvest data to derive an index of proximity to a core area within each of the three bear regions in Sweden (Fig. 2) by calculating a kernel density estimate of female bears shot between 1997 and 2008. 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 ensure that any density effects estimate was always interpreted within the context of its region.

Probability of reproducing.—Reproduction (yes or no) by female bears in Sweden was determined by observations of cubs and inspection of adult females captured shortly after emergence from the winter den, along with inspections of dens for signs of cub activity. We applied logistic regression to these data to model the probability that a breeding-age female (≥ 4 years) in our study areas in Sweden emerges from the winter den with cubs in a given year. The most complex model considered included age, year, region (north, south), and density of shot bears modified by region. Preliminary analysis indicated that the effect of age was nonlinear; therefore

we modeled age using piecewise-cubic splines. Because individual females were observed in multiple years, we also considered using a mixed-effects model by including an individual identifier as a random effect. However, accounting for between-individual variation through inclusion of the random effect did not improve the model (likelihood ratio test: $\chi^2 \sim 0$, df $= 1$, $P \sim 1$), 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 model complexity and fit. The final model included age and region. The higher frequency and earlier age of reproduction in the southern study area (Fig. 4) are consistent with previous findings on Scandinavian brown bears (Swenson et al. 2001, Zedrosser et al. 2009).

Age distribution.—Previous investigations have indicated that bear hunting in Sweden shows little age-specific bias (Bischof et al. 2009). Cubs 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 one year old and older. However, the female age distribution may vary spatially with 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 of harvested bears as the continuous response, and density and region as 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 the core areas.

The age distribution of hunted bears is incomplete, as cubs are excluded from legal hunting. To augment the age distribution with cubs, we estimated their number by using the age distribution of breeding-age females (≥ 4 years), their age- and region-specific probability of producing cubs, and an estimate of litter size. Details of the augmentation process are provided in Appendix A. This approach resulted in an age distribution (Appendix A: Fig. A1) where 22.5% of the female population consists of cubs, which corresponds well with previous predictions of the proportion of cubs (122 cubs out of 619 total, which is ~20% (Swenson et al. 1994). We used this as the source distribution to sample ages for stochastic age assignment to female Norwegian bears in step 1 of each simulation.

Home range size.—We calculated kernel home ranges for VHF-monitored females with relocations in at least six separate weeks between week 18 (May) and week 40 (September). To reduce autocorrelation, we only used one relocation per four-day period for each bear in a given year. Because of an insufficient sample size and

Fig. 4. GLM-predicted age-dependent probability (and associated 95% CI bands) of adult female brown bears producing cubs in two subpopulations in Sweden (red represents south; black represents north). Sample sizes are shown as sunflower plots (red represents south; black represents north), where each leaf represents a single bear-year.
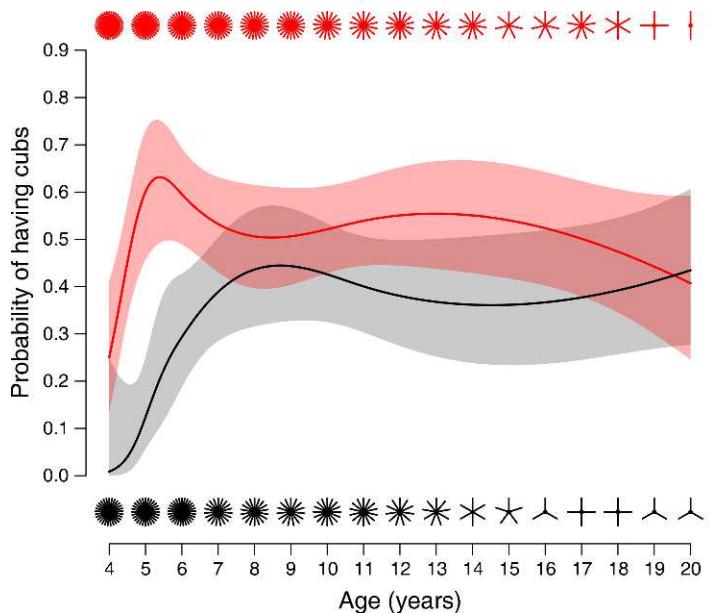
lower reliability of VHF data from the northern study area in Sweden, we only included data from bears monitored in the southern study area in this analysis. This is not likely to constitute a significant source of bias, because previous analysis gave no indication of a difference in home range sizes between the northern and the southern study areas (Dahle and Swenson 2003).

