Estimating population size and trends of the Swedish brown bear *Ursus arctos* population

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Estimating population size and trends are key issues in the conservation and management of large carnivores. The rebounding brown bear *Ursus arctos* population in Sweden is monitored by two different systems, both relying on voluntary resources. Population estimates have been calculated using Capture-Mark-Recapture methods, based on DNA-based scat surveys in five of the six Swedish counties with established bear populations. A total of 1,358 genotypes were identified using DNA extracted from collected scats. An independent ongoing programme, the Large Carnivore Observation Index (LCOI), was initiated in 1998. The LCOI uses effort-corrected observations of bears by moose *Alces alces* hunters during the moose hunt (> 2 million observation hours/year) and has shown a good correlation with relative population density of bears using the DNA-based method. From this, we have calculated population trends during the period 1998-2007. Using an exponential model, we estimated the yearly increase in the bear population to be 4.5% at the national level, varying between 0 and 10.2% in different counties. We used the regional population estimates and the trends from the LCOI, taking the variation from both systems into account using parametric bootstrapping, to calculate the regional as well as the national population size in Sweden in fall 2008. In one case (the northernmost county; Norrbotten) a DNA-scat survey was lacking, so we used assumptions based on data from the neighbouring county to estimate population size. We estimated the Swedish brown bear population to be 3,298 individuals (2,968-3,667; 95% confidence intervals) in 2008. Our results suggest that reliable information, necessary for the management of the brown bear population can be obtained from volunteers using standardised methods.

Key words: brown bear, DNA, faeces, genetic, monitoring, observations, population size, survey, Ursus arctos, volunteers

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Population size and trends are important parameters for the management and conservation of large carnivore species (Kendall et al. 1992, Mowat & Strobeck 2000). These parameters are used to assess population status, decide quotas for harvested populations, evaluate the effects of management measures or decisions (Wilson & Delahay 2001), or to obtain parameters for conservation principles

including the IUCN criteria for Red-listing evaluations (Vié et al. 2009). This is even more important for low-density populations of rare and elusive animals that are long-lived and with relatively low reproduction rates; in addition these species are particularly difficult to monitor (Thompson 2004). The brown bear *Ursus arctos* is a typical example of a cryptic animal with these characteristics, it occurs at relatively low densities, even within established areas, and it avoids humans (Nielsen et al. 2004, Nellemann et al. 2007). The public often demands an accurate knowledge of population size. Thus, managers are faced with challenges of estimating population sizes and trends and evaluating the population's response to hunting and other management measures, often within short time spans.

Current methods for monitoring brown bears range from field observations to intensive collection of material for identification of individual bears by DNA analysis (Linnell et al. 1998). Observations are used both for estimation of population size and trends (Mattson 1997, Kojola et al. 2006, Schwartz et al. 2008, Kindberg et al. 2009), and most observation-based methods focus on females with cubs (Knight et al. 1995, Eberhardt & Knight 1996, Harris et al. 2007, Ordiz et al. 2007, Schwartz et al. 2008), because they are easier to recognise in the field and are the most important segment for populations stability. Observations can also be used in combination with other methods, e.g. in Mark-Resight studies, where radio-marked bears are used in combination with aerial surveys (Swenson et al. 1994, Miller et al. 1997, Solberg et al. 2006). The introduction of non-invasive DNA-based methods in the 1990s (Taberlet & Bouvet 1992, Höss et al. 1992, Taberlet et al. 1996, 1999, Mills et al. 2000, Paetkau 2003) made it possible to accurately distinguish individuals in an area without the need to capture and handle them. The prevailing methods for non-invasive DNA sampling are hair snagging using baits (Boulanger et al. 2002, Kendall et al. 2009) and collection of scats (Bellemain et al. 2005). Population size estimations have benefitted from the development of analysis methods using Capture-Mark-Recapture (CMR) software (White & Burnham 1999) and better field methods for improving capture rates (Woods et al. 1999, Mowat & Strobeck 2000, Kendall et al. 2009).

After centuries of persecution, the brown bear population in Sweden was reduced to a few remote areas in the 1930s with an estimated lowest population size of 130 individuals (Swenson et al. 1995).

