

1 **Evaluation of winter population density estimates of**
2 **moose (*Alces alces*) – a long-term study**

3

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24

1 **Abstract**

2 Different census methods are used to monitor and manage ungulate populations and the
3 choice of optimal method depends on accuracy of estimates, objective of management,
4 and economical constraints. Here we compare estimates of population size and
5 development between four different methods (aerial counts, hunter observations, pellet
6 group counts and a reconstruction of the population from shot moose with known age).
7 A Swedish moose population was studied between 1973-2005 in the Grimsö Wildlife
8 Research Area (135 km²). The highest correlation was found between the
9 reconstruction and the aerial counts ($r = 0.69$, $P < 0.05$) and the hunter observations and
10 the aerial counts ($r = 0.76$, $P < 0.10$). The pellet group counts showed low correlations
11 with the other methods probably because prior to 1997 the sample plots were located
12 within a small part of the research area and the moose were shown to use different parts
13 of the research area in different years. The analysis showed that there was considerable
14 immigration of males during a five-year period in the late 1970's when a local hunting
15 strategy with large proportion of shot males was implemented. We conclude that a
16 combination of methods is important to use for accurate monitoring of ungulate
17 populations.

18

19

20 **Introduction**

21 A successful management of wildlife populations requires knowledge about the status
22 and trends of the managed population, which should be obtained from some kind of
23 census. An effective monitoring system within the management and decision making
24 includes reliable data on the number of animals, growth rate, sex and age composition,
25 and reproduction. Over the years several different census methods have been used to

1 monitor ungulate populations, including aerial surveys, pellet group counts, direct
2 observations (e.g. hunter observations and drive counts), hunters' harvest statistics and
3 snow track counts (Timmerman 1974, Mayle 1999, Solberg & Sæther 1999). Three of
4 these methods are commonly used within the Fennoscandian moose management;
5 aerial surveys, pellet group counts and hunter observations (Haagenrud et al. 1987,
6 Lavsund et al. 2003).

7

8 Aerial surveys are the dominating monitoring method in Sweden (Haagenrud et al.
9 1987). It easily covers large and remote areas and provides data on number of animals,
10 sex ratio and number of calves per female (Haagenrud et al. 1987). However, the
11 method is costly and demands trained personnel and good snow and weather
12 conditions, which often restrict the use of aerial surveys (Timmerman 1974, Mayle
13 1999, Barnes 2001).

14

15 Hunter observations are provided by questionnaire reports from Swedish moose
16 hunters. Hunters are asked to report their moose observations, the number of active
17 moose hunters per day and the time (hours) spent hunting moose per day during the
18 first week of the hunting season. This gives an index of population size in terms of the
19 number of moose observations per hunter day but also sex ratio and reproduction
20 (calves per cow) (Haagenrud et al 1987, Ericsson & Wallin 1999, Solberg & Sæther
21 1999). This method has been used mainly in areas larger than 500 km² (Sylvén 2000).

22

23 Pellet group counts are a widely used method in the management of deer populations
24 (Neff 1968, Timmermann 1974, Mayle 1999). The accuracy of this method has been
25 questioned (Fuller 1991; White 1992; Fuller 1992), but several studies have also shown

1 realistic estimates and consistency in population trends and size between different
2 independent methods (Neff 1968, Mandujano & Gallina 1995, McIntosh et al. 1995,
3 Barnes 2001). Pellet group counts provide indices that can be calculated into absolute
4 number of animals (Neff 1968, Timmerman 1974, Mayle et al. 1999). However,
5 reliable interpretation of absolute numbers requires estimates of the rate of defecation
6 (i.e. number of pellets groups produced per individual and day) and knowledge about
7 the total time period of pellet accumulation. However, the defecation rate of moose
8 varies between studies and seems to depend on the type of habitat, forage quality, and
9 forage composition (Neff 1968, Andersen et al 1992). A variation in defecation rate has
10 a large impact on the calculated absolute number of individuals in an area. However,
11 the transformation of pellet groups count index into absolute numbers is not only a
12 function of the defecation rate and the time of pellet accumulation but also depend on
13 the detectability and rate of decomposition during the time of accumulation (Persson
14 2003).

15

16 Data from the three different monitoring techniques presented in this paper differ in
17 precision, accuracy, assumptions, costs and gained information. For example, pellet
18 group counts do not provide demographic information as aerial counts do, but pellet
19 group counts are instead less affected by weather and a less expensive method
20 compared to aerial counts. Further, the pellet group count reflects the moose population
21 during the entire period between leaf fall and the date of census, whereas the aerial
22 count gives an instantaneous view of the size and distribution of the moose population
23 (Leresche & Rausch 1974, Timmerman 1974, Jordan & Wolfe 1980, Ericsson &
24 Wallin 1999, Barnes 2001, Campbell et al. 2004). These differences make it difficult in

1 a cost effective manner to select the most suitable method for management and it is
2 therefore important to further evaluate the accuracy of methods.

3

4 Cohort analyses have previously been used to study moose population dynamics
5 (Fryxell et al. 1988, Ferguson 1993, Solberg et al. 1999). A reconstructed population
6 using cohort analysis may give a reliable estimation of the number of moose in an area
7 where harvest is the main cause of mortality, as the moose population is in Sweden
8 (Cederlund & Markgren 1987). Thus, by using a cohort analyses an independent
9 estimate of population size and development, comparisons can be done with other
10 methods in order to further evaluate the accuracy of different methods.

11

12 The objectives of this study was to combine information from several census methods
13 in a long-term study to i) improve our understanding of the accuracy, concordance and
14 usefulness of these methods, and ii) improve our understanding of the population
15 development within the study area in terms of animal numbers, age-sex structure and
16 migration.

