Management and Conservation Article

Hunting Patterns, Ban on Baiting, and Harvest Demographics of Brown Bears in Sweden

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ABSTRACT We analyzed harvest data to describe hunting patterns and harvest demography of brown bears (*Ursus arctos*) killed in 3 geographic regions in Sweden during 1981–2004. In addition, we investigated the effects of a ban on baiting, instituted in 2001, and 2 major changes in the quota system: a switch to sex-specific quotas in 1992 and a return to total quotas in 1999. Brown bears ($n = 887$) were harvested specifically by bear hunters and incidentally by moose (*Alces alces*) hunters. Both hunter categories harvested bears 1) using dogs (37%), 2) by still hunting (30%), 3) with the use of bait (18%), and 4) by stalking (16%). The proportion of bears killed with different harvest methods varied among regions and between bear- and moose-oriented hunters. We found differences between male (52%) and female bears (48%) with respect to the variables that explained age. Moose-oriented hunters using still hunting harvested the youngest male bears. Bears harvested during the first management period (1981–1991) were older and had greater odds of being male than during the subsequent period. It appears that hunters harvesting bears in Sweden are less selective than their North American counterparts, possibly due to differences in the hunting system. When comparing the 4 years immediately prior to the ban on baiting with the 4 years following the ban, we found no differences in average age of harvested bears, sex ratio, or proportion of bears killed with stalking, still hunting, and hunting with dogs, suggesting that the ban on baiting in Sweden had no immediate effect on patterns of brown bear harvest demography and remaining hunting methods. As the demographic and evolutionary side effects of selective harvesting receive growing attention, wildlife managers should be aware that differences in harvest systems between jurisdictions may cause qualitative and quantitative differences in harvest biases. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):79–88; 2008)

KEY WORDS age, baiting, brown bear, demography, hunting, sex, Sweden, *Ursus arctos*.

Brown bears (*Ursus arctos*) in Scandinavia have experienced a drastic decline in numbers to near extinction by the early 1900s as a result of aggressive persecution (Swenson et al. 1995). This decline was followed by a period of recovery, due to protective measures that were implemented in Sweden as early as the late 1800s (Bjärvall 1990, Swenson et al. 1995). Brown bears are currently hunted through most of their range in Sweden, with the annual harvest in 2005 estimated at ranging from 4.1% to 5.1% of the total population estimate (2,350–2,900; Kindberg and Swenson 2006). Bear populations have a relatively low rate of increase and are vulnerable to over-harvest (Miller 1990), so information about the harvest and the relative vulnerability of sex and age groups to different harvest methods is relevant to our understanding and management of the Swedish brown bear population and bear populations in general.

Demographic data derived from harvested animals are typically biased and should be used with caution when drawing conclusions about the sex and age composition or density of the population from which the sample was collected. Despite this caveat, harvest data should not be discarded (Martinez et al. 2005, Mysterud et al. 2006); even with biases, and sometimes because of them, harvest data are important for management-oriented research and life history studies. Several studies on bears (e.g., McLellan and Shackleton 1988, Derocher et al. 1997, Noyce and Garshelis 1997, Kohlmann et al. 1999, McLellan et al. 1999) have shown that harvest is demographically biased and that biases could at least in part be explained by heterogeneities in the bear population (e.g., behavior, mobility, and morphology) and interplay of these heterogeneities with differences in harvest methods, hunter selectivity, and regulations. Although results differ between studies investigating bias and vulnerability in bear harvests, persistent findings shared by most investigations have been 1) harvest is generally biased towards males, 2) young and subadult animals (particularly young M) are more vulnerable than older animals, and 3) harvest sex and age biases differ among harvesting methods. The explanations offered for these biases are wide-ranging. For example, male bias in the harvest is generally explained with greater male mobility, hence greater probability of encountering hunters (Litvaitis and Kane 1994, Noyce and Garshelis 1997, Kohlmann et al. 1999, McLellan et al. 1999), but male bias also has been attributed to the legal protection of females with dependent young (McLellan and Shackleton 1988, Kohlmann et al. 1999, McLellan et al. 1999), longer denning periods for pregnant females and thus reduced availability for harvest (Derocher et al. 1997), active hunter selection for larger-bodied animals, which are more likely males (McLellan et
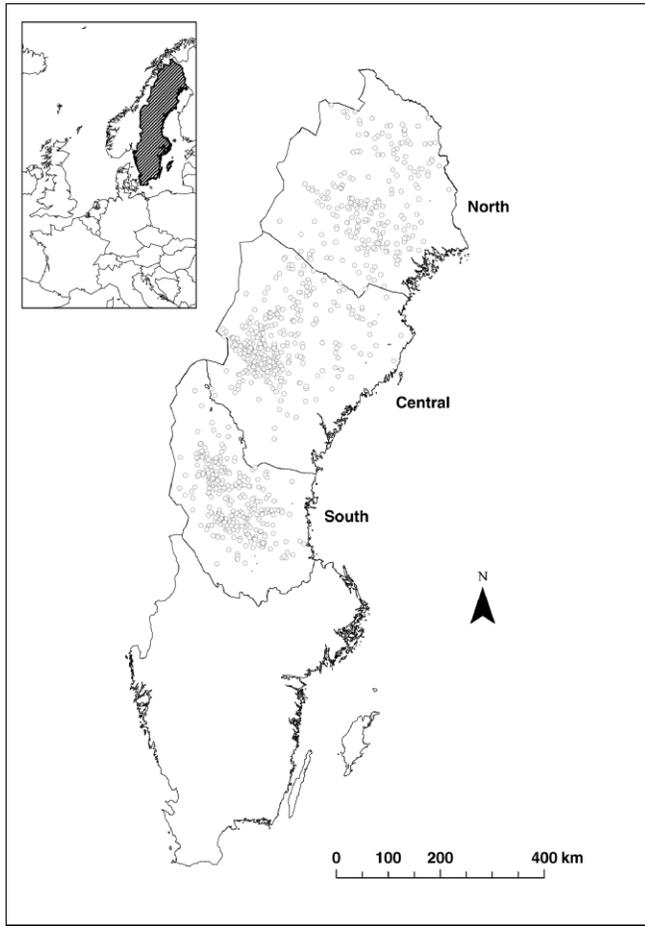
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Figure 1. Map of Sweden, showing the 3 regions of our study area (northern, central, and southern) and harvest locations for 883 brown bears with sufficient spatial information from 1981 through 2004 (circles).

al. 1999), and greater male tolerance towards feeding near other bears and humans (Noyce and Garshelis 1997).