After effective conservation measures were implemented in the early 20th century, various methods of estimation indicated a steady increase in population numbers and distribution (Swenson et al. 1995). However, these population estimates were made using different methods, mainly based on inquiries of presence or various methods of estimation and also lacked variance estimates, so they could not be compared or used to determine population trends. The first population estimate made by the Scandinavian Brown Bear Research Project (SBBRP) used several methods, including observations of marked and unmarked bears from helicopter surveys during the mating season and among harvested bears (Swenson et al. 1994). Today population estimates are based on DNA surveys using hunter-collected bear scats, which was introduced in 2001 (Bellemain et al. 2005), and monitoring of population trend is based on systematic effort-corrected observations of bears by moose *Alces alces* hunters, introduced in 1998 (Kindberg et al. 2009). These methods, together with data from harvested bears and research by the SBBRP, are the main sources of information used for the management of the bear population in Sweden.

In this article, we describe how we estimated population trends and population size of brown bears in Sweden and in the individual counties in 2008 using the methods described above. We have also used these data to estimate population size, even in areas where DNA surveys had not been conducted. This has been extremely useful for bear managers in Sweden and perhaps it can be used as a model for wildlife managers in other countries or jurisdictions as well.

Material and methods

Study area
Brown bears are unevenly distributed in the northernmost ⅔ of Sweden (Fig. 1). The population is expanding from four former relict core areas (Swenson et al. 1998, Manel et al. 2004), which results in a skewed sex ratio in the expansion areas (Swenson et al. 1998, Kindberg et al. 2009). The habitat is mainly boreal forest with the Scandinavian mountain range in the west and the more populated areas along the eastern coast. Large carnivore management is mainly administrated at the county level, and therefore most surveys are conducted and reported at this scale.
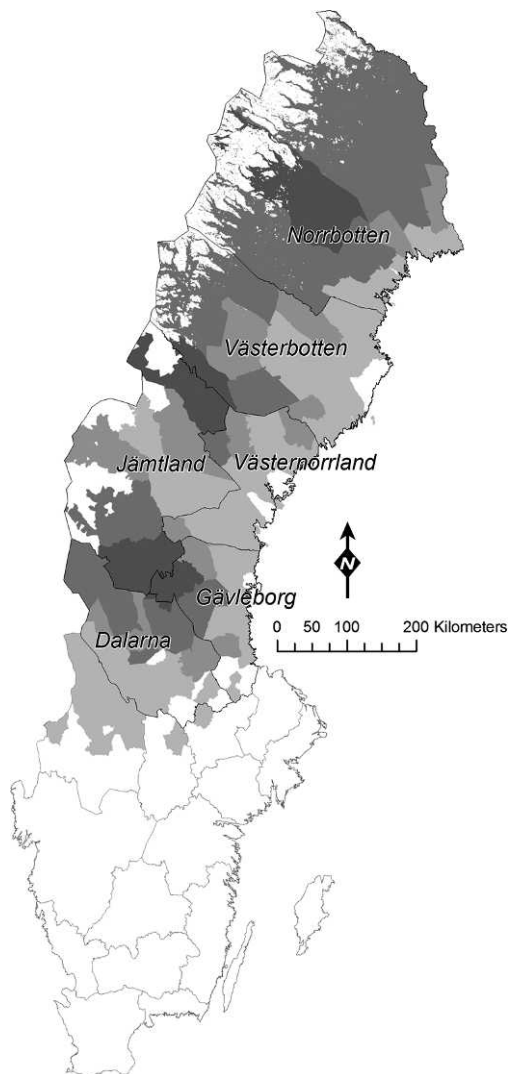
Figure 1. The different Swedish counties and the distribution of bears as an index of average bear density from the LCOI (1998-2006) in gray shading (higher densities have darker nuances).

Collection of scats and genetic analysis

We collected bear scat samples within the counties throughout the study area, except for the northern-most county (i.e. Norrbotten; see Fig. 1). We conducted these collections even where bears were very rare or non-existent. We collected samples opportunistically by cooperating with moose hunt-ers, volunteers and personnel from the SBBRP. Hunters picked up each scat sample using a stick of wood and put 1 cm³ of the sample into a 20-ml collection bottle. They used a different stick and bottle for each sample. For each scat sample the volunteers recorded the sampling date, the geo-

graphical location, the names of the hunting teams and the coordinates (Swedish RT90 2.5 gon V).