17

18 Estimates obtained from reconstruction of the moose population are compared to the
19 three other census methods (aerial counts, pellet group counts and number of moose
20 observations per hunter day) with data collected over a thirty-year period in the 135
21 km² large Grimsö Wildlife Research Area. Age-specific natural mortality was
22 estimated from radio-collared moose in order to provide input parameters important to
23 the reconstruction of the moose population. By comparing methods we also estimated a
24 conversion factor for transforming pellet group counts into aerial counts and evaluate
25 the importance of migration as a contributing factor to population development.

1

2 **Material and Methods**

3 **Study area**

4 The 135 km² Grimsö Wildlife Research Area, located in the south-central Sweden
5 (59°5'N, 15°5'E), is a rugged plateau with elevations ranging from 100 to 150 m above
6 sea level and composed of low flat ridges with till and boulders interspersed with bogs
7 and swamps. The area consists of 72% forests, 18% bogs, 7% lakes and rivers, and 3%
8 meadows and farmlands. Mature forest stands are dominated by Scots pine (*Pinus*
9 *silvestris*), Norway spruce (*Picea abies*), and birch (*Betula pubescens* and *B.*
10 *pendula*). Rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), and willows (*Salix*
11 spp.) are preferred moose browsing species that rarely occur within the stands. Forest
12 management is intensive with clear-cutting of 3-10 ha patches and old forest replaced
13 by planting. The period of rotation in the forest stands are is 80-100 years. Early
14 succession after logging consists of birch, aspen and willow with an under-story of
15 common hair grass (*Dechampsia flexuosa*), bilberry (*Vaccinium myrtillus*), cowberry
16 (*Vaccinium vitis-idea*), and heather (*Calluna vulgaris*). Climate is typical of inland,
17 central Sweden, with winter temperatures down to -20° C and summer temperatures up
18 to 25° C and mean daily temperature in July is 16.3° C and -4.4° C in January,
19 respectively. Snow cover is normally present from December to March with a mean
20 snow depth of 25-30 cm in February. Annual precipitation averages 670 mm with peak
21 values in July (average=86 mm) (Swedish Meteorological and Hydrological Institute).

22

23 **Calf and adult survival**

24 The survival rates and causes of mortality other than hunting were estimated using
25 radio-collared moose (both adults and calves). During 1980 to 2000, 63 adult females

1 and 44 adult males were captured and equipped with radio collars. Radio tracking was
2 normally performed once a week (Cederlund & Lemnell 1979). For further details on
3 adult moose tagging see Cederlund et al. (1989).

4

5 Calf survival rates were estimated by observing radio-collared moose cows and
6 counting their calves at different occasions during the year, and also by using radio-
7 collared calves. Newborn calves (1-10 days old) were captured from ground within
8 Grimsö Wildlife Research Area between 1993 and 2001. See Ericsson et al. (2001) for
9 further details on moose calf tagging.

10

11 **Reconstruction from harvest data**

12 Since 1973 the number of moose shot each year within the Grimsö Wildlife Research
13 Area has been recorded. The data used in the present study included 2065 observations
14 of shot animals of known sex and age. Another 53 moose (2.5%) were shot in the
15 research area but were excluded from further analyses due to missing information on
16 age or sex.

17

18 **Aerial counts**

19 Between the years 1977 to 2006, the size of the moose population in the Grimsö
20 Wildlife Research Area was estimated by aerial counts from helicopter at 12 occasions.
21 The method used 1977 to 2002 was total counts of moose based on line-transect
22 surveys with 300 m between line transects (LeResche & Rausch 1974, Tärnhuvud
23 1988). The surveys were performed in winter after the moose hunt and prior to the
24 calving period and only during good snow conditions 1-2 days after snow fall and with
25 at least 20-40 cm snow cover and temperature below 0° C. In 2006 an aerial count was

1 performed as a sample of the research area including 15 plots of 2 by 2 km (equal to
2 44% of the research area). A correction factor for sightability in 2006 was achieved by
3 applying a mark-recapture procedure of plots that were surveyed twice by using two
4 different helicopters and observers. The first helicopter to survey a plot worked along
5 north-south transects and positioned all moose observations by GPS. These
6 observations were treated as marked moose. The second helicopter repeated the survey
7 along east-west transects as soon as the first helicopter left the plot (recapture). The
8 total number of observed moose was achieved as:

$$9 \quad N_{obs} = obs_c + \frac{obs_1 + obs_2}{2}$$

10 Where obs_c is the number of moose seen by both observers, obs_1 is the number of
11 moose seen only by the first observer and obs_2 is the number of moose seen only by the
12 second observer. To get the best estimate of the number of observed moose in a
13 surveyed plot the mean of obs_1 and obs_2 was used. The “true” number of moose in the
14 surveyed plots was then achieved using standard capture-recapture methods following
15 Seber (1982) and Krebs (1999):

$$16 \quad N_e = \frac{(M+1)(C+1)}{(R+1)} - 1$$

17 where N_e is the estimate of the population at time of marking, M is number of marked
18 individuals in the first sample (obs_c+obs_1), C is the total number of individuals captured
19 in the second sample (obs_c+obs_2) and R is number of individuals in the second sample
20 that are marked (obs_c). The sightability factor (S) was estimated as:

$$21 \quad S = N_{obs}/N_e$$

22 The sightability factor was estimated from an expanded survey covering more than the
23 Grimsö Wildlife Research Area (42 surveyed plots and 244 moose observations).

24

1 **Moose observations**

2 Between 1984 and 2005 the number of moose observed by each hunter during the first
3 week of the regular hunting season was recorded within the research area. This method
4 has been widely used in both Sweden and Norway since the mid 1980's as an index of
5 moose population size (Jaren 1992, Ericsson & Wallin 1999, Solberg & Saether 1999)
6 and is based on the assumption that a change in observation rate per time unit reflects a
7 true change in the population. Each observation of an individual moose is recorded as
8 adult male, adult female without calves, adult female with one calf, adult female with
9 two calves, lone calf, or moose of unknown status. In this study the data is presented as
10 the number of moose observations per day per hunter (Table 1).