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 cubs as fixed effects, and individual ID as the random effect. The final model (lowest AIC value) showed an increase in home range size with increasing distance from a core area ($\beta = -85.36 \pm 15.91$ (mean $\pm$ SE), $t_{160} = -5.37$, $P < 0.001$), and smaller home ranges for females that had emerged from the winter den with cubs in a given year ($\beta = -0.39 \pm 0.05$, $t_{160} = -7.27$, $P < 0.001$; Fig. 5). These findings are consistent with those obtained during 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 between 1998 and 2008 ($\beta = -0.04 \pm 0.012$, $t_{160} = -3.69$, $P < 0.001$), presumably due to an overall increase in bear densities.

Based on the results of the regression analysis, we decided to draw home ranges for simulations from 35 annual home ranges from females that had produced cubs (16 individual bears) within the lower 30% of the distribution of the density index (to the left of the vertical dashed line in Fig. 5). 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. We chose to use actual home ranges with UD information 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 $\geq r$ 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 (Fig. 6) 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 decreases from the center toward 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 provides a way to assess the proportion of utilization that falls within the focal region (Fig. 7).

Model validation

At the onset of this project, we set aside 91 bear-years of SBBRP individual long-term monitoring data (one year each for 91 individuals). The remaining monitoring data (1149 bear-years, 252 individuals) were used as the training data, i.e., for the estimation of required parameters. To be representative of brown bears detected in Norway, the cross-validation data were randomly selected from all VHF relocation sets (one VHF relocation set = all VHF capture locations of a given female in a given year) with centers within a 75-km buffer around the Swedish/Norwegian border.
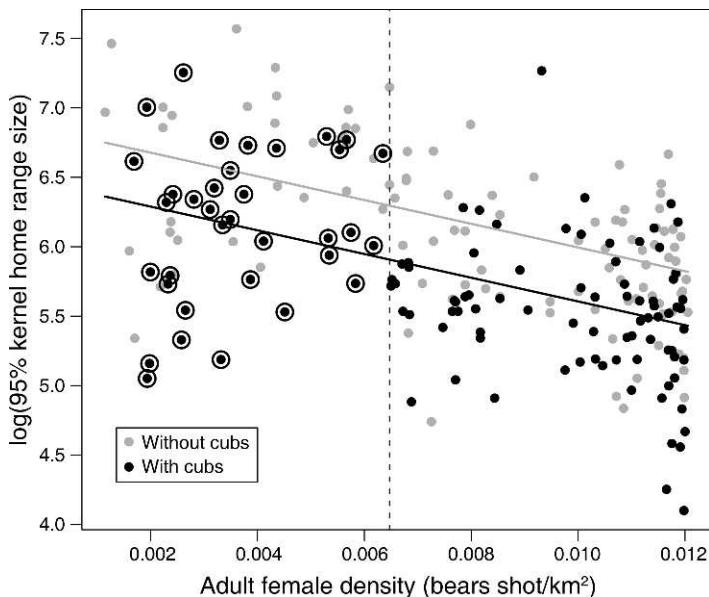
Fig. 5. The log-transformed 95% kernel home range size (originally measured in square kilometers) of adult (≥4-year-old) female brown bears, dependent on the density of female bears killed by hunters in Sweden between 1997 and 2008. Points represent the data (annual home ranges), and the solid lines indicate the regression slopes predicted with a linear mixed-effects regression model (gray for bear-years without cubs and black for bear-years with cubs). Additional circles indicate annual home ranges that were selected for use during simulations in the model for estimating the number of reproductions in Norway (left of the dashed vertical line).