For every collected scat sample, DNA extractions and amplifications were performed at the Labora-toire d'Ecologie Alpine, Grenoble, France, as de-scribed in Bellemain et al. (2005). Each DNA extract was first screened for species-diagnostic amplifica-tion with one microsatellite marker (G10P; Paetkau & Strobeck 1994). After this, six microsatellite loci (Mu10, Mu23, Mu50, Mu51, Mu59, G10L; Paetkau & Strobeck 1994, Taberlet et al. 1997) and a sex marker (Bellemain & Taberlet 2004) were amplified, following the multiplex preamplification method (Piggott et al. 2004, Bellemain & Taberlet 2004). The detection and sizing of fragments was performed in an ABI Prism 3100 DNA sequencer (Applied Bio-systems, Foster City, California, USA). Amplifica-tions were repeated four times. We typed samples as heterozygous at one locus if both alleles appeared at least twice among the four replicates, and as ho-mozygous if all the replicates showed identical homozygous profiles. If neither of those cases occurred, the alleles were treated as missing data. The gels were analysed using the Genemapper (version 3.0) software package (Applied Biosys-tems, Foster City, California, USA). We grouped samples according to their genotypes and identified the unique genotypes.

Population trends

Since 1998, the Swedish Association for Hunting and Wildlife Management has collected observa-tions of bears annually through the LCOI pro-gramme during the moose hunt, as complementary information to their 'moose observation' survey (Ericsson & Wallin 1999, Sylvén 2000, Liberg et al. 2010). The LCOI is based on bear observations made by moose hunters during the first seven days of the hunt and is corrected for effort using man-hours. The index has been evaluated and the observations corrected for effort are closely corre-lated with relative bear density, as determined from individuals genetically identified during the popu-lation censuses (see below; Kindberg et al. 2009). Because the monitoring is carried out yearly, it has been used to calculate population growth rate in each county, as well as for Sweden as a whole.

We calculated population growth rate as the 'instantaneous rate of increase' (r) for the period 1998-2007 using an exponential growth model, except for the county of Gävleborg, where we used the period 1998-2006. The reason for the shorter

Table 1. Brown bear scat surveys and genetic identification in the studied counties in Sweden, i.e. the number of scat samples collected and analysed, the number of samples successfully genotyped for 5-7 loci (including the sex locus) and the number of unique genotypes identified.

County	Survey year	Number of analysed scats	Number of genotyped scats	Number of unique genotypes identified
Dalarna & Gävleborg	2001	1066	728	311
Dalarna & Gävleborg	2002	838	665	239
Västernorrland	2004	690	434	140
Västerbotten	2004	940	524	223
Jämtland	2006	3000*	2400	684

* 3,000 scats were randomly selected to be analysed among the 5,185 collected scats.

period was that data collection changed in parts of the county of Gävleborg in 2007. Thus, we cannot be certain that the 2007 datum is comparable with earlier data. With regard to the national growth rate, these areas in the county of Gävleborg were removed (for the entire period 1998-2007), so that only areas which continuously submitted reports using the same protocol were used for the national growth rates.

Population estimates

Counties with DNA-based estimates
The counties of Dalarna and Gävleborg were surveyed in 2001 and 2002 to evaluate the technique and were followed by Västernorrland and Västerbotten in 2004 and Jämtland in 2006 (Bellemain et al. 2005, Solberg et al. 2006). To estimate total population size in each county, we identified individual bears using DNA analysis from the scats collected by volunteers (Table 1), and we analysed the data using CMR methods available in program MARK (White & Burnham 1999), with each week

used as a session for capture and recapture (11 weeks for Dalarna and Gävleborg and 12 weeks for the other surveys). We used closed population models and model selection using Akaike's Information Criterion (AIC_c) values and model averaging where appropriate (Burnham & Anderson 2002; Table 2). For the counties of Jämtland and Västerbotten, only the top model was used, as they just had one model with a $\Delta AIC_c < 2$ (Burnham & Anderson 2002). For Västernorrland two models were included in the model averaging and, because the lower bound confidence limit was less than the number of identified individuals, confidence limits were calculated by hand as described by Williams et al. (2002). All high-ranking models included individual heterogeneity in capture probabilities and time effects. This seemed to be reasonable, because search effort varied among capture sessions, with the highest effort attained during the first week of the moose hunt (Bellemain et al. 2005). Heterogeneity among individuals can arise due to factors that cannot be recognised from DNA, such as age and reproductive status (Boulanger et al. 2008). We modelled