11

12 **Pellet group survey**

13 Since 1977 moose pellet group surveys were carried out annually on the research area.
14 From 1977 to 1998 only the south-eastern part of the research area (approximately 20%
15 of the total research area) was used. Permanent squares (5x10 m) were distributed 100
16 m apart along transects with 200 or 400 m between the line transects. The number of
17 squares included in the survey was approximately 400, except for the first two years
18 when only 175 and 209 were counted (Table 1).

19

20 In 1997 an additional moose pellet group survey was commenced (hereon named *new*
21 *pellet group survey*). This new survey included 32 permanent squares 1 by 1 km
22 systematically distributed over the total research area. Each square had permanent 20 (5
23 along each side) circular sample plots of 100m² (Figure 1). The survey included in total
24 600 sample plots.

25

1 For both moose pellet group surveys all sample plots were annually checked and
2 cleaned from all moose pellet groups in the fall (early October) and the number of new
3 pellet groups were counted in the spring (late April to early May). Thus, we received
4 data on the number of new pellet groups produced by moose during a specific time
5 period (i.e. no. of days) during the winter season.

6

7 **Reconstruction of the moose population**

8 The moose population size and composition during 1973-2005 was reconstructed from
9 data collected from animals shot within the research area during the same period. The
10 maximum age recorded for shot females and males was 21 years and 13 years,
11 respectively. Therefore, all males born before 1990 and all females born before 1984,
12 were assumed to have died before the end of the study period. These are the *complete*
13 *cohorts*, whereas male cohorts born after 1990 and female cohorts born after 1984 are
14 referred to *not complete cohorts* below. For animals shot between 1973 and 1990, 99%
15 of the females were shot before the age of 15 years and 99% of the males were shot
16 before the age of 7 years (Figure 2).

17

18 Complete cohorts

19 Following the method developed by Fryxell et al. (1988) and extended by Solberg et al.
20 (1999) we reconstructed the complete cohorts for each sex separately from the
21 following equation (eq (2) in Fryxell et al. (1988)):

22

$$23 \quad N_{i,t} = (N_{i+1,t+1} / p_i + K_{i,t}) \quad (1)$$

24 where

25 $N_{i,t}$ = no. of animals of age i year t

1 p_i = age specific survival

2 $K_{i,t}$ = no. of animals shot aged i year t

3

4 The number of animals in each sex-age class was then calculated by using equation (1)
5 recursively with $N_{i,t} = K_{i,t}$ for males in age class $i = 13$ and for females in age class $i =$
6 21. The adequacy of this method assumes that there is a maximum age beyond which
7 no animals survive, that age-specific survival is known and constant over years, and
8 that the population is closed with no migration (Fryxell et al. 1988).

9

10 Not complete cohorts

11 The expected number of animals born before 2005, and to be shot after 2005, was
12 calculated

13 following Solberg et al. (1999). Hence, the expected number of animals to be shot in
14 the future was predicted from sex-specific curves of cumulative proportions shot
15 (Figure 2). The number of animals in each cohort born after 1990 was then calculated
16 from the observed numbers shot within the cohort and the expected number to be shot
17 in the future using equation (1).

18

19 The estimates of the expected number of animals to be shot in the future assumes a
20 constant hunting effort on the population among years and also that there has not been
21 a shift in hunting strategy. During the years 1984 to 1998 (where complete data on total
22 number of hunter days was available) the number of hunter days was proportional to
23 the reconstructed population size ($\ln(\text{hunter days}) = 0.97\ln(\text{population size})$, SE =
24 0.008). It was therefore concluded that the hunting effort was constant. The hunting
25 strategy, however, changed around the year 1982 from a male biased hunting strategy

1 to a strategy for an even sex ratio. Consequently, the sex-specific curves of the
2 cumulative proportion shot were therefore different before and after 1982, but in a
3 preliminary analysis these differences did not show any considerable changes in the
4 reconstruction. The sex-specific curves of cumulative proportion shot were therefore
5 estimated for all years from 1973 to 1990 where complete cohort information is
6 available.

7

8

9 **Statistical analyses**

10 The probability of calf survival was modelled with logistic regression. Calves from the
11 same mother were treated as repeated measurements. Proc Genmod in SAS was used
12 for the analysis. The explanatory variables included were; age = the age of the mother
13 in years; $age^2 = age * age$; yr = the birth year of the calf; $yr^2 = yr * yr$; twin = binary
14 dummy variable equal to 1 if the calf was born as a twin and 0 otherwise. Sex was not
15 included as a possible explanatory variable because this character was not always
16 determined during capture.

17

18 Adult survival was analyzed with Cox regression and possible differences between
19 sexes and cohorts were tested. The survival library in the statistical package R
20 (<http://www.r-project.org>) was used for these analyses. Life histories of shot or lost
21 moose were treated as right censored, since the focus of the analysis was on natural
22 mortality.

23

24 The new pellet group counts of moose were analyzed in order to gain an understanding
25 of the geographical distribution of moose density within the research area. The number

1 of pellet groups per sample plot was analyzed as a dependent variable in a generalized
 2 linear model with log link function (i.e. a log-linear model). The explanatory variables
 3 were year (class effect), four sub-regions (class effect) and the interaction of year and
 4 sub-region (class effect). In a preliminary analysis the distance from the mid-point of
 5 the research area was also included as covariate. The four sub-regions correspond to the
 6 four large quadrates (NE,SE,SW,NW) in Figure 1. The GLM library in the statistical
 7 package R (<http://www.r-project.org>) was used for these analyses and P-values were
 8 based on likelihood ratio tests.

