GENETIC MONITORING OF SCANDINAVIAN BROWN BEAR EFFECTIVE POPULATION SIZE AND IMMIGRATION

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Abstract: We used microsatellite marker data taken from Scandinavian brown bear (*Ursus arctos*) tissue samples collected by hunters and biologists to estimate population genetic parameters important for bear management. Specifically, we show evidence of a small effective population size (N_e = 44.8; 95% CI: 30.9 to 73.2) and low rates of immigration ($\hat{m}$ = 0.01; 95% CI: 0.00 to 0.05) into the brown bear population along the southern edge of their range in Scandinavia. The ratio of genetic effective size to population size is approximately 0.06–0.14, which falls within the range of values found in previous studies of brown bears. The large confidence intervals around the immigration estimate reflect considerable uncertainty. Nonetheless, these values deserve attention because they are near thresholds of short-term management concern and worthy of long-term monitoring. If the genetic effective size remains this small and immigration remains low, then this population could be subject to the loss of fitness as a consequence of inbreeding effects.

Key words: abundance, brown bears, demography, effective population size, genetic monitoring, immigration, population size, non-invasive sampling, Scandinavia, *Ursus arctos.*

Studies employing non-invasive genetic techniques have focused on estimating or indexing wildlife population sizes (Kohn et al. 1999, Boulanger et al. 2002, Eggert et al. 2003). However, genetic samples also may provide another obvious, but underappreciated, opportunity: the means to monitor population genetic properties and processes (Schwartz et al. 1998, Miller and Waits 2003) such as effective population size (N_e) and rate of immigration into a population. The expected rate of loss of genetic variation per generation (ΔH) is inversely proportional to N_e; ΔH = 1 − 1/2N_e (Crow and Kimura 1970:102). The effective size is the ideal population equivalent of the natural population of interest, controls the rate of loss of selectively neutral genetic variation, dictates the rate of inbreeding effects, and influences the ability of a population to respond to natural selection. Natural populations with a small N_e can be a serious management concern because the loss of genetic variation and inbreeding effects have been shown to lower demographic rates and raise extinction risks (Newman and Pilson 1997, Westermeier et al. 1998, Madsen et al. 1999). Effective population size can be as small as 10% of the population size (Frankham 1995), and researchers have suggested that $\hat{N_e} \leq 50$ is a serious short-term management concern due to the negative fitness effects of inbreeding (Mace and Lande 1991). More recently, researchers have suggested that a N_e of 1 or 2 orders of magnitude larger than 50 is necessary to maintain adaptive genetic variation and avoid buildup of deleterious variation (Franklin and Frankham 1998, Lynch and Lande 1998).

Knowing the rate at which individuals immigrate and successfully breed each generation (m) is also useful because this rate provides insight into the amount of connectivity a population has to others (e.g., Mills et al. 2003). The immigration of 1 or a few individuals has been shown to alleviate the negative fitness consequences of inbreeding and the loss of genetic variation in experimental populations (Newman and Tallmon 2001) and can lend demographic stability to small populations (Beier 1993). Recent observational studies from different taxa suggest that even small amounts of immigration into small inbred populations can facilitate population rebound (Westermeier et al. 1998, Madsen et al. 1999, Keller et al. 2001, Vilà et al. 2002, Tallmon

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et al. 2004). Mills and Allendorf (1996) suggested that between 1 and 10 migrants/generation might be necessary to alleviate the negative genetic effects of isolation in wild populations, and Hedrick (1995) found positive fitness effects of low levels of immigration into the inbred Florida panther (*Felis concolor coryii*) population.

We used 18 years of genetic data taken from conventional tissue samples of the well-studied southern population of brown bears in Sweden (Swenson et al. 1994, 1995). We applied the new estimator of Wang and Whitlock (2003) to obtain $\hat{N}_e$ and $\hat{m}$ jointly. This population of bears merits monitoring for several reasons. First, this population of bears is on the southern periphery of the brown bear range in Scandinavia and is recovering from an extreme population bottleneck ($N < 50$) that occurred in the last century (Swenson et al. 1995). As a population that suffered an extreme bottleneck only a few generations ago, it may be susceptible to negative effects of breeding among relatives. In addition, this population has a high frequency of a mtDNA haplotype not found elsewhere in Scandinavia, and so may represent an important maternal evolutionary lineage for conservation (Taberlet and Bouvet 1994, Taberlet et al. 1995, Manel et al. 2004; but see Waits et al. 2000). As a peripheral population increasing in size (Sæther et al. 1998), it represents the forefront of brown bear range and may serve as the source of individuals for further range expansion south in Sweden and west into Norway (Swenson et al. 1998). Our study demonstrates how genetic samples can be used to monitor important population processes that have not received much attention and gives an example of the type of information, in addition to population size estimates, that can be provided by non-invasive samples in the future.