Table 2. The top three ranked closed population Capture-Mark-Recapture models used to estimate brown bear population size in the different counties. For a summary of the counties of Dalarna and Gävleborg in 2001, see Bellemain et al. (2005).

County	Models*	ΔAIC_c	Weights	Average capture probability
Västernorrland 2004	M_{th2}	0.00	0.73	0.14
	$M_{th2*sex}$	1.93	0.27	
	M_t	18.41	0.00	
Västerbotten 2004	$M_{th2*sex}$	0.00	0.89	0.11
	M_{th2}	4.19	0.11	
	M_t	19.61	0.00	
Jämtland 2006	$M_{th2*sex}$	0.00	0.95	0.15
	M_{th2}	5.73	0.05	
	M_t	157.21	0.00	

* $M_{th2*sex}$ = Heterogeneity and temporal variation in detection probabilities for each sex;
M_{th2} = Heterogeneity and temporal variation in detection probabilities;
M_t = Temporal variation in detection probabilities.

heterogeneity using the Pledger model with two mixtures (Pledger 2000, White 2008).

The estimate for Dalarna and Gävleborg in 2001 (Bellemain et al. 2005) also had time and heterogeneity in the selected model. For that survey, it was necessary to divide the original population estimate, which had been determined for the two counties combined, to obtain the population size for each of the counties. We assumed that the population was distributed between the two counties in the same way as the identified genotypes, which gave a 52/48% split of the joint population of 550 bears (52% in Dalarna). Only 4% of the genotypes were found in both counties.

Because the surveys were conducted in different years over a 5-year period, it was not possible to analyse overlap between adjacent populations in the different surveys. However, an analysis of all available genotypes (including the 2002 survey in Dalarna and Gävleborg) in 2008 showed that 2.8% of the genotypes were present in more than one county (E. Bellemain, unpubl. data).

County without a DNA-based estimate

At the time of our analysis, no DNA-based population estimate had been conducted in the county of Norrbotten, which is also the region with the largest area and lowest human density. A survey was eventually conducted in 2010, but no results are available yet. We estimated the brown bear population for Norrbotten based on the LCOI in 2004 (to compare with the adjacent county of Västerbotten in 2004 when the scat survey was made there), the relationship between the LCOI and the relative density of bears previously found for the county of Västerbotten (Kindberg et al. 2009) and the estimated density of brown bears in the county of Västerbotten from the DNA-based population estimate. We calculated the estimate of the 2004 population for Norrbotten using an area equivalent to the registered moose areas determined by the Norrbotten County Board (ca 78,800 km^2). This method entailed the assumption that the relation between the LCOI and bear density was similar to an adjacent county with comparable forest density and structure. This is an important assumption, because the slope of the relationship varies within Sweden (Kindberg et al. 2009). To improve our confidence in using the relationship from Västerbotten as a proxy for Norrbotten, we compared the relationship in Jämtland with the relationship found in Dalarna-Gävleborg and Västernorrland. These counties also have a similar forest density and structure, but the relationship between the LCOI and population density in Jämtland was not included in the study by Kindberg et al. (2009). If the slopes of the relationships were similar in these counties, it would strengthen our assumption that it would also be similar for Norrbotten and Västerbotten.