Brown bears in Sweden are hunted in the fall by sit-and-wait (still hunting), by stalking, with dogs, and with bait. In 2000, the Swedish Environmental Protection Agency issued a ban on baiting for bears to start in 2001, mainly because of concerns about human safety (Naturvårdsverket 2000). Additional issues regarding the impact of baiting on bear management had also been raised, namely 1) the perceived increasing prevalence of baiting in the annual brown bear harvest and 2) the suspicion that certain age and sex groups were more vulnerable to baiting than others (Naturvårdsverket 2000). On the other hand, proponents of baiting have argued that, among the available hunting techniques, baiting actually allows for a more deliberate selection due to increased visibility and the more controlled setting that it provides, reducing the risk of inadvertently shooting females with dependant young (Fujita 2000). The ban on baiting was and continues to be controversial among hunters and wildlife managers, in part because of the scarcity of quantitative information about the consequences of this or other harvest methods on bear populations, particularly brown bears. We also note that the legality of the ban

according to Swedish law is currently being evaluated by the Swedish court system.

We examined the demographic composition of harvested brown bears in Sweden in relation to harvesting methods from 1981 to 2004, with added emphasis on hunting over bait and the ban on baiting. Specifically, we ask the following main questions: 1) What is the age and sex composition of harvested bears and is it affected by harvest method? 2) Did the ban on baiting affect the prevalence of bears taken by different hunting techniques and the age and sex composition of harvested bears? 3) Did changes in the quota system (i.e., sex- vs. non–sex-specific quotas) during the study period coincide with changes in demographic composition of the harvest?

STUDY AREA

Our study area consisted of 3 contiguous regions in Sweden (northern, central, and southern), spread over 292,000 km^2, approximately the northern 65% of the country, from about 60° to 69° N (Fig. 1). We based the region delineation on 3 genetically distinct subpopulations that matched 3 geographical clusters of bears with no or very little interchange of females (Manel et al. 2004). All 3 regions occurred within the southern, intermediate, and northern boreal vegetation zones, which were dominated by coniferous forests on primarily granite and gneiss bedrock, with small adjoining alpine zones on the western edge and the Baltic Sea to the east of each region. The area was cool and moist, with 120–160 days per year $\geq 6°$ C and primarily 500–700 mm annual precipitation. The dominating tree species were Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), but birches were also common (*Betula* spp.). The primary land use throughout this area was clear-cut forestry (Nordisk ministerrådet 1984, Bernes 1994).

METHODS

Brown Bear Hunting in Sweden

During our study (1981–2004), the brown bear hunting season occurred annually in the fall in Sweden, generally starting in late August or early September and lasting 1–2 months. No specific license was required for harvesting brown bears; all hunters with hunting rights on a hunting ground and a legal weapon for big game hunting could harvest bears. During 1981–1985, cubs of the year and females with cubs of the year were protected; after 1985 family groups were protected, regardless of the cubs' age. Bears were shot by hunters who were hunting specifically for bears and by hunters who were hunting primarily for moose (*Alces alces*; Swenson et al. 1998). Both bear- and moose-oriented hunters harvested bears 1) by stalking, 2) by still hunting (generally waiting for moose), 3) with dogs, and 4) by hunting over bait. Although the requirements for training and stamina differ between moose and bear dogs (Sandegren and Swenson 1997), methods for hunting bears with dogs were typically identical for bear- and moose-oriented hunters and generally consisted of on- or off-leash pursuit with 1–3 dogs, after which the dog or dogs (off-

leash) kept the bear in place until it was shot by the hunter. Baiting used by bear hunters generally consisted of deliberately placing meat bait (often domestic animal carcasses or slaughter remains from wild and domestic animals) to attract bears at a location chosen by the hunter. Bears shot incidentally by moose hunters over bait were attracted to moose entrails left after a previous moose hunt in the same area.

Guided hunts, financially motivated by trophy hunting, are rare in Sweden. There was no limit on the number of bears that an individual hunter was allowed to harvest in a given year, and the hunting season continued each year until the scheduled season end date or until the harvest quota was reached (whichever came first). The authorities informed hunters of the number of bears that remained on the harvest quota via the media and a 24-hour telephone number (beginning in the mid-1990s). During 1981–1991 (management period 1), harvest quotas (nonspecific for sex) were based on political units (municipalities or groups of municipalities), rather than biological units (subpopulations). During 1992–1998 (management period 2), a double quota system, with a total quota and a female quota (between 29% and 33% of the total quota) in each of 4 subpopulations recognized at that time regulated the maximum number of bears that were harvested annually (Swenson et al. 1994). This sex-specific quota system stipulated that the bear season ended if either the female quota or the total quota was filled, whichever came first. In 1999 (management period 3, 1999–2004), the hunting system changed again; female quotas were removed and quotas were set at the county (i.e., län) level, rather than by subpopulation. A ban on hunting bears over bait was implemented starting with the 2001 hunting season and was in place throughout the remainder of our study.

Reporting

Successful brown bear hunters were required to present bear carcasses to an officially appointed inspector on the day of the harvest and to provide information about harvest methods, sex of harvested bears, body mass, and harvest location to the Swedish Hunters Association (1986–2001) and the National Veterinary Institute of Sweden (after 2001). If the inspector was suspicious of the accuracy of information provided by the hunter, the hunter was required to take the inspector to the reported harvest site. In addition, hunters had to submit a premolar tooth from harvested bears for age determination via cementum annuli counts (Mattson's Inc., Milltown, MT; Craighead et al. 1970). The information and samples were archived by the National Veterinary Institute of Sweden.

Analysis

We analyzed data from hunter reports collected between 1981 and 2004. No data were available for unsuccessful hunts or hunters, therefore, our analysis was restricted to data associated with harvested bears, without a measure of harvest effort. We excluded from analysis bears harvested outside of regular harvest activities. We used log-linear analysis to evaluate the effect of harvest method, hunter category, and population on the number of bears harvested between 1981 and 2000. We used linear regression to detect temporal trends in arcsine-transformed proportions (e.g., proportion of F in the harvest), after ensuring that the data were not autocorrelated over years. We used generalized linear models (GLM) to test effects of independent variables and meaningful 2-way interactions between variables on the log-transformed age of harvested bears. Preliminary analysis of our data and review of the literature suggested differences between male and females with respect to the effect of age on vulnerability to hunting, hence we calculated separate models for each sex. The independent variables used in the initial model for each sex were 1) method (baiting, dog hunting, still-hunting, stalking), 2) hunter category (moose-oriented, bear-oriented), 3) region (north, south, central), 4) management period (periods 1, 2, and 3), and 5) year (covariate).