9
 10 A calibration between the aerial counts and pellet group counts was estimated where
 11 the daily defecation rate per moose was estimated from the population size obtained
 12 from the aerial counts in the years 2002 and 2006 together with the number of pellet
 13 groups counted in these two years. These were the only two years for which estimates
 14 from the entire research area from both aerial counts and pellet group survey were
 15 available. The estimates were obtained as $x/(yz)$ where x is the estimated number of
 16 pellet groups in the area, y is the estimated number of moose, and z is the mean number
 17 of days that the pellets have been accumulated between early October to late April. The
 18 variances (V_x , V_y and V_z) of the three estimates (x , y and z , resp.) used in the formula
 19 were combined using the delta-method (Casella & Berger 2001) to obtain a standard
 20 error of the daily defecation rate:

$$21 \quad SE = \sqrt{\left(\frac{1}{yz}\right)^2 V_x + \left(\frac{x}{y^2 z}\right)^2 V_y + \left(\frac{x}{yz^2}\right)^2 V_z} \quad (2)$$

22 The aerial count is a snapshot of the population size during one day in late winter,
 23 whereas the pellet group counts give accumulation of pellets over the whole winter. In
 24 the calculations of V_y it was assumed that the animals observed in the central parts of
 25 the research area (more than 1 km from the border) were within the area the whole

1 winter, whereas those closer to the border could move randomly over the border. It was
 2 also assumed that the population density was the same on both sides of the border.

3 Hence, V_y was equal to the number of animals less than 1km from the border.

4

5 Time series analysis

6 A correlation analysis was performed to compare the similarities between the estimates
 7 of moose density. The pairwise comparisons were based on a variable number of years
 8 because the different methods started at different times during the total study period.

9

10 The time series of moose population density were compared pairwise. The time series
 11 $y_1(t)$ and $y_2(t)$ were analyzed as two random walks around the means μ_1 and μ_2 . The
 12 modelled random walks $u_1(t)$ and $u_2(t)$ included an auto-correlation with a one year
 13 time lag such that:

$$14 \quad \begin{aligned} u_1(t) &= r_1 u_1(t-1) + \varepsilon_1(t) \\ u_2(t) &= r_2 u_2(t-1) + \varepsilon_2(t) \end{aligned} \quad (3a)$$

15 and

$$16 \quad \begin{aligned} y_1(t) &= \mu_1 + u_1(t) \\ y_2(t) &= \mu_2 + u_2(t) \end{aligned} \quad (3b)$$

17 where r_1 and r_2 are the two auto-correlation coefficients, and the residuals ε_1 and ε_2 are
 18 normally distributed with variances σ_1^2 and σ_2^2 , respectively. The residuals are
 19 independent between years and within time series, but correlated between time series
 20 for common t :

$$21 \quad Cov(\varepsilon_1(k), \varepsilon_2(l)) = \begin{cases} \rho \sigma_1 \sigma_2 & \text{for } k = l \\ 0 & \text{for } k \neq l \end{cases} \quad (4)$$

22 where ρ is the cross-correlation between the time series, which is a measure of
 23 dependency between the two time series. Note that if there is no auto-correlation then
 24 ρ is simply the correlation between $y_1(t)$ and $y_2(t)$.

1

2 The maximum likelihood estimates of m_1 , m_2 , σ_1^2 , σ_2^2 , r_1 , r_2 and ρ were obtained with
3 Fisher scoring (Pawitan 2001). The main parameter of interest is ρ and we, therefore,
4 tested the null hypothesis $\rho = 0$ with a likelihood ratio test. This analysis was not
5 performed on the aerial counts since there were several years between each count and
6 the effect of auto-correlation could therefore be ignored. Furthermore, the number of
7 years was too few in which both the old and the new pellet group surveys were
8 performed for a time series analysis.

9

10 **Results**

11 **General**

12 Moose harvest in the research area increased dramatically during the 1970's and
13 peaked in 1982 with harvest rates more than four times higher compared to 1973
14 (Figure 3). In the late 1970's a local hunting strategy within the research area was
15 applied with the objective to reduce the number of adult males per female in the living
16 population. Thus, harvest of adult males exceeded the harvest of adult females by 5 to 6
17 times during 1976-1983. Since 1984 sex ratio of harvested adult animals has been
18 relatively stable averaging 51.5% males and 48.5% females among years and the
19 proportion of calves of all harvest moose has been around 54 %.

20

21 **Survival analysis**

22 Calf survival

23 In the years 1993 to 2001, 85 marked calves (27 females, 37 males and 21 calves with
24 unknown sex) from 32 different females were checked for survival from August to
25 April. Nineteen (22.3%) of the calves were born as twins. Nine of the 85 (10.6%)

1 calves died of natural causes during their first winter (Table 2) resulting in an average
2 survival of 0.89 for all calves. Survival was not significantly related to birth year, birth
3 year², twin or single, age of mother or age of mother² (P>0.2).

4 5 Adult survival

6 During the total study period each radio collared male moose were followed for on
7 average of 2.4 (S.D. 1.8) years and female moose for 5.6 (S.D. 3.6) years. Mean age of
8 all radio collared males and females was 4.8 (S.D. 2.9) and 9.9 (S.D. 5.3) years,
9 respectively, whereas the maximum age for males and females was 12 and 21 years,
10 respectively. In the spring of 2005, none of the males and 9 females were still alive. In
11 total, 68% of the males were shot during the hunting season, 18% died of natural
12 causes, and contact were lost for 14% of the collared moose due to malfunctioning of
13 radio-collars. Among females, 48% were shot during the hunting season, 30% died of
14 natural causes, 8% were lost from the study for unknown reasons (possibly due to
15 malfunctioning of radio-collars) and 14% were still alive in the spring of 2006.