Statistics

To calculate the uncertainty in the estimates that included both the population size calculations based on DNA and population growth rates according to the LCOI, we used parametric bootstrapping to create 10,000 values of both population estimates and growth rate, using the same mean and variance as our results. We used the rlnorm and rnorm functions in the statistical software R 2.8.1 (R Development Core Team 2008). We averaged the standard errors from the somewhat skewed confidence limits from the MARK estimates, which usually were smaller in the lower bound, because the population cannot be lower than the number of identified individuals. We used the lognormal distribution to improve the variance estimate of the population size, as it has been suggested to be close to this type of confidence limits (Chao 1989). Regardless of the lack of a perfect fit, the mean of the estimates will be the same and this only minimally affects the size of the variance. We derived the estimated population for each county in 2008 from the mean of the 10,000 population values and the 95% confidence limits calculated using the 2.5 and 97.5 percentiles. We estimated the total number for Sweden by randomly adding the 10,000 county estimates and calculating the mean and confidence as described above.

To evaluate if the relationships between the LCOI and the minimum density of bear from the DNA-scat surveys differed among counties, we tested the regression slopes between Jämtland and Västernorrland, as well as among all the five counties (Dalarna and Gävleborg were combined) using a-nalysis of covariance.

We considered results to be significant at P $\leq$ 0.05.

Results

Genetic identification of individuals

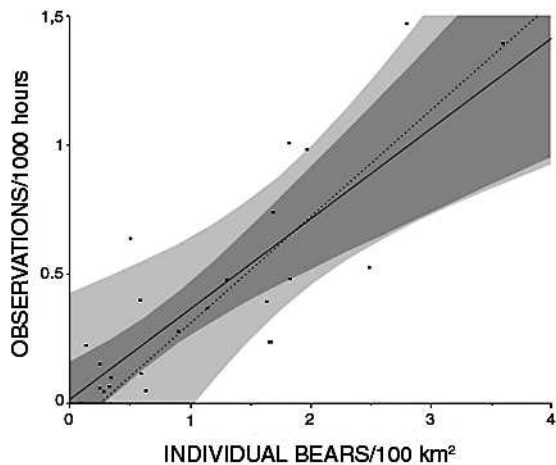The number of scat samples collected and analysed

Figure 2. The relationship between the LCOI and density of individuals from DNA-based scat surveys in two adjacent counties. The county of Västernorrland is shown with the slope as a solid line and dark gray prediction interval (95%) and the county of Jämtland is shown with a dotted line and light gray prediction interval (95%).

in the laboratory, the number of samples successfully genotyped for 5-7 loci (including the sex locus), as well as the number of unique genotypes identified are shown in Table 1.

Relationships between the LCOI and minimum bear density

There was no significant difference between the slopes from the regression of observations/1,000 hours and minimum bear density from the DNA-scat survey in Jämtland and Västernorrland (P = 0.46; Fig. 2). We also tested the slopes from all the counties and only the slope of Västerbotten was significantly different (P < 0.001).

Population trends

The LCOI indicated that the bear populations had a significantly positive growth rate during the period 1998-2007 in all but two counties: Väster-

botten and Dalarna, which showed no significant trend (Table 3). The highest growth rates were found in Gävleborg (r = 0.097, P < 0.007), based on data from 1998-2006, and Västernorrland (r = 0.095, P < 0.017). Both counties are considered to be expansion areas. In the counties of Jämtland and Norrbotten, which include several core areas of reproduction, the growth rates were lower (r = 0.054, P < 0.007 and r = 0.050, P < 0.004, respectively), but were still judged to be relatively high. The total Swedish bear population had a positive trend with an instantaneous rate of increase (r) of 0.045 (P < 0.008), as calculated from the LCOI.

Population estimates

The counties of Dalarna and Västerbotten had no significant population trend, and therefore the population estimates and confidence limits (95%) for 2008 were assumed to be the same as calculated from the scat surveys, 286 (range: 251-337) for Dalarna in 2001 and 309 (range: 265-401) for Västerbotten in 2004. The other populations had a significant observed population trend and bootstrapped estimates of initial population size, and we used the trends in an exponential model to estimate the population size for 2008 with 95% confidence limits. The Jämtland population was estimated to be 1,009 (range: 878-1,151) bears in 2008. Gävleborg and Västernorrland, which had the highest observed growth rates, were estimated to have 529 (range: 352-759) and 255 (range: 171-364) bears, respectively, in 2008. The estimated population size in Norrbotten was calculated to be 910 bears (range: 713-1,152) in 2008, using the relationship between observation rate and population density in Västerbotten.