METHODS AND MATERIALS

Study Area and Sample Collection.—The brown bear distribution in Scandinavia is structured into 4 geographically separated female concentration areas (Swenson et al. 1998). Tissue samples were taken from bears in the southern concentration area and adjacent areas covering 60,000 km^2 in Dalarna, Jämtland, and Gävleborg counties, south-central Sweden (S; Fig. 1). In addition, bears were sampled from 3 populations further north (M, NS, and NN; Fig. 1). Between 1985 and 2002, samples were collected during the marking of live bears for demographic studies and from harvested bears and stored in 95% alcohol until DNA extraction.
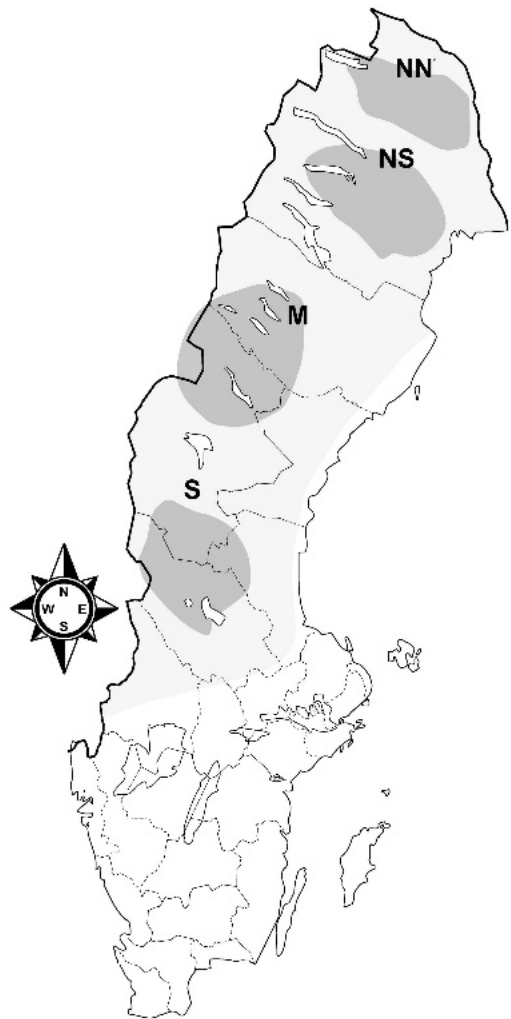

Fig. 1. Map of the Scandinavian brown bear range (light shading) in Sweden and the concentration areas (dark shading) of the focal population (S) and potential source populations further north (M, NS, NN).

Lab Analyses.—We used microsatellites primers described in Paetkau and Strobeck (1994), Paetkau et al. (1995), and Taberlet et al. (1997) to amplify brown bear DNA in a polymerase chain reaction. Eighteen microsatellite loci cloned from an American brown bear DNA library (G1A, G1D, G10B, G10C, G10L, G10P, G10X, G10H, G10O, G10J) and a European brown bear library (Mu05, Mu10, Mu15, Mu23, Mu50, Mu51, Mu59, Mu61) were amplified to obtain a multilocus genotype for each bear tissue sample. We synthesized 1 primer of each pair with a fluorescent dye group (6-FAM, TET or HEX) on the 5′ end to allow detection and sizing of fragments on an

Table 1. Expected ($\hat{H}_{exp}$) and observed ($\hat{H}_{obs}$) number of heterozygotes, as well as the heterozygote excess (F_{is}) within population at each locus in 2 samples collected from the southern Scandinavian brown bear population in 1985–1987 (*n* = 22) and 2000–2002 (*n* = 127).

Locus	Sample 1 (1985–1987)			Sample 2 (2000–2002)		
	$\hat{H}_{exp}$	$\hat{H}_{obs}$	$\hat{F}_{is}$	$\hat{H}_{exp}$	$\hat{H}_{obs}$	$\hat{F}_{is}$
G1A	14.302	16	−0.122	73.846	82	−0.111
G1D	12.442	12	+0.036	73.825	74	−0.002
G10B	15.744	17	−0.082	83.494	88	−0.054
G10C	13.744	13	+0.055	85.988	86	−0.000
G10O	17.837	20	−0.124	96.490	95	+0.016
G10L	16.884	14	+0.174	95.577	97	−0.015
G10P	8.930	12	−0.355	41.637	46	−0.105
G10J	12.442	12	+0.036	72.268	69	+0.045
G10X	12.674	16	−0.270	63.935	69	−0.080
Mu15	14.907	18	−0.213	82.545	82	+0.007
Mu51	16.953	21	−0.246	96.333	95	+0.014
Mu61	12.209	12	+0.018	68.243	67	+0.018
G10H	11.070	15	−0.367	49.017	56	−0.143
Mu05	13.605	14	−0.030	76.924	83	−0.079
Mu59	17.256	18	−0.044	94.699	94	+0.007
Mu10	17.698	17	+0.040	100.120	97	+0.031
Mu23	16.209	17	−0.050	89.100	92	−0.033
Mu50	16.325	16	+0.020	82.289	81	+0.016