We used logistic regression to test effects of the above independent variables, age (log-transformed covariate), and meaningful 2-way interactions between variables on sex of harvested bears. We did not include the ban on baiting (before and after) in these models because the ban was defined by the presence or absence of baiting, already a model component as a level of the categorical variable "method." Prior to including the harvest year as a covariate, we looked for autocorrelation in proportion of females and average age, using autocorrelation factor plots, and found no indication of autocorrelation among years. For all models, we removed model terms in a stepwise fashion until we arrived at the model with the lowest Akaike's Information Criterion (AIC) value. For the final GLMs with age as the dependent variable, we inspected the residuals for normality and found no gross deviations. For the age analysis, we excluded age data from the years 1981–1985 because ages from those years were only available for a small subset (3–12%) of harvested bears and are unlikely to represent random samples of the harvest. To test whether geographic differences on a scale smaller than the study region were important enough to be included in final age models, we initially included commune (a political unit below county level) as a random effect in the age model. We omitted the random effect from final age models because its impact was negligible and did not improve model fit (e.g., for M: AIC = 745.192 for model including commune as a random factor vs. AIC = 743.192 for model without the random factor).

To test effects of the ban on baiting on harvest demography and harvest patterns, we compared the 4 years immediately prior to the ban on baiting (1997–2000) with the 4 years immediately following the ban (2001–2004). We felt that this comparison would 1) enhance balance, in terms of years and sample size, and 2) make the comparison more robust, because shrinking the overall time frame reduced (although not eliminated) the opportunity for potentially confounding temporal changes in environmental conditions, harvest effort, and population attributes. To verify that our data were sufficiently independent (i.e., that we did not have
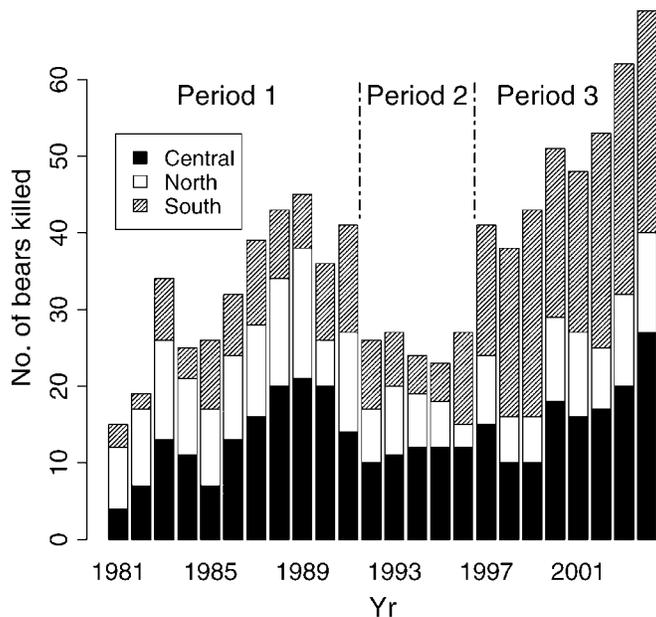
Figure 2. Number of brown bears killed per year within the northern, central, and southern study areas in Sweden between 1981 and 2004. Periods with different quota systems are separated by hatched lines. A noticeable depression in total harvest coincides with management period 2, during which sex-specific harvest quotas were implemented. $n = 887$.

a few hunters taking a large portion of bears harvested), we calculated the number of bears shot per individual hunters for years for which hunter identity data were available (1981–2003). We used the statistical programming language and environment R 2.4.0 for statistical analysis (R Development Core Team 2006).

RESULTS

During 1981–2004, hunters reported harvest of 1,053 brown bears in Sweden. We used data from 887 bears with sufficient information for our analysis. Of these, 232 (26%) were harvested in the north, 336 (38%) in the central region, and 319 (36%) in the south. As a result of increasing quotas, the number of bears harvested or lethally wounded annually increased during our study, from 16 bears in 1981 to 101 in 2004, attributable mainly to harvest increases in

the southern region and to a lesser degree in the central region (Fig. 2). Only 3.1% of hunters (22 of 700) harvested >1 bear during 1981–2003, with 2, 3, 4, 5, and 17 bears harvested by 16, 2, 2, 1, and 1 hunter(s), respectively. On 14 occasions 2 bears were shot by a hunter in one year, and on one occasion a hunter shot 3 bears during the same year. The one hunter that harvested 17 bears did so within the same municipality over a period of 18 years (1986–2003, never >2 bears/yr) and shot bears both incidentally while hunting for moose and specifically, using stalking and baited hunting.

Harvest Patterns

Of the 887 bears we used in our analysis, 159 (18%) were harvested using baiting, 329 (37%) by using dogs, 137 (16%) by stalking, and 262 (30%) by still hunting. We identified hunter category for 771 bears, of which 351 (46%) were harvested by bear-oriented hunters and 420 (55%) by moose-oriented hunters. Only the saturated log-linear model (containing all possible interactions among model terms) sufficiently explained the observed number of bears harvested (pre-bait ban, Table 1) relative to hunting method, hunter category, and population (3-way interaction: deviance = 15.385, df = 6, $P[\chi^2] = 0.018$). Inspection of predicted values from the model and associated standard errors suggested 1) bear-oriented hunters harvested more bears with baiting in the south than with any other technique in any of the 3 regions (between 1.7 and 7.7 times more, depending on method and region), 2) moose-oriented hunters harvested more bears in the central region with still hunting than with any other technique in any of the 3 regions (between 1.7 and 10.5 times more, depending on method and region), and 3) still hunting in all 3 regions was more important for moose hunters than for bear hunters but was least important in the north (18 bears vs. 34 in the south and 63 in the central region; Fig. 3).

We used linear regression analysis to test whether the relative importance of baiting had increased during 1981–2000 and found that, contrary to one of the arguments made by opponents of baiting, the proportion of bears harvested by baiting was stable prior to the bait ban for bear hunters

Table 1. Number of brown bears harvested by moose- and bear-oriented hunters in 3 regions using 4 methods in Sweden before the ban on baiting (1981–2000) and after (2001–2004).