16
17 Survival analyses, excluding harvest-related mortality of adult moose, showed that
18 there were no significant effects of birth year (P=0.25), and no significant differences
19 between the sexes (P=0.22). Thus, survival was analysed for males and females
20 combined (Figure 4). The survival rate for both sexes combined corresponds
21 approximately to an age-specific survival of: 0.95 for 1- to 13-year-olds, 0.9 for 14-
22 year-olds, 0.85 for 15-year-olds and 0.6 for older animals (Figure 4).

1 **Reconstruction**

2 Reconstruction of the moose population in the research area showed that the population
3 size changed from an all time low in 1973 with 0.5-0.6 moose per km² to a peak in
4 1981 with 1.9 moose per km² (Figure 5). After 1981 the moose population decreased
5 continuously during the 1980's and 1990's reaching a level of approximately 0.7-0.8
6 moose per km² in the late 1990's and early 2000's. The pattern of a sharp increase
7 during the 1970's and a somewhat slower decline in the late 1980's follow the general
8 pattern of the Swedish moose population (Cederlund & Markgren 1987, Lavsund &
9 Sandegren 1989).

10

11 **Comparison of population density estimates among methods**

12 Population density

13 Aerial counts did not show the same strong increase during the 1970's as compared to
14 the reconstruction estimates. However, aerial counts did not start until 1977 and the
15 first year produced a relatively high estimate compared to aerial counts in the two
16 following years. Despite the lack of consistent pattern in the late 1970's a significant
17 correlation between the aerial counts and the reconstructed population size was found
18 for the period 1977-2002 (n=11, P = 0.02; Table 3). The estimated correlation between
19 hunter observations and the aerial counts was also high ($r=0.76$) but non-significant
20 (n=6, $P<0.10$). However, estimates from these two methods were comparable for only
21 6 years. All other correlations between time-series estimates were low and non-
22 significant, indicating that aerial counts, reconstruction, and hunter observations were
23 estimates of population density that are more similar than other estimates (pellet
24 surveys).

25

1 The time-series calculated with the reconstruction method showed high auto-
2 correlation (Table 3), which was expected since the calculation of year-specific
3 population size in the reconstruction depends on the population size in the previous
4 year. The hunter observation data also showed high auto-correlation (Table 3), which
5 was more surprising since there is no mathematical connection between estimates in
6 two consecutive years for these data.

7

8 Correction factors for sightability

9 The aerial counts performed 2006 gave an estimate of 73% (S.D. 0.03) of the animals
10 in the population being observed during the aerial survey. This corresponds relatively
11 well with the average proportion of animals with radio collars observed in previous
12 aerial counts (0.67, S.D. 0.22, Table 1). It is therefore likely that the aerial counts prior
13 to 2006 underestimated the true population size, and that the correction factors
14 suggested by Tärnhuvud (1988) generally produced underestimates of the true
15 population size.

16

17 Estimated defecation rate

18 The daily defecation rate was estimated from the aerial survey and pellet group counts
19 in the years 2002 and 2006. The number of moose within the research area estimated
20 from the aerial counts was 225 and 163, in 2002 and 2006 respectively. The variance of
21 the mean winter population size (V_y in eq. (2)) was calculated given the proportion of
22 animals <1 km within the border. This proportion was 0.32 in 2002, whereas for 2006
23 the yearly average (1977-2002, Table 1) 0.427 was used. The estimated variances were
24 then 72 and 69 in the years 2002 and 2006, resp. The estimated total number of pellet
25 groups within the research area was 638,500 (S.D. 1441) and 440,100 (S.D. 1218). The

1 number of days that the pellet groups had accumulated was 197 (S.D. 5.0) and 202
2 (S.D. 7.1) in the years 2002 and 2006, respectively. This resulted in a daily defecation
3 rate of 14.41 (S.E. 0.71) and 13.36 (S.E. 0.83) for the years 2002 and 2006,
4 respectively.

5

6 **Old and new pellet group counts**

7 Data from the older pellet group survey was obtained from the south-eastern quadrat
8 of the research area whereas the newer pellet group survey includes sampled squares
9 throughout the entire research area (Figure 1). Therefore it was possible to test whether
10 the south-eastern sub-region was a representative part of the research area. This was,
11 however, not the case. The moose density varied significantly ($P < 0.001$) between
12 different sub-regions (Figure 8), which is likely to explain the poor correspondence
13 between the old pellet group survey and the other three measures of moose density
14 (Figure 5), and also the poor correspondence between the old and the new pellet group
15 survey in 1997 and 1998 (Figure 5). In the same analysis, we found no evidence
16 ($P = 0.2$) for the moose density to increase (or decrease) in the peripheries of the
17 research area, which means that the border effects is not greater (nor less) than could be
18 expected from the size of the research area. The deviance divided by the degrees of
19 freedom in the log-linear model was close to one (1.3) indicating that the number of
20 pellet groups was randomly distributed throughout the research area (after adjusting for
21 the class effects of year, sub-region, and the interaction of year and sub-region).

1 **Sensitivity analysis of reconstruction**

2 Assumption of no migration

3 During the years 1976 to 1983, an excess of male adults were shot. Contrary to what
4 was expected, however, the proportion of adult males was unrealistically high during
5 the years 1973 to 1980 in the reconstruction analysis (Figure 6).

6

7 Estimated survival

8 The estimated reconstruction was found to be sensitive to the estimated age-specific
9 survival of females older than 15 years, previously estimated to 0.6. This parameter
10 was estimated from the survival analysis of radio-collared moose and had relatively
11 large standard errors (Figure 4). A change in the age-specific survival of old females
12 from 0.6 to 0.5 resulted in a change in the maximum density in 1981 from 19.0 to 22.8
13 moose per 1000 ha, whereas an increase in old female survival from 0.6 to 0.7 results
14 in a lowered density in 1981 to 17.6 moose per 1000 ha.