ABI Prism 377 DNA sequencer. The amplification and analysis of microsatellites was carried out following the protocol described in Waits et al. (2000). We analyzed the gels using GENESCAN (Applied Biosystems 2001) and GENOTYPER (Applied Biosystems 2001).

Hardy-Weinberg Proportions.—We tested for Hardy-Weinberg proportions for each locus in our 2 samples (1985–1987 and 2000–2002) from the southern population of brown bears using a heterozygote excess test (F_{is}; Weir and Cockerham 1984), as implemented in the online version of GENEPOP (Raymond and Rousseau 1995), with a Bonferroni adjustment for multiple statistical tests (Table 1). We did not test for Hardy-Weinberg proportions in the northern populations because samples were pooled across the M, NS, and NN populations for our analyses and such pooling would not lead to an expectation of Hardy-Weinberg proportions. Allele frequency data are available from the authors upon request.

Effective Population Size and Migration Rate Estimation.—Wang and Whitlock (2003) derived a likelihood-based estimator of N_e and *m*. The associated software program (MLNE; Wang and Whitlock 2003) uses as input allele frequency data from the focal population and from the source population that might provide immigrants into the focal population. Three samples are required to use this method; 2 from the focal population taken 1 or more generations apart and 1 sample from the potential source population. The 2 samples from the southern population (focal) were collected in 1985–1987 (*n* = 22) and 2000–2002 (*n* = 127). Data from the middle and northern populations were collected from 1985 to 2001 and combined to form the putative source population sample (*n* = 91). All samples were from sexually mature bears (i.e., bears ≥3 years-of-age; J. Swenson, unpublished data). The direction and magnitude of changes in allele frequencies in samples from the focal population determine $\hat{N}_e$ and $\hat{m}$. Stochastic changes in allele frequencies of the focal population reflect the influence of genetic drift and small effective size, whereas directional changes reflect the influence of gene flow from the source population. This estimator assumes a large source population of potential immigrants into a finite focal population, that samples are a random subset of the population, that sampling does not change the pool of potential breeders, and that marker loci are independent and not under selection.

A primary uncertainty surrounding our N_e and *m* estimates is the generation time for this population. Thus, we used MLNE to provide $\hat{N}_e$ and $\hat{m}$ over a range of generations (1–3) that may have passed between the first and second sample collections. The generation time of this population was estimated to be approximately 10 years (based on the mean age of parents in this population), but to be conservative, we considered a range of possibilities.

RESULTS

The large samples collected during our study and large number of polymorphic molecular markers used provided precise N_e estimates. We found no evidence of a statistically significant departure from Hardy-Weinberg proportions in the southern Scandinavian bear population (Table 1). However, N_e of this population was small ($\hat{N}_e$ = 44.8, 95% CI: 30.9 to 73.2). This assumes that 1 generation passed between sampling periods of 1985–1987 and 2000–2001, as

inferred from the long-term demographic data collected from this population, and provides an estimate of N_e at the time of the first sample period. Importantly, $\hat{N}_e$ was robust to variation in the generation time and fell between 40 and 90 whether we assumed from 1 to 3 generations passed between the 2 sample collection periods (Table 2). The estimated immigration rate also appeared to be quite low ($\hat{m} = 0.01$; 95% CI: 0.001 to 0.05). This estimate was slightly less robust to variation in generation time, with the point estimate ranging from 0.01 to 0.003, assuming 1–3 generations between sample collections (Table 2). The 95% confidence intervals around all of the immigration estimates are large and reflect considerable uncertainty in these estimates.

DISCUSSION

The southern population of Scandinavian brown bears has an estimated effective population size ($\hat{N}_e = 44.8$) that is considerably smaller than the estimated population size (approx 700; Bellemain et al. 2005). The fact that $\hat{N}_e$ was below 100, which is closer to the International Union for the Conservation of Nature red-book criterion of 50 for endangered species (Mace and Lande 1991), means that this population may be susceptible to negative effects of small N_e. These effects include the loss of genetic variation and inbreeding depression.