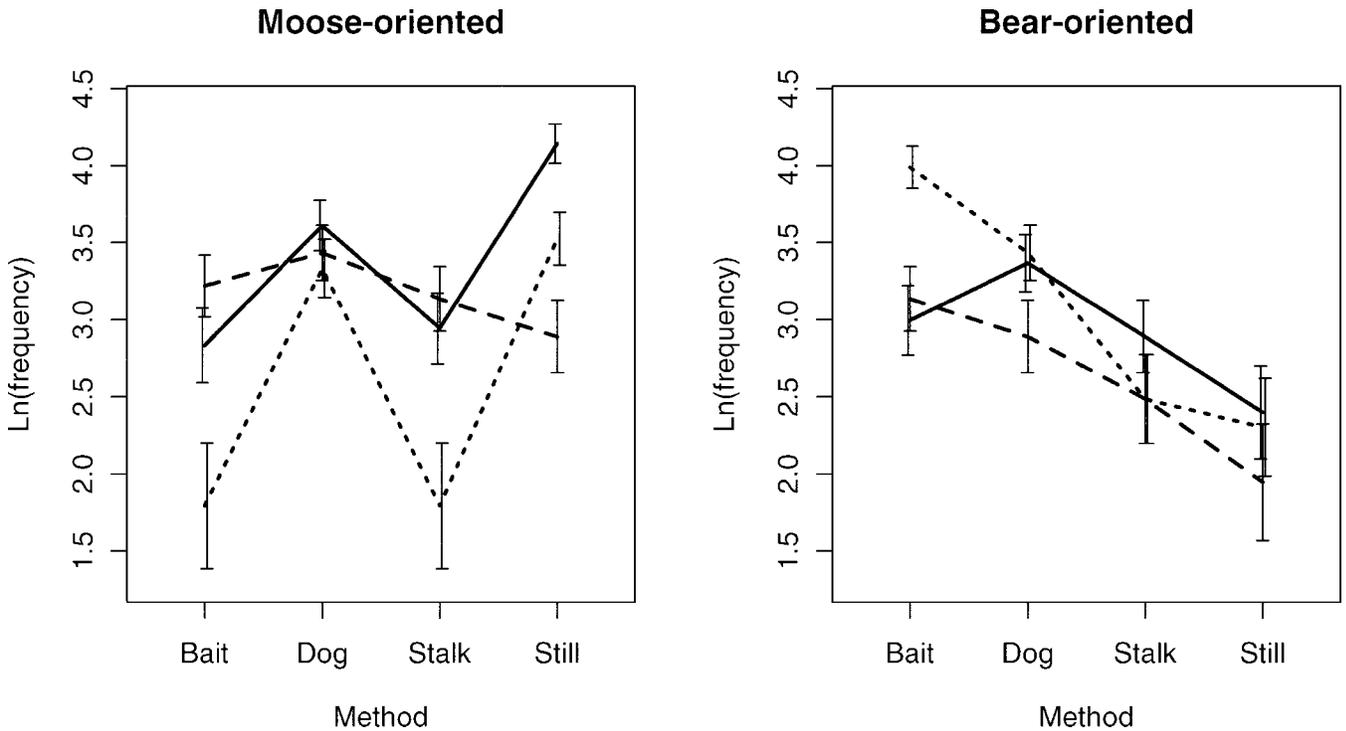|		Hunter category							
		Bear-oriented				Moose-oriented			
Period	Method	North	Central	South	Total	North	Central	South	Total
1981–2000	Bait	23	20	54	97	25	17	6	48
	Dog	18	29	31	78	31	37	28	96
	Stalk	12	18	12	42	23	19	6	48
	Still	7	11	10	28	18	63	34	115
	Total	60	78	107	245	97	136	74	307
2001–2004	Dog	7	24	33	64	10	11	18	39
	Stalk	3	2	8	13	7	3	4	14
	Still	0	13	16	29	13	26	21	60
	Total	10	39	57	106	30	40	43	113

Figure 3. Predicted brown bear harvest frequencies in Sweden (log-transformed) and standard error bars from the log-linear model with hunting method, hunter category, and region (solid = central, dashed = north, dotted = south) as model factors, during 1981–2000. Because model selection (Akaike's Information Criterion [AIC]) resulted in the saturated final model (3-way interaction between the predictor variables), predicted and observed frequencies are identical. We added a small amount of noise to the location of error bars along the x-axis to allow distinction of overlapping error bars.

and had decreased during the same period for moose hunters at a rate of approximately 1% per year (Table 2, Fig. 4).

Harvest Demography

Of the 887 bears we used in the analysis, 422 (48%) were female and 465 (52%) were male. Regression analysis showed no temporal trend in the proportion of females (arcsine-transformed) in the harvest during our study (linear regression, $F_{1,22} = 0.268$, $\beta = 0.002$, $P = 0.61$). Age information was available for 644 bears. Male and female age distributions were similar (M: $\bar{x} = 4.823$ yr, SD = 4.142, min. = 1, max. = 22 yr; F: $\bar{x} = 5.048$ yr, SD = 4.907, min. = 1, max. = 33 yr; Fig. 5), although there was some indication

Table 2. Regression results for temporal trends in the proportion (arcsine-transformed) of brown bears harvested by moose- and bear-oriented hunters in Sweden while using bait, dogs, stalking, and still hunting during 1981–2000.

Method	β	SE	$F_{1,18}$	P
Bear-oriented				
Bait	0.001	0.009	0.006	0.941
Dog	0	0.008	<0.001	0.985
Stalk	−0.012	0.014	0.701	0.414
Still	0.015	0.007	4.649	0.045
Moose-oriented				
Bait	−0.024	0.007	10.76	0.004
Dog	0.015	0.007	5.231	0.035
Stalk	−0.018	0.005	10.7	0.004
Still	0.014	0.007	4.085	0.058

of an elevated male:female ratio in the harvest among the 4- to 7-year-olds. Subadults (1- to 3-yr-olds) made up 51.6% of the harvest ($N = 644$). The 4 oldest animals (23 yr, 24 yr, 32 yr, and 33 yr) were females.

Variable selection resulted in different final GLMs for males and females (Tables 3, 4). For males, region, management period, and method modified by hunter category were variables predicting age (Table 3). Male bears shot by moose hunters using still hunting were 24–50% younger than males shot with other methods, although there seemed to be no recognizable difference among ages of males shot with the different methods by bear hunters. Inspection of model residuals and histograms over age by hunter category and method suggest differences in the age distribution among the groups, most notably a bias towards yearling males by moose hunters using still hunting (Fig. 6). Harvested males were approximately 32% younger in the north than in other regions. For females, region, management period, and hunter category modified by year remained in the final model (Table 4). Region did not have an effect on age but remained in the model as an adjusting variable. The interaction between hunter category and year indicated that average age of females harvested by moose hunters increased during our study, whereas there was no linear temporal trend in the average age of females harvested by bear-oriented hunters. Both males and females harvested during management period 1 were older than during the subsequent period.