15

16 Hence, the population density in 1981, calculated from the reconstruction, was
17 sensitive to the age-specific survival of old females. This sensitivity was mainly caused
18 by one female born in 1979 and shot at the age of 21 years in the year 2000. In the
19 reconstruction analysis, this single female corresponds to 54 calves born in 1979 when
20 the age-specific survival of old females is 0.6, and to 163 calves born in 1979 if the
21 same age-specific survival is 0.5. If we would calibrate this parameter given the
22 population size estimated from the aerial counts, then the age-specific survival of old
23 females would be 0.52.

1 Estimates for incomplete cohorts

2 After 1990, the reconstruction of the moose population was based on incomplete
3 cohorts and the precision of the estimated moose density therefore declines towards the
4 end of the study. For the complete cohorts an additional female calf shot increases the
5 total number of females by one, whereas if an additional female calf was shot in the
6 cohorts born after the year 2002 the total number of females increased by 1.5. Thus, the
7 estimates were concluded not to be sensitive to the number of calves shot.

8
9 We also studied how a small change in the cumulative proportion shot (Figure 2)
10 affected the reconstruction results. If the cumulative proportion shot was decreased by
11 one percent unit for all ages up to the age of 10 years, then the estimated number of
12 females increased by 1% in year 1997, 4% in year 2002 and 5% in year 2005. It was,
13 therefore, concluded that the estimates of the population density in the year 2002 and
14 later was especially sensitive to the cumulative proportion shot and that the
15 reconstruction results may, therefore, be less accurate after the year 2002.

16

17 **Discussion**

18 In this paper we compared and evaluated the results from four different methods of
19 estimating moose density in a long-term study of one moose population: aerial counts,
20 reconstruction from harvest data, pellet group survey, and hunter observations. All
21 methods used gave similar results regarding the size and development of the moose
22 population during the thirty-year period in our study area. This included a low initial
23 population size expressing a fast growth with a peak in the early 1980's with a
24 subsequent slower decline during the mid 1980's and 1990's to an intermediate size in
25 the early 2000th. However, different methods gave somewhat different absolute

1 estimates of the population size and of the population development during the last 10
2 years of the study. By comparing the results between these methods some general
3 conclusions for each of the four methods can be drawn.

4

5 *Aerial counts*

6 Aerial counts provide absolute estimates of population size at a certain time point
7 during the annual population cycle. This method may yield estimates of high accuracy
8 given that relevant correction factors for the proportion of non-observed moose are
9 available. A number of studies in North America have provided a wide range of
10 estimates of sightability (mean: 0.71, range: 0.38-0.97; Timmermann 1993), or a
11 sightability correction factor (SCF) (1.03-2.60) among studies, and this estimate is
12 known to be dependent on a number of factors such as the type of aircraft (helicopter or
13 fixed wing), type of forest, moose density, experience of crew, and snow and weather
14 conditions (Timmermann & Buss 1998).

15

16 Based on a number of aerial counts from different areas including radio collared moose
17 in Sweden during the 1980's Tärnhuvud (1988) suggested correction factors that
18 mainly were based on the type of weather conditions during aerial counts. However,
19 the average proportion of radio-collared moose observed (67%) of the total number
20 present within the study area ($n_{\text{total}} = 82$) during aerial counts over a number of years
21 were clearly lower than estimates presented by Tärnhuvud (1988) for good (95%) and
22 intermediate (84%) snow conditions using a helicopter with experienced personnel.
23 This is also corroborated by the fact that the sampling-resampling technique used at the
24 end of the study period (2006) provided estimates of sightability (73%) that
25 corresponded well with the average proportion of radio collared moose observed over

1 the whole period. We conclude that general application of sightability estimates should
2 be avoided and that area and census specific estimates should be developed.

3

4 *Cohort analyses*

5 Reconstruction of historical population size can be a good complement for analyzing
6 trends in population development. However, this method depends on a number of
7 assumptions and requires independent estimates of natural mortality in the study
8 population. Unlike most other moose populations, natural mortality could be estimated
9 from radio collared animals for this study population but was biased towards young and
10 mid-aged individuals. Unfortunately, reconstructed population size showed to be very
11 sensitive to survival estimates among old females (>15 years), resulting in relatively
12 large confidence intervals for this age class, and thus contributing to uncertain
13 estimates of population size.

14

15 Also, this method rests on the assumption of no net immigration or emigration, an
16 assumption that showed to have been violated in the current study during the initial
17 phase of the study period due to seasonal immigration of males during the mating- and
18 harvest season. However, this was likely a result of an extreme harvest strategy aiming
19 to drastically reduce the male segment of the adult moose population. Nevertheless, if
20 no aerial counts have been performed during this period erroneous conclusion about
21 population size (in Figure 5) and the adult sex ratio (in Figure 6) may have been drawn.

22

23 Furthermore, a reconstruction analysis is difficult to use as a management tool since the
24 estimates of population size in the most recent years are the ones most uncertain. In our
25 dataset, complete cohorts of the population could be reconstructed only up to 1990 with

1 the decreasing precision of estimated population size after this year. However,
2 sensitivity analyses of how a change in the cumulative proportion of animals shot
3 affected more recent estimates showed that estimates of the model population size were
4 relatively robust up to 2002, i.e 4 years previous to analyses of data.