We explored the sensitivity of model predictions to violations of several assumptions made during model implementation. This analysis was focused on age-dependent detectability of brown bear scats during NGS, spatial heterogeneity in home range sizes of female bears with dependent cubs, and variation in the probability of detecting reproductions during long-term monitoring by the SBBRP. The cross-validation and
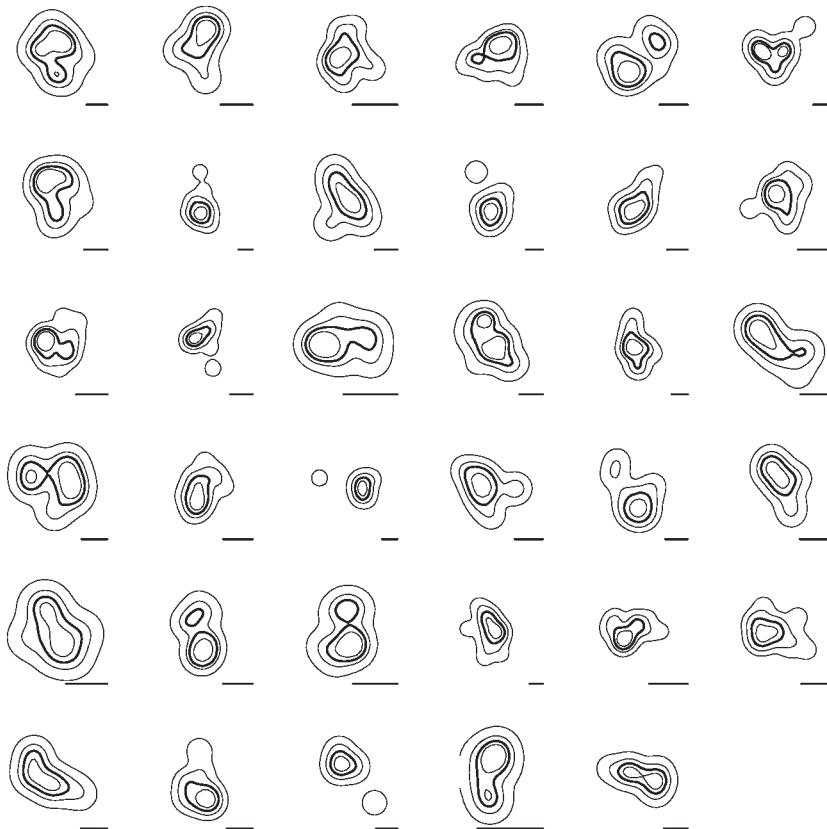

Fig. 6. Sample kernel home ranges (35 bear-years from 16 different female bears with cubs of the year) used for simulating home ranges for female brown bears detected in Norway. Contour lines represent 25%, 50% (thicker), 75%, and 95% kernel density volumes, from the center of each home range outward. A horizontal 10-km size reference is provided below each home range.

FIG. 7. Example of how the proportion of a home range within a focal polygon (shaded area) is determined. Annual 95% kernel home ranges are represented as utilization distribution (UD) grids, where the size of each point on the grid indicates its relative utilization intensity, i.e., the relative probability of encountering the individual at that point vs. another point on the grid. The UD grid point values 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 (solid circles).

5 km
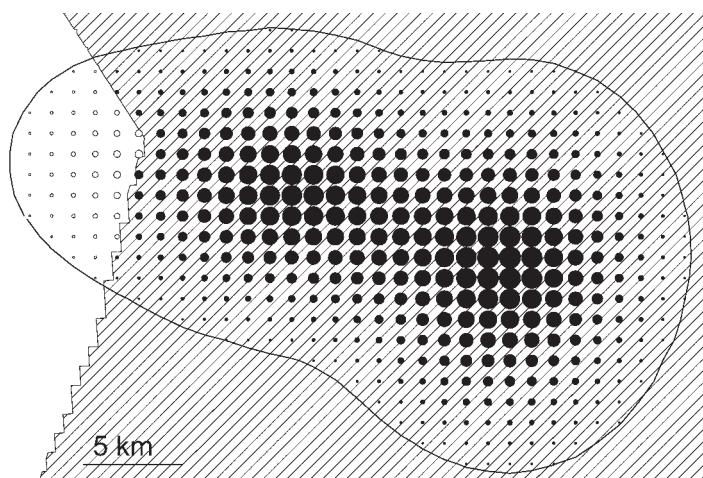
sensitivity analysis are described in detail in Appendices B and C, respectively.

Implementation and computing

Most statistical analyses and modeling were conducted using the statistical programming environment R (R Development Core Team 2010) and functions contained in various packages, including *lme4* (Bates et al. 2008), *adehabitat* (Calenge 2006), *PBSmapping* (Schnute et al. 2008), and sp (Pebesma and Bivand 2005). We used the Spatial Analyst extension in ArcGIS 9.3 (release year 2008) for Kernel density estimation of shot bears and the Hawth's Tools extension (Beyer 2004) for associating density estimates with point locations.

RESULTS

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 4.3 (95% CI is 1.1–8, Fig. 8). In 2009, we estimated 5.7 reproductions (95% CI is 2–9.9; Fig. 8), associated with the 49 individual females detected through DNA collection. 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 by ~30% in both years (2008, estimate = 5.6, 95% CI is 2–10; 2009, estimate = 7.5, 95% CI is 3–13). Convergence testing suggested that standard deviation in the mean estimates changed little after ~1000–2500 runs; estimates reported here are based on 5000 simulation runs.

Cross-validation indicated good correspondence between actual and model predicted values of the number of reproductions. The results of the cross validation and sensitivity analysis are provided in Appendices B and C.