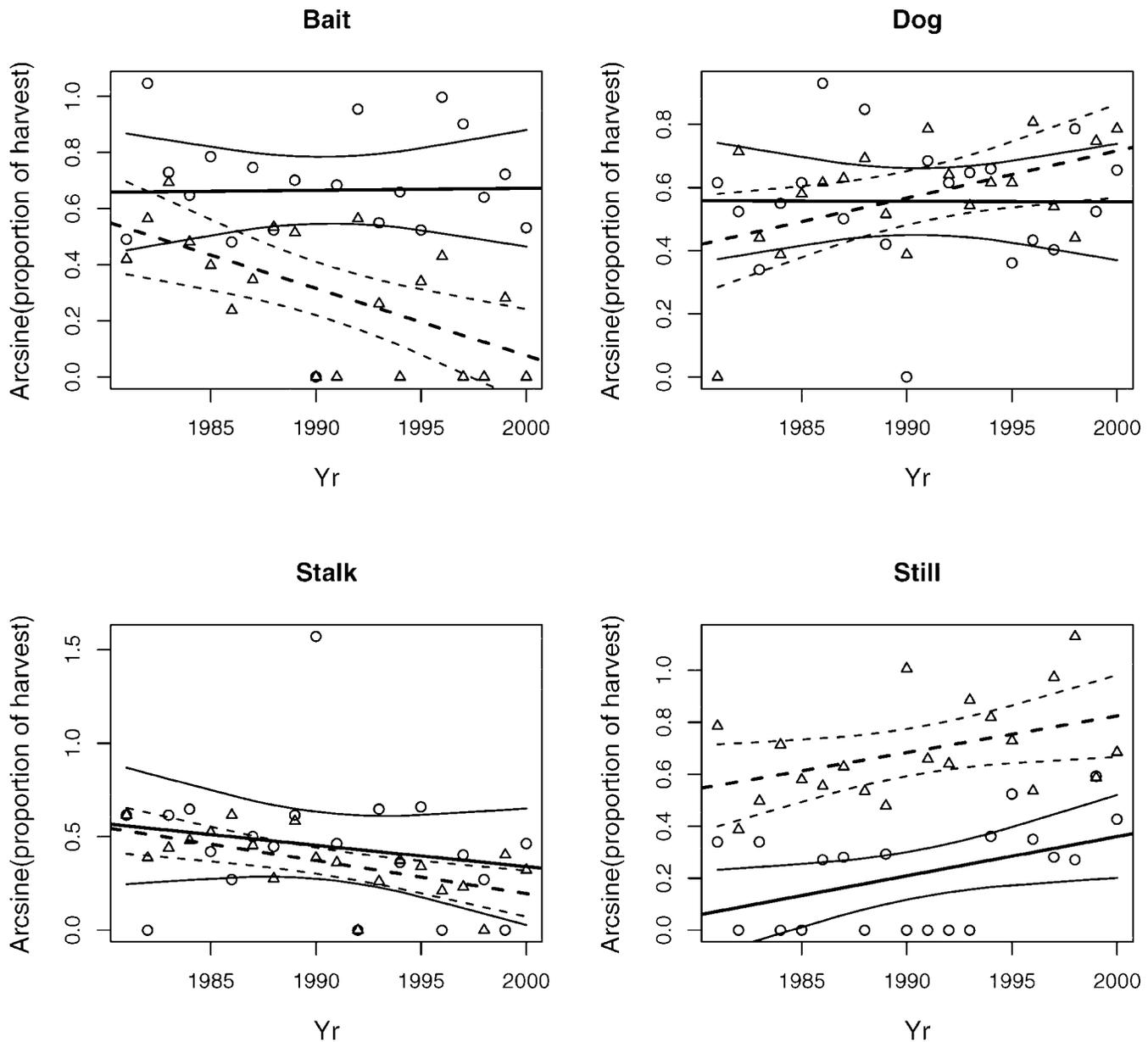Management period, age modified by hunter category, and

Figure 4. Proportion (arcsine-transformed) of brown bears killed annually with each of 4 hunting methods by bear- (circles and solid lines) and moose-oriented hunters (triangles and dashed lines) in Sweden between 1981 and 2000, including linear regression lines (bold lines) and 95% pointwise confidence bounds (thin lines) for the fitted lines.

age modified by region remained as predictors in the final logistic regression model with sex as the dependent variable (Table 5). Odds of a harvested bear being male were greatest during management period 1 (between 24% and 33% greater than during the other 2 management periods). The interaction between age and region suggests decreasing odds with increasing age that bears harvested in the northern region were male, which is consistent with the findings of the GLM with age as the dependent variable for males. Neither method nor harvest year were predictors for the sex of harvested bears.

Effects of the Ban on Baiting

We found no difference between the 4 years before and the 4 years after the ban on baiting with respect to relative

importance (representation in the harvest) of stalking, still hunting, and hunting with dogs ($\chi^2 = 0.202$, df = 2, $P = 0.904$). There was no difference in the proportion of males and females harvested between the 2 periods (bear hunters: $\chi^2 = 0.012$, df = 1, $P = 0.914$; moose hunters: $\chi^2 = 0.209$, df = 1, $P = 0.648$; combined: $\chi^2 = 0.284$, df = 1, $P = 0.594$). We also found no difference between pre- and postban years in the age (log-transformed) of bears harvested (F: $t = 1.204$, df = 184, $P = 0.23$; M: $t = 0.799$, df = 193, $P = 0.425$; combined: $t = 1.439$, df = 379, $P = 0.151$). The removal of baiting as a harvest method in 2001 did not reduce the ability of hunters to reach the annual harvest quota (Table 6), as would have been expected if baiting were substantially more efficient than the remaining hunting methods.

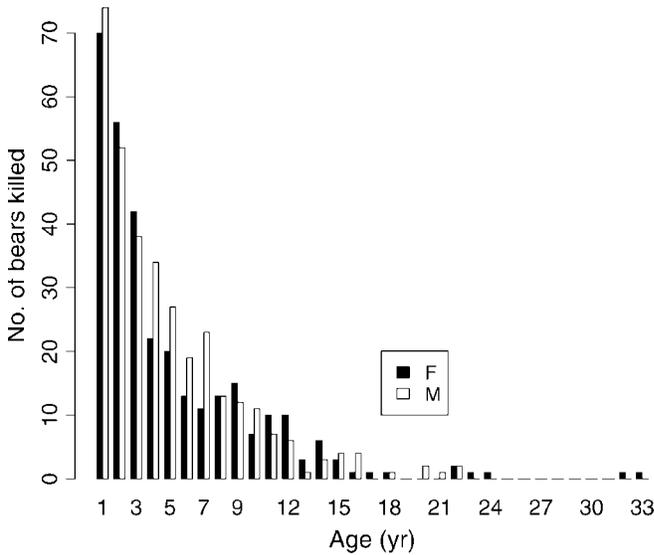Before the ban, baiting was most prevalent in the southern

Figure 5. Number of female ($n = 310$) and male ($n = 334$) brown bears killed by age in Sweden during 1981–2004.

area (Table 1); hence we speculated that the southern area may be where impacts of the ban on baiting on the relative proportion of harvest methods would be the most pronounced, particularly for bear-oriented hunters. However, we found no difference between the 4 years before and after the ban on baiting with respect to the proportion of bears harvested by hunting with dogs, stalking, and still hunting in the southern area by bear-oriented hunters ($\chi^2 = 0.593$, df $= 2$, $P = 0.744$).