The total population estimate for Sweden was calculated by randomly adding the 10,000 county estimates. The total estimate was a brown bear population of 3,298 (range: 2,968-3,667) for 2008.

Table 3. Brown bear population estimates based on DNA in scats and trends estimated from the Large Carnivore Observation Index (LCOI) surveys in the different Swedish counties. The trends are based on data from 1998-2007 (1998-2006 for Gävleborg) and figures within brackets show confidence limits (95%).

County	DNA survey year	CMR population estimate	Growth rate (r)	P	Population estimate 2008
Dalarna	2001	286 (251-337)	0	0.590	286 (251-337)
Gävleborg	2001	264 (232-311)	0.097 (0.036-0.157)	0.007	529 (352-759)
Västernorrland	2004	173 (148-249)	0.095 (0.022-0.169)	0.017	255 (171-364)
Jämtland	2006	906 (821-1043)	0.054 (0.019-0.088)	0.007	1009 (878-1151)
Västerbotten	2004	309 (265-401)	0	0.300	309 (265-401)
Norrbotten	none	-	0.050 (0.021-0.079)	0.004	910 (713-1152)

Discussion

In this article, we have used two independent methods which we have developed and tested for monitoring the Swedish brown bear population. They provide management authorities with an index to follow the population trends in different areas over time, as well as distribution, and with statistically robust estimates of population size. All the counties in Sweden with an established bear population, except the northernmost county of Norrbotten, were surveyed between 2001 and 2006 to obtain population size using DNA from collected scats and CMR methods. These surveys cover > 160,000 km² and encompass almost all areas where we can expect bears, apart from the mountain range. In addition, the LCOI has provided yearly indices of bear density since 1998, covering all counties in Sweden with bears, as well as the counties without a current bear population.

A common limitation in bear monitoring is that it is difficult to obtain large enough sample sizes for CMR estimations, due to resource limitations and the huge areas which must be covered (Mills et al. 2000). In this connection, the role of volunteers is important to keep costs low, but also to allow the survey of the huge areas needed (Newman et al. 2003). Another important advantage of using volunteers is that involving them in the monitoring process increases their knowledge and understanding of the procedures (Newman et al. 2003). The interest among volunteers must be maintained, with feedback as one of the most important factors, for obtaining the long data series, 8-10 years, required for trend estimations (Maxwell & Jennings 2005, Harris et al. 2007). The use of LCOI as an addition module to the ongoing moose observations system will help to keep this interest as the moose is the primary motivation for most hunters. However, this means that the system is somewhat dependent upon the moose hunting situation.

The politically decided minimum population goal in Sweden was in 2001 set at 100 yearly reproductions equalling about 1,000 individuals. This was supplemented in a governmental decision in 2008 stating that the population should be maintained at about current levels on a national scale, but allowed it to increase or decrease at local scales, based on the local situation regarding conflicts, e.g. livestock depredation (including semi-domestic reindeer *Rangifer tarandus*), competition for game and problem individuals.

Our objective was to provide estimates of brown bear population size by county, because bear management operates at that scale in Sweden. That means that the spatial structure of bear population management does not correspond to the current bear population distribution (see Fig. 1). This will have an impact on the results, i.e. violation of population closure assumptions, as parts of the same population will be surveyed at different times in different areas.

There are a number of confounding factors for both methods. For scat surveys, they can occur during the collection of scat samples (unevenly distributed or that some areas are completely missing; see Bellemain et al. 2005), the handling of samples, the analysis of DNA and the choice of models for estimating population size. We used closed capture models for estimating population size, as these are better suited for estimating the number of individuals (Amstrup et al. 2005), but bears move across large areas and therefore some bears can appear in several counties, violating closure assumptions (Miller et al. 1997, Schwartz et al. 2003). We believe that this is a minor issue, as the sampling takes place within a limited period (maximum 12 weeks) during the hyperphagia period when there is little immigration/emigration and also that the surveys cover large areas, thus encompassing most of the individuals (Kendall et al. 2009).