5

6 *Reasons for differences between aerial counts and cohort analyses?*

7 Estimates of population size from the reconstruction yielded consistently lower
8 estimates than aerial counts corrected for a sightability of 70%. A number of
9 explanations may be invoked to explain this difference. Seasonal migration into the
10 study area during the winter season may have resulted in higher winter estimates
11 compared to reconstruction. However, earlier studies of radio-collared moose do not
12 support this explanation (Cederlund & Sand 1991, Cederlund & Sand 1994). Stochastic
13 annual variation in moose population distribution along the border of the research area
14 might have resulted in variable estimates of population size between years but is
15 unlikely to consequently result in higher estimates as received from aerial counts unless
16 seasonal migration is a common behaviour in the moose population. A third
17 explanation may be that sightability of moose during aerial counts was underestimated.
18 This is also unlikely because sightability from both radio collared moose and the
19 sampling-resampling technique give strong support for an average sightability close to
20 70%. Another possibility is that double counting of individual moose were an extensive
21 and a recurrent phenomenon during aerial counts covering the total study area i.e. all
22 aerial counts except in 2006. In 2006 a sample of the research area were counted (2*2
23 km² squares similar to a chess pattern) which minimized the risk of double counting
24 individual moose. Although reliable estimates of population size from the
25 reconstruction for 2006 is not yet at hand and the accuracy of estimates is declining

1 towards the end of the study the population trend presented up to 2005 still suggests
2 higher estimates from aerial counts compared to reconstruction, i.e. data does not
3 support such an explanation. The only logical explanation that we could find for the
4 discrepancy between aerial counts and estimates from reconstruction is that the natural
5 mortality of radio collared moose has been overestimated and that reconstruction
6 estimates were sensitive to the existence of a few old shot females in the dataset.
7 Calibrating the reconstruction with the aerial counts corrected for a 70% sightability
8 gives a natural mortality of old females slightly less than 50% which is lower than the
9 average estimate for this age class but well within the confidence interval of the
10 survival analysis (Figure 4).

11

12 *Pellet group counts*

13 Pellet group survey may constitute a good method to analyse population trends but
14 merely gives an index of population density if not combined with an estimate of animal
15 defecation rate. Hence, accurate estimate of the species and population specific
16 defecation rate is required to achieve accurate estimates of population density.

17

18 Our results show that the defecation rate derived by comparing aerial counts and pellet
19 group counts in the field for specific years (14 pellet groups per moose and day) is
20 similar to, or in the lower range of, those reported for moose in captivity (Franzmann et
21 al. 1976, Oldemeyer & Franzmann 1981) and for some free-ranging populations
22 (Jordan & Wolfe 1980, Joyal & Ricard 1986, Andersen et al. 1992, Jordan et al. 1993).
23 Several authors (Andersen et al. 1992, Neff 1968, Person 2003) have shown that the
24 defecation rate may depend on the herbivore population structure and the amount and
25 quality of available forage. Therefore, pellet group surveys should be used with caution

1 in areas where the population structure or the availability of different browsing species
2 changes considerably between years or over time. In this study, moose population size
3 did not change dramatically between the two aerial estimates (2002 and 2006) when the
4 defecation rate was estimated. Nor did forestry practices or age distribution or
5 composition of forest stands change dramatically during this five-year period. This fact
6 may be an important cause of the high correspondence between the two estimates.

7

8 The old pellet group survey showed low correlation to other estimates of population
9 size but the overall trend, estimated as a three-year average, was similar to other
10 estimates. Our analysis of the data in the new pellet group survey points out the
11 importance of having sampling units distributed over the total study area.

12

13 The new pellet group survey indicated a constant population size in the years 1997-
14 2001 that was similar to the reconstruction and hunter observation data, but during
15 2002-2004 the new pellet group survey showed a peak that was not supported by the
16 other methods and could not be explained by our further analysis. One possible
17 explanation is that annual variation in forage quality may result in variable defecation
18 rates among years in the moose population. If true this will significantly reduce the
19 potential for using this method as a good estimate of both population size and trends.
20 Hopefully, the discrepancy with the reconstruction will become clearer in the future
21 when we more years are added to the reconstruction analysis and more reliable
22 estimates for these years are available.

23

24 *Hunter observations as a management tool*

25 Solberg & Saether (1999) and Sylvén (2000) have shown that hunter observations can

1 be a useful tool to moose population management, since several population measures
2 can be derived from these: population size index, sex ratio and recruitment rate. Sylvén
3 (2000), however, found that an area of 500 km² is needed to be able to use the hunter
4 observations as an accurate population index, whereas our results indicate that hunter
5 observations could also be a useful tool for estimating long-term population trends
6 even in smaller areas (130 km²).

7

8 Sylvén (2000) did not include spatial auto-correlation between hunter observations in
9 smaller areas. Hunting districts close to each other are more likely to have similar
10 observation statistics even though the area of each district is small. Our results indicate
11 that hunter observations can be useful over a long time period in moderately sized
12 areas, and if support could be gained from surrounding hunting districts then this
13 should be improved even further.

14

15 *Harvest strategy affected moose behaviour*

16 The most logical explanation for the combination of male biased shooting strategy in
17 the late 1970's and the high proportion of adult males found in the reconstruction
18 analysis is a substantial amount of male immigration into the area. A low proportion of
19 males within the research area could have induced an immigration of adult males
20 during the mating season, since there were more females available per male than in the
21 surrounding population. Some of these males were then likely to have been shot within
22 the research area (since the hunting season follows directly after the rut) and the
23 reconstruction analysis does not take immigration into account. Consequently,
24 immigrating males were assumed to be born within the research area, resulting in a
25 high proportion of males in the reconstruction analysis during years with immigration

1 and also in several years prior to the actual immigration. From the reconstruction
2 analysis it was concluded that over 80 adult immigrated males must have been shot
3 within the research area during the second half of the 1970's in order to have a
4 proportion of males equal to 0.5 in the population, as estimated from aerial counts. In
5 the years after 1980, however, no evidence for changes in net migration could be found
6 since the proportion of males was constant (Figure 6). Hence, this behavioural change
7 was caused by differences in the adult sex ratio within and outside the research area,
8 with fewer males per female inside the research area. This means that local harvest
9 policies may result in behavioural changes of individuals that may affect population
10 structure, demography, and harvest in adjacent populations.