Table 3. Parameter estimates and test statistics for the generalized linear model[a] explaining age (log-transformed) of male brown bears harvested in Sweden during 1986–2004. We based model selection on Akaike's Information Criterion. One level of each categorical variable serves as a contrast ($\beta = 0$) for the remaining levels of that variable.

Explanatory variables	df	β	SE	t	P(>|t|)
Method	3				
Dog		0			
Bait		0.199	0.19	1.049	0.295
Stalk		−0.048	0.236	−0.204	0.839
Still		0.071	0.19	0.373	0.71
Hunter category	1				
Bear-oriented		0			
Moose-oriented		0.153	0.166	0.921	0.358
Region	2				
South		0			
Central		0.054	0.114	0.477	0.634
North		−0.366	0.132	−2.77	0.006
Management period	2				
1986–1991		0			
1992–1998		−0.317	0.142	−2.237	0.026
1999–2004		−0.182	0.135	−1.349	0.179
Method:hunter category	3				
Bait:moose-oriented		−0.238	0.296	−0.804	0.422
Stalk:moose-oriented		−0.259	0.321	−0.807	0.421
Still:moose-oriented		−0.702	0.24	−2.929	0.004

[a] Model $R^2 = 0.14$.

Table 4. Parameter estimates and test statistics for the generalized linear model[a] explaining age (log-transformed) of female brown bears harvested in Sweden during 1986–2004. We based model selection on Akaike's Information Criterion. One level of each categorical variable serves as a contrast ($\beta = 0$) for the remaining levels of that variable.

Explanatory variables	df	β	SE	t	P(>|t|)
Hunter category	1				
Bear-oriented		0			
Moose-oriented		−146.8	44.36	−3.31	0.001
Region	2				
South		0			
Central		−0.165	0.129	−1.277	0.203
North		0.183	0.153	1.193	0.234
Management period	2				
1986–1991		0			
1992–1998		−0.666	0.317	−2.104	0.036
1999–2004		−0.83	0.496	−1.674	0.095
Yr	1	0.006	0.036	0.157	0.876
Hunter category:yr	1				
Moose-oriented		0.074	0.022	3.31	0.001

[a] Model $R^2 = 0.08$.

One of the arguments of proponents of baiting was that females with cubs were easier to identify as such over bait and thus less likely to be harvested. Due to the low sample size, we were not able to carry out statistical tests; however, 5 of the 6 females with known dependent offspring were harvested with the use of dogs, and 3 of them were harvested after the ban on baiting. In addition, of the 12 cubs-of-the-year harvested during hunting (not included in the other analyses), 8 were harvested using dogs, 3 by still hunting, and one over bait. Of the 12 cubs, 6 were harvested after the ban on baiting was implemented, 2 with dogs and one with still hunting.

DISCUSSION

Differences in age and sex composition among harvest methods in Sweden were not as pronounced as the differential biases that similar investigations have shown to exist for brown and black bear (*Ursus americanus*) harvests in North America (e.g. McLellan and Shackleton 1988, Kohlmann et al. 1999). For example, we found no effect of method on the sex of harvested bears and few age-specific biases. In addition, our models explained only a small proportion of the overall variation in age (14% for M, 8% for F), which we attribute in part to differences in hunter selectivity. Active hunter selectivity of bears based on sex or age is unlikely to be a major factor causing demographic bias in the Swedish harvest. Given a relatively low probability of encountering a bear, the lack of individual bag limits, combined with a harvest that is limited by season quotas, there is little incentive for Swedish hunters to pass up a shot at a legal brown bear they encounter, other than a fee that has to be paid to the owner of the hunting rights (the landowner). The low encounter rate is further illustrated by the small proportion of hunters (3.1%) that shot >1 bear during our study. It remains to be seen whether a growing bear population in Sweden (and correspondingly increasing
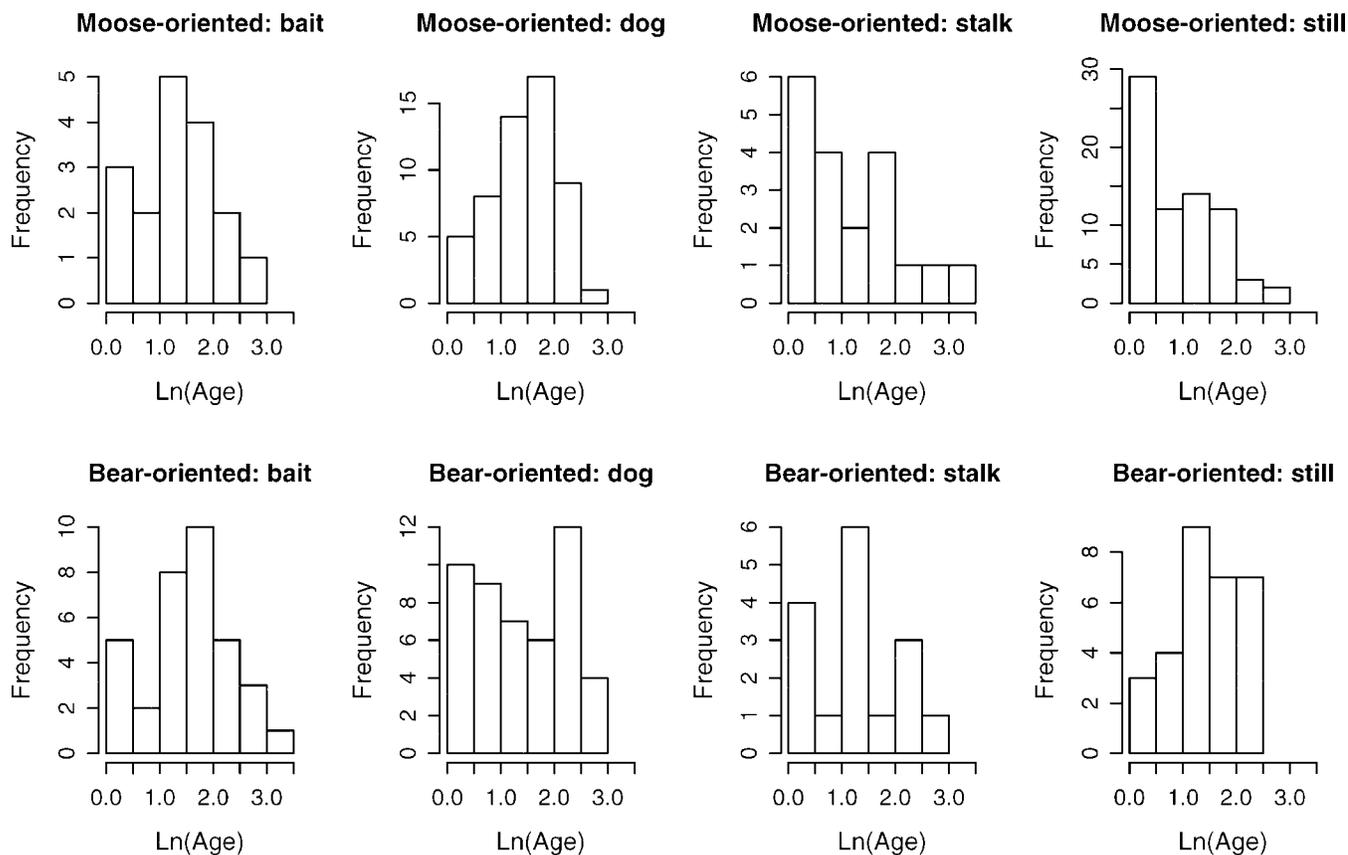
Figure 6. Histograms of male brown bear ages (log-transformed) harvested by moose and bear oriented hunters using 4 different methods from 1986 to 2004 in Sweden.