Using observations for estimating population size has been criticised, with several studies showing these to underestimate population size (Swenson et al. 1995, Schwartz et al. 2008, Kendall et al. 2009), but for estimating trends in population size, they seem to give estimates comparable to demographic methods (Harris et al. 2007, Brodie & Gibeau 2007; but also see Fernandez-Gil et al. 2010). This, in addition to our evaluation of the LCOI (Kindberg et al. 2009), supports our assumption that we can use the LCOI to obtain trends in the population. The conditions in each area should also be as similar as possible throughout the period. If changes occur in e.g. the manner in which the hunting is conducted, the reporting protocol, the areas involved or the composition of the brown bear population, it could affect the LCOI.

We calculated population growth (r) as exponential growth. This is a simple model, as it for example does not include density-dependent effects; on the other hand it does not require any other assumptions. The difference between different growth models should be minor in our case, and we only included the years for which we have data.

Harvest rates have increased rapidly in recent years (quotas increased from 55 in 1999 to 233 in 2008) and all the effects of the most recent quotas cannot be fully seen in the calculated growth rate, which is based on data from the entire period. This means that the projected growth that we have used may be somewhat higher than it actually was at the end of period. The estimated sustainable harvest in the Swedish population of brown bear has been estimated at 11.2% of the females (C.I: 8.2-13.5%) based on long-term monitoring data from the study area in central Sweden (Bischof & Swenson 2009). When more data are available, future trend estimations should include curvilinear models in competition with the current model as used elsewhere (see Harris et al. 2007).

The estimate for Norrbotten was largely dependent on assumptions based on the survey in Västerbotten. It is most likely that the relationship between the number of bears and the LCOI is more similar to the situation in the adjacent county of Västerbotten than in the other counties. But Norrbotten contains two former core areas for female bears, whereas Västerbotten only shares one with Jämtland (Manel et al. 2004). We were able to verify the assumption that this relationship was statistically the same between Jämtland and the adjacent Västernorrland (see Fig. 2). Nevertheless, we must await the results of the 2010 scat survey in Norrbotten to test the assumptions used here. Until then, this population estimation for Norrbotten should be used carefully.

The LCOI shows a clear linear relationship when compared to the relative density of bears in the DNA surveys (Kindberg et al. 2009), but the relationships are different in different areas, as with moose (Ericsson & Wallin 1999). However, these relationships might change both over time and with changing bear density. One should therefore periodically, perhaps every 5-7 years, correct bear observations with other surveys (DNA scats) to reduce the risk of over- or underestimates. The need for a complementary DNA-survey can be accelerated if the LCOI indicates a major change in the population trend, especially a decline (Hauser et al. 2006). It is also important that the method of the collection of bear observations is constant over time.

It is important to conduct new population estimates in the counties on a regular basis. At this time, Dalarna and Gävleborg have the oldest estimates. However, it would probably be more valid biologically to conduct the surveys to include entire subpopulations of bears (Manel et al. 2004), rather than at the county level, to avoid violations of the assumptions of closed population models. It is important to continuously evaluate our models against estimates from future DNA-based scat surveys. This will allow us to test the accuracy of the estimates, verify the trend calculations from the LCOI and learn from the process, i.e. adaptive management.

Our calculations have not taken immigration, emigration or deaths into account, but they should be considered for future surveys. A common genetic database has recently been constructed, containing all bears that have been sampled and analysed, which will allow this to be evaluated. Bears that are located south of the counties of Gävleborg and Dalarna have not been considered in our national estimate, because they represent a relatively small part of the Swedish population. Other elements that should be included in future analysis (as discussed above) are the effects on growth rate caused by hunting, both in the short- and long-term, various growth models and diffusion and density. Heterogeneity in capture probabilities may occur because some individuals are located in less accessible areas. A solution to this might be to model distance to roads as a covariate for individuals (Huggins 1989). The sex ratio of the population should be followed, as a change in the ratio might indicate a shift from an expansion area (with fewer females; Swenson et al. 1998) to a more stable population structure with more reproducing females.

The use of the two independent methods we have developed and tested for monitoring the Swedish brown bear population provides management authorities with an index to follow the population trends in different areas over time, as well as distribution and statistically robust estimates of population size. It is possible that these methods are suitable for other large brown bear populations where volunteers are available and willing to contribute.

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