The ratio of $\hat{N}_e$ to estimated population size ($\hat{N}$) for our focal population was approximately 0.06–0.14, if one interprets our results conservatively and assumes $\hat{N}_e$ lies between 40 and 100. Previous studies of brown bears in the United States and Canada have suggested that this ratio lies between 0.037 and 0.32 (Allendorf et al. 1991, Paetkau et al. 1998, Miller and Waits 2003). That $\hat{N}_e / \hat{N}$ for our focal population fell within the range of values found in previous studies is encouraging and lends confidence that our results are trustworthy.

The estimated immigration rate ($\hat{m} = 0.01$) also was quite small and suggests that little genetic variation from populations further north is replenishing the genetic variation. However, the large confidence intervals around this estimate and the fact that it lies near the parameter boundary of zero suggest that our estimate should be interpreted cautiously. The problem of N_e and m estimation in finite, age-structured populations has not been addressed rigorously using simulation or analytical models. Therefore, as this population undergoes changes in age structure, growth rate, and generation length, we will have difficulty

Table 2. Genetic effective size (N_e) and immigration rate (m) estimates (95% CI) for the southern Scandinavian brown bear population as a function of the number of generations between samples.

Generations	N_e	m
1	44.8 (30.9 to 73.2)	0.010 (<0.001 to 0.05)
2	64.4 (41.4 to 117.2)	0.005 (<0.001 to 0.03)
3	88.3 (53.8 to 172.8)	0.003 (<0.001 to 0.02)

assessing how our estimates might be affected by nonequilibrium demographic conditions in this population. This uncertainty, and the potentially complex interactions of nonequilibrium conditions and sampling error, warrant conservative interpretation of our parameter estimates.

Nonetheless, our low estimate of $\hat{m}$ is supported by a separate genetics study, employing different analytical methods, which identified the genotype of only 1 individual being the result of a cross between a resident and a bear from the more northern populations (P. Taberlet et al., unpublished data). Previously, Taberlet et al. (1995) recorded no females and 2 males entering the northern edge of the southern population from the northern populations using telemetry and mtDNA data, though successful breeding was not confirmed. Manel et al. (2004) found highly variable—though generally low—estimates of immigration into this population depending on the approach used and the associated assumptions. Because our samples are from the southern edge of brown bear range in Scandinavia and social structures may limit the distance that northern immigrants disperse and successfully reproduce, the "trickle-down" effects of successful immigration by bears from northern populations may take several years before immigrant alleles reach the southern edge of brown bears (Waits et al. 2000). Consequently, monitoring of immigration over the next few generations is warranted, as the small effective size we observed will lead to the loss of genetic variation unless immigrants replenish this variation.

Despite evidence for small N_e and m, we are not overly concerned about this population at present. At least 1 migrant per generation ($N_e m = 1$) is thought to be a useful management goal to maintain genetic variation in local populations that have historically been connected (Mills and Allendorf 1996), and experimental evidence supports this (Spielman and Frankham 1992, Newman and Tallmon 2001). The estimated number of immigrants in our focal population ($\hat{N}_e \hat{m} = 0.45$) was lower than this level. However, this population was recently found to have the highest

population growth rate yet reported for the species (Sæther et al. 1998). This suggests that past bottlenecks and inbreeding have not translated into serious negative consequences for population fitness, and that assumptions of equilibrium conditions between drift and gene flow, upon which population genetic model predictions are based, may be violated. Consequently, we are still optimistic about the future of this population, though future monitoring of immigration and inbreeding effects are warranted because demographic impacts of inbreeding can be expressed at any time.

MANAGEMENT IMPLICATIONS

The southernmost Scandinavian population of brown bears has a small estimated effective size and low rates of detectable immigration by individuals from populations to the north. Our results suggest that continued monitoring of these population genetic parameters is important, as inbreeding and the loss of genetic variation could become a management concern over the coming decades if this population remains at the inferred N_e and low level of connectivity to other populations. The phenotypic expression of inbreeding effects is context dependent, so a negative change in the environment could cause inbreeding depression even without increases in existing inbreeding levels. Mitigating these concerns is the long generation time of this bear population, which will slow the rate of loss of genetic variation and inbreeding effects in absolute time, and the recent positive growth rate of this and other populations in Sweden (Sæther et al. 1998). If the Scandinavian bear populations continue to grow in size and expand their ranges as they have over the past few decades, then rates of inbreeding will slow and immigration rates also may increase over time as populations further north mix with our focal population along the southern edge of their range. However, our estimated parameters serve as a useful source of baseline information for directing monitoring resources and monitoring future population trends.

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