encounter rates) will result in greater hunter selectivity in the future. We found that hunters in Sweden did not distinguish between male and female brown bears when encountering them in the field, because sex-specific quotas that were meant to encourage hunter selectivity did not have that effect. We recognize that active hunter selectivity accounts for only a portion of the demographic patterns observed during harvest analyses of other bear populations, and differential vulnerability of sex and age groups to harvest methods would not be eliminated solely by lack of hunter selectivity. Thus, another explanation for the comparatively small difference in age and sex composition among different methods in our results could be that differential vulnerabilities among sex and age groups are not as pronounced in the Scandinavian bear population as in North America and that a larger sample size than the one available to us is needed to detect them.

The ban on baiting had no recognizable effect on harvest patterns and demographic composition of the harvest, at least when comparing the 4 years leading up to the ban with the 4 years following it. We note that we only had 4 years of postban data to evaluate. Data from future harvest years may be required to uncover delayed or small, but long-term, impacts on harvest demographics.

Our models suggested that average age was highest for bears harvested during management period 1 (most pronounced in comparison with management period 2)

and that odds of a harvested bear being male were greater during management period 1 than during the subsequent periods. Interpretation of these results is difficult, because our analysis does not allow us to distinguish potential temporal effects, perhaps associated with a changing population, from effects of changes in the quota system. The percentage of the annual quota that was filled showed an upward trend during the study period, with a noticeable depression during 1992–1998 (Table 6), because hunters reached the female quota, and hence ended the season, prior to reaching the total quota during the time period with sex-specific quotas.

We found that younger male bears (particularly yearlings) were more vulnerable to still hunting (when used by moose-oriented hunters) than to other hunting methods. Method-specific vulnerabilities are more likely to show up with incidentally shot bears (moose-oriented hunters), because they are not as prone to be masked or confounded by other factors associated with active targeting or seeking of bears (bear-oriented hunters). Others have attributed harvest bias towards young animals (particularly M) to their greater mobility compared with other sex and age cohorts, increasing the probability of encountering a hunter (Litvaitis and Kane 1994, Noyce and Garshelis 1997, Kohlmann et al. 1999, McLellan et al. 1999). In our case, because still hunters are sedentary, vulnerability of bears to still hunting is likely to increase with increasing mobility of bears.

Table 5. Parameter estimates and test statistics for the logistic regression model explaining sex (F = 0, M = 1) of brown bears harvested in Sweden during 1981–2004. We based model selection on Akaike's Information Criterion (AIC). One level of each categorical variable serves as a contrast (β = 0) for the remaining levels of that variable.[a]

Explanatory variables	df	β	SE	z	LCL	OR	UCL	$P(>|z|)$
Age (log)	1	0.256	0.166	1.546	0.934	1.292	1.788	0.122
Hunter category	1							
Bear-oriented		0						
Moose-oriented		0.861	0.315	2.734	1.276	2.366	4.386	0.006
Region	2							
South		0						
Central		−0.539	0.354	−1.523	0.292	0.584	1.167	0.128
North		0.809	0.408	1.981	1.009	2.245	4.996	0.048
Management period	2							
1981–1991		0						
1992–1998		−0.631	0.281	−2.248	0.307	0.532	0.922	0.025
1999–2004		−0.500	0.262	−1.906	0.363	0.607	1.014	0.057
Age:hunter category	1							
Moose-oriented		−0.353	0.207	−1.704	0.468	0.702	1.054	0.088
Age:region	2							
South		0						
Central		0.309	0.233	1.330	0.864	1.362	2.149	0.184
North		−0.803	0.274	−2.930	0.262	0.448	0.766	0.003

[a] LCL = lower 95% CL; UCL: upper 95% CL; OR = odds ratio.

The average age of male bears was lowest for animals harvested in the northern region of the study area, which was not likely a result of distribution of hunter categories and harvest methods, because still hunting, the technique we found to be biased towards younger animals compared with other methods, comprised a smaller portion of the harvest in the north than elsewhere. Instead, this regional bias towards younger males in the harvest may represent a difference in age structure of the male population or greater subadult male vulnerability in the north (Zedrosser et al. 2007).

We found differences in the relative importance of the 4 hunting methods used for harvesting brown bears in Sweden, as well as regional and temporal variation in harvest patterns and differences between bear- and moose-oriented hunters. The complex interaction between hunting method, hunter category, and harvest region in terms of the number of bears harvested means that conclusions about the effect of either factor can only be drawn when the remaining 2 factors are also considered. Differences among regions in the prevalence of bears harvested with different hunting methods are attributable at least in part to regional differences in hunting traditions and the ratio of bear- to moose-oriented hunters and likely also to variation in the demographic structure of the different populations.

Table 6. Annual harvest quota and number of brown bears killed or lethally wounded by hunters in Sweden during 1981–2004. We show female quotas and the number of females harvested for the time period with sex specific quotas (1992–1998). The number of brown bears harvested exceeded the quota in some years, due to a small time lag between the filling of the quota and the announcement of the end of the season.