DISCUSSION

By combining NGS and information available from traditional monitoring sources, such as harvest records, and telemetry-based research, we were able to derive an estimate of the number of annual reproductions by female bears detected in Norway using NGS: 4.3 reproductions in 2008 and 5.7 reproductions in 2009. 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 that their potential reproductions consequently only partially "belong" to Norway. This adjustment is a crucial component of the estimation procedure and reduces the risk of counting the same individual multiple times in different jurisdictions. Estimates of the annual number of reproductions were ~30% higher when no spatial adjustment was made (Fig. 8), and the difference is bound to remain relevant as long as most female bears detected in Norway continue to be near the country's land borders. The Norwegian national goal of 15 annual brown bear reproductions is modest for a country with an area of ~300 000 km² and a historical bear population estimated at >3000 individuals (Swenson et al. 1995). Yet this goal remains beyond the upper 95% CI limit of estimated number of annual reproductions, regardless of whether or not adjustments are made for home ranges partially outside of Norway (Fig. 8.). Without the adjustment for spatial extension beyond Norway's borders, we estimated that in 2009, 15% of females detected in Norway reproduced. Given the late age of first reproduction and long litter interval of brown bears, these estimates are not unusually low; in fact the Scandinavian population is the most productive brown bear population studied (Nawaz et al. 2008).

Like any model, ours is a simplification of a complex real-life system. This facilitates comprehension and permits a certain degree of generalization when making predictions (Starfield 1997). On the other hand, simplification and a restricting set of assumptions mean that model predictions have to be interpreted cautiously.

Habitat.—Although the model is spatially explicit, it does not consider habitat differences or latitudinal or longitudinal gradients. The most relevant spatial fea-
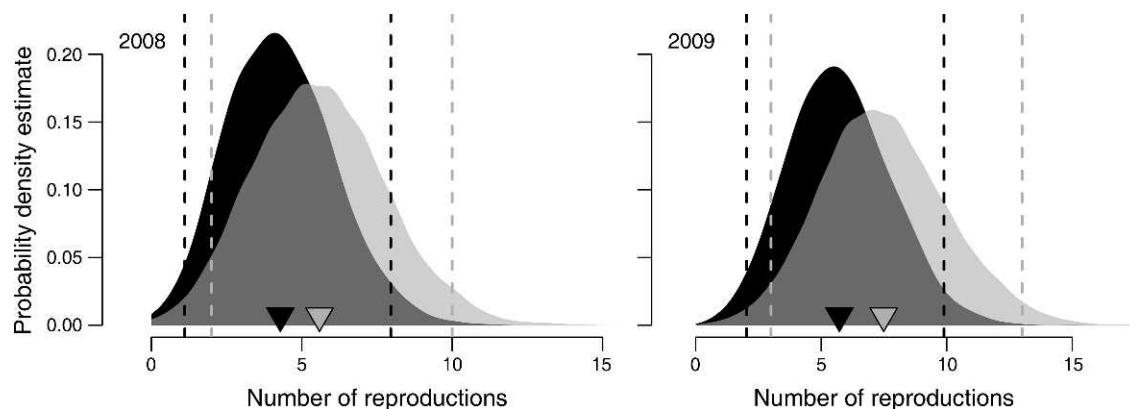
Fig. 8.   Distribution (black, adjusted for potential home range extension beyond Norway; gray, unadjusted) of model-predicted number of annual reproductions of brown bears in Norway based on the number and location of individual females detected in 2008 and 2009. Triangles (black, adjusted; gray, unadjusted) mark the mean of each distribution (i.e., the expected number of annual reproductions), and the vertical dashed lines indicate the lower and upper 95% confidence limits of the distribution. Results are based on 5000 simulation runs.

tures considered were proximity to Norwegian land borders and location (southern vs. the northern study area). Habitat differences were indirectly addressed during model parameterization by using density of harvested bears as a proxy for location relative to the core areas. This is justified, because the regression model for home range size in the southern subpopulation explained >40% of the variation in home range size, with only density of harvested bears, year, and reproductive status as the predictors.

Russia and Finland.—The model was parameterized using available information from an intensely monitored population in Sweden. This is appropriate, as many of the bears in Norway originate from Sweden; in fact bears in southern and central Norway and Sweden are part of the same population (Swenson et al. 1998). However, Russia and Finland are additional sources of brown bears in northern Norway, 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 northern Swedish population), it be incorporated into the present model to increase its predictive accuracy.

Male bears.—Because the goal was to estimate the number of females producing cubs 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 by 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 cause differences in vital

rates, for example by influencing the incidence of infanticide.

Age structure.—In our opinion, the weakest assumption of the model is that the predicted 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 cubs. The evidence that provides some justification for this assumption is (1) the lack of an obvious effect on age of either region or location relative to the core area, and (2) the lack of strong age-specific vulnerability to hunting for bears in Sweden, with the exception of cubs (Bischof et al. 2009). Similarly, Kojola and Heikkinen (2006) detected no difference in the age of male or female brown bears harvested in Finland along a north–south or east–west gradient. Although these findings and the outcome 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 based on fecal collection.

Despite these limitations, results of the cross-validation and the consistency of our estimates with previous estimates of the number of reproductions based on observations of females with dependent cubs (3–5 females with cubs per year during 1998–2002 [Swenson et al. 2003]) encourage confidence in model predictions.

An important strength of NGS is that it permits the application of CMR methods for estimating various population parameters, including abundance (Mills et al. 2000, Lukacs and Burnham 2005), while accounting for capture probabilities <1. Norwegian management authorities continue to base management targets on counts of individuals detected rather than a total estimate (for similar approaches see, e.g., Sloane et al. 2000, Creel et al. 2003, Bhagavatula and Singh 2006). To answer the specific question posed by Norwegian

management authorities, we based the analyses presented here on the number of individual females identified rather than an estimated female population size. With minor modification the model could also base its predictions on a total estimate of females obtainable from NGS-based capture–mark–recapture methods. Estimating abundance of females rather than obtaining minimum counts converted to number of reproductions should be seen as a desirable and logical evolution of brown bear monitoring in Norway and would make greater use of the potential of NGS. The Norwegian brown bear population is an extension of the bear population in Sweden; therefore abundance estimates in Norway should not be generated in isolation from the remainder of the species' range in Scandinavia. A CMR analysis accounting for spatial structure and movement (e.g., Brownie et al. 1993) will require collection and compilation of NGS data from both Norway and Sweden, as well as matching individual genetic profiles between the two countries' growing databases. This work is ongoing, and we hope that the present article can serve as a foundation and set the stage for a planned comprehensive CMR analysis and for a revision of how management goals are expressed. The latter is the subject of an ongoing debate in the Norwegian Parliament, with one proposal being a change to expressing the goal in the number of female bears, rather than the number of annual reproductions.

Regardless of whether managers use minimum counts or abundance estimates to monitor populations in their management areas, we recommend that they consider the possibility that individuals detected by their surveys also could be detected in neighboring management areas. This could lead to such individuals being credited to multiple jurisdictions, therefore inflating population estimates. Various methods have been devised to justify closure assumptions or deal with their violation during analysis of invasive and noninvasive CMR data and to estimate density for a defined area (Efford 2004, Royle et al. 2009, Obbard et al. 2010). The simulation-based method we described may be useful in other situations involving trans-border populations.

Aside from the difficulties inherent in the study of rare and highly mobile species, nontrivial challenges arise when monitoring wild populations over large areas with permeable boundaries. Monitoring methods suitable for application on the level of countries or regions may not always represent direct ways for obtaining the measures desired by managers or policy makers. Ecological studies might benefit from combining NGS with other sources of information in order to augment genetic data, validate results obtained from NGS, and verify that assumptions of NGS-based CMR are met, with the ultimate goal of increasing the reliability and resolution of studies based on NGS (for example see Solberg et al. 2006, Meijer et al. 2008, and Mondol et al. 2009). CMR approaches that allow for the analysis of data from multiple sources of information (Lebreton et al. 1999) are bound to further increase the utility of NGS. Nonetheless, when combining NGS data with other sources of information, one should take care to determine whether knowledge obtained from alternative sources is applicable to the system explored via NGS. Some parameters, such as those related to age structure and reproductive potential, did not seem to be affected by a female bear's location relative to the core areas in Sweden. On the other hand, average home range size was likely larger for individuals in areas subjected to NGS in Norway in comparison with the part of the population that formed the basis for model parameterization. In addition to testing for differences between that part of the population from which noninvasive genetic samples were collected and those individuals that served as the basis for alternative data collections, sensitivity analyses and cross-validation using a data set representative of the NGS-population should be employed to ensure that model predictions are reliable.

Coordinated monitoring and management across multiple jurisdictions sharing a common population would reduce the inherent uncertainty in population status and in the outcome of management actions. Even in the likely case where management does not transcend manmade boundaries, decision-making, including monitoring design and interpretation, in each spatial entity might at least consider that the population is shared with others and recognize that, through this link, jurisdictions are mutually impacted by their respective management actions.

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Supplemental Material

Appendix A

Age distribution augmentation (*Ecological Archives* A022-023-A1).

Appendix B

Cross-validation (*Ecological Archives* A022-023-A2).

Appendix C

Sensitivity analysis (*Ecological Archives* A022-023-A3).