Yr	Quota	No. harvested	F quota	F harvested
1981	36	16		
1982	35	21		
1983	42	34		
1984	42	27		
1985	40	27		
1986	45	35		
1987	57	41		
1988	60	45		
1989	59	49		
1990	58	42		
1991	51	46		
1992	50	34	16	8
1993	50	34	16	18
1994	50	30	16	16
1995	50	36	16	14
1996	58	30	17	18
1997	69	48	23	24
1998	78	49	26	27
1999	55	51		
2000	56	57		
2001	60	63		
2002	64	62		
2003	74	75		
2004	101	101		

We found anecdotal evidence that cubs and females with dependent young may be more vulnerable to be harvested when hunted using dogs than by other methods, but our sample size was too small to determine the magnitude of this effect, if in fact it exists. Females with dependent young could be more vulnerable to dog hunting than other hunting methods, if they move slower and through more accessible terrain, leave a wider scent trail, and if they are more likely to face their attackers in order to protect their cubs. In addition, it is possible that hunters will not recognize a female with dependent young as such if she is separated from her cubs (e.g., by sending them up a tree) before they are noticed by the hunter. We recommend that future studies investigate the vulnerability of females with dependent young at bait stations (e.g., do females take their young with them when visiting bait stations?) and when hunted

with dogs (e.g., are hunters able to see and recognize the cubs when a female pursued with dogs has dependent young?).

Milner et al. (2006) recommended that harvesting regimes mimic natural mortality patterns more closely to minimize demographic side effects as well as evolutionary consequences of selective harvesting. If and when hunting regimes closer to natural mortality patterns become an objective for the management of the Scandinavian brown bear, it will require information about the demography and natural mortality patterns in unhunted brown bear populations, preferably in Scandinavia. In addition, to further identify and to explain biases in Swedish brown bear harvest and to account for potentially confounding variation in bear populations and harvest effort over time and space, future analyses should provide context through information about population(s) from which the harvest sample is drawn, as well as some measure of harvest effort.

MANAGEMENT IMPLICATIONS

Wildlife managers can expect to find differences in harvest biases among jurisdictions with different harvest systems. Biases in Swedish brown bear harvest primarily reflect differences in inherent vulnerability, whereas in North America investigators often have to distinguish between biases that are a result of active hunter selectivity and those that are caused by differential vulnerability of sex and age groups in the population. Furthermore, we found no demographic effect of the ban on baiting in Sweden on the harvest, hence an evaluation of the advantages and disadvantages of the ban should continue to concentrate on the human dimensions of hunting using bait. These include concerns about human safety (for example if bears are accustomed to forage on food provided by humans or if hikers inadvertently stumble onto a bear at a bait station), as well as ethical issues, such as discussions about fair chase (Loker and Decker 1995).

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LITERATURE CITED

Bernes, C. 1994. Biologisk mångfald i Sverige; en landstudie. Naturvårdsverket Förlag, Solna, Sweden. [In Swedish.]

Bjärvall, A. 1990. The brown bear in Sweden. Aquilo, Serie Zoologica 27: 17–19.

Craighead, J. J., F. C. Craighead, Jr., and H. E. McCutchen. 1970. Age determination of grizzly bears from fourth premolar tooth sections. Journal of Wildlife Management 34:353–363.

Derocher, A. E., I. Stirling, and W. Calvert. 1997. Male-biased harvesting of polar bears in western Hudson Bay. Journal of Wildlife Management 61:1075–1082.

Fujita, R. 2000. Bait-hunting for brown bear in Sweden: temporal and spatial occurrence and potential effects on the population. Thesis, Agricultural University of Sweden, Uppsala, Sweden.

Kindberg, J., and J. E. Swenson. 2006. Populationsberäkning av björnstammen i Sverige 2005. Report No. 2006–2. Scandinavian Brown Bear Research Project, Ås, Norway. [In Swedish.]

Kohlmann, S. G., R. L. Green, and C. E. Trainer. 1999. Effects of collection method on sex and age composition of black bear (Ursus americanus) harvest in Oregon. Northwest Science 73:34–38.

Litvaitis, J. A., and D. M. Kane. 1994. Relationship of hunting technique and hunter selectivity to composition of black bear harvest. Wildlife Society Bulletin 22:604–606.

Loker, C. A., and D. J. Decker. 1995. Colorado black bear hunting referendum: what was behind the vote? Wildlife Society Bulletin 23:370–376.

Manel, S., E. Bellemain, J. E. Swenson, and O. François. 2004. Assumed and inferred spatial structure of populations: the Scandinavian brown bears revisited. Molecular Ecology 13:1327–1331.

Martínez, M., C. Rodríquez-Vigal, O. R. Jones, T. Coulson, and A. San Miguel. 2005. Different hunting strategies select for different weights in red deer. Biology Letters 1:353–356.

McLellan, B. N., F. W. Hovey, R. D. Mace, J. G. Woods, D. W. Carney, M. L. Gibeau, W. L. Wakkinen, and W. F. Kasworm. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management 63:911–920.

McLellan, B. N., and D. M. Shackleton. 1988. A comparison of grizzly bear harvest data from Montana and southeastern British Columbia. Wildlife Society Bulletin 16:371–375.

Miller, S. D. 1990. Population management of bears in North America. International Conference on Bear Research and Management 8:357–373.

Milner, J. M., E. B. Nilsen, and H. P. Andreassen. 2006. Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:36–47.

Mysterud, A., P. Tryjanowski, and M. Panek. 2006. Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right place. Biology Letters 2:632–635.

Naturvårdsverket. 2000. Åtgärdsprogram för bevarande av björn (Ursus arctos). Swedish Environmental Protection Agency, Stockholm, Sweden. [In Swedish.]

Nordisk ministerrådet. 1984. Naturgeografisk regionindelning av Norden. Berlings, Arlöv, Sweden. [In Swedish.]

Noyce, K. V., and D. L. Garshelis. 1997. Influence of natural food abundance on black bear harvests in Minnesota. Journal of Wildlife Management 61:1067–1074.

R Development Core Team. 2006. R: a language and environment for statistical computing. <http://www.R-project.org>. Accessed 17 Aug 2007.

Sandegren, F., and J. E. Swenson. 1997. Björnen, viltet, ekologin och människan. Svenska Jägareförbundet, Spånga, Sweden. [In Swedish.]

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

Swenson, J. E., F. Sandegren, and A. Söderberg. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. Journal of Animal Ecology 67:819–826.

Swenson, J. E., P. Wabakken, F. Sandegren, A. Bjärvall, R. Franzén, and A. Söderberg. 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. Wildlife Biology 1:11–25.

Zedrosser, A., E. Bellemain, P. Taberlet, and J. E. Swenson. 2007. Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. Journal of Animal Ecology 76:368–375.

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