11

1 **Conclusions**

2 Our results emphasize the importance of developing area-specific estimates of
3 sightability correction factors for aerial counts of moose. This could be done either by
4 using radio-collared moose or by using the sampling-resampling technique of sample
5 plots during field counts.

6

7 If pellet group counts should be used as a measure of population size and trends this
8 method should in some years be combined with aerial counts to estimate accurate rate
9 of defecation. Furthermore, pellet group counts should be distributed to cover the
10 whole study area so that inference of population size over the whole area can be made,
11 since the distribution moose in the local population may be variable among years.

12

13 Our results, also indicate that hunter observations can be used to follow long-term
14 population size development, even in relatively small sized management areas. A
15 management strategy resulting in a strongly skewed adult sex ratio may result in
16 behavioural changes of individuals that may affect population structure, demography,
17 and thus size of harvest in adjacent populations.

18

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17 change - a comment. - Journal of wildlife management 56: 611-612.

1 Table 1. Comparison of different survey methods in moose

	Aerial counts	Pellet group counts	Hunter observations
Sex structure	Yes	No	Yes
Reproduction (calf/cow)	Yes	No	Yes
Remote areas	Good	Harder ^a	Good ^b
Large areas >1000km ²	Good	Harder ^c	Good
Costs	Costly	Intermediate	Cheap
Absolute numbers	Yes	No	No
Surveyed time window	Snapshot	Entire winter period	Snapshot
Weather sensibility	High	Low	Low

2 ^a Accessibility – need of forest roads for transportation

3 ^b Surveys are conducted in areas where hunting takes place

4 ^c Short time period with good conditions i.e. many field workers needed during a short
5 period when surveying large areas

6

1 Table 2. Descriptive statistics for data used in estimating moose population size by: Aerial counts, Pellet group counts, Hunter observations and Cohort analysis. The data was
 2 collected within the Grimsö Wildlife Research Area, Sweden, in the years 1973 to 2006. Numbers of observed moose per 1000 ha from the aerial counts are given without
 3 correction for sightability. The ratios of marked moose observed during the aerial surveys are given as (No. marked moose observed) : (Total no. marked moose in the area).

Year	Area surveyed (1000 ha)	Aerial counts		Proportion <1 km from border	Pellet group surveys ^e		Hunter observations		Cohort analysis
		Observation per 1000 ha	Ratio of marked moose observed		Old survey. Pellet groups per 100 m ² .	New survey. Pellet groups per 100 m ² .	Number of adult moose observed	Observations per hunter and day	Number of adult moose per 1000 ha
1973			-						5.49
1974			-						6.32
1975									6.91
1976									8.76
1977	11.5	18.2 ^a	-	37%	0.312 ^d				11.66
1978	13.5	14.7 ^a	-	49%	0.105 ^d				12.57
1979	13.5	13.3 ^a	-	47%	0.746				14.03
1980					0.534				18.43
1981	10.5	19.2 ^b	-	48%	0.554				19.09
1982	13.5	21.0 ^a	-	45%	1.139				18.01
1983					0.690				17.06
1984	13.5	14.2 ^a	3:9	35%	0.715		127	0.900	15.21
1985	13.5	17.7 ^a	4:5	52%	0.515		190	1.021	15.56
1986					0.417		159	0.815	13.69
1987	13.5	14.0 ^a	21:24	44%	0.469		85	0.574	13.51
1988	13.5	12.7 ^a	5:13	37%	0.357		106	0.675	13.02
1989					0.656		75	0.568	13.53
1990					0.385		103	0.715	13.51
1991					0.444		89	0.689	13.43
1992					0.609		70	0.404	13.82
1993					0.504		63	0.443	12.86
1994	13.5	13.9 ^b	12:17	53%	0.571		59	0.404	12.92
1995					0.770		50	0.364	11.46
1996					0.386		26	0.273	10.31
1997					0.360	0.328	35	0.472	8.84
1998					0.520	0.322	28	0.358	7.81
1999						0.317	39	0.469	6.82
2000						0.343	52	0.520	7.23

2001					0.331	53	0.563	6.86
2002	13.0	12.2 ^c	10:14	32%	0.471	40	0.388	6.41
2003					0.453	39	0.475	7.54
2004					0.573	54	0.587	6.45
2005					0.347	45	0.417	5.62
2006	13.5	8.3 ^c	-	-	0.326			

1 ^a 95% observed according to guidelines by Tärnhuvud (1988)^b 84% observed according to guidelines by Tärnhuvud (1988). ^c Estimated percentage of moose observed from
2 sampling-resampling equal to 73%. ^d Only 200 sample plots (50 m²) surveyed. 400 sample plots were surveyed in 1979 to 1998. ^e The annual ratio between the variance and
3 the mean of pellet groups per plot was between 1.1 and 6.1 for the Old Pellet Group Survey and between 1.8 and 3.3 for the New Pellet Group Survey.

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2
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4
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1 **Table 3** Auto-correlations within time-series (lower diagonal^a) and the correlation
 2 between the time-series (upper diagonal^b). Number of years in each analysis is shown
 3 in parentheses

	Reconstruction	Hunter observations	Old pellet survey	New pellet survey	Aerial counts ^c
Reconstruction	-	0.20 (22)	-0.06 (22)	-0.03 (9)	0.69* (9)
Hunter obs.	0.94\1.00	-	-0.37 (15)	0.31 (9)	0.76 [†] (6)
Old pellet survey	0.18\0.96	0.03\1.00	-	^d	0.40 (10)
New pellet survey	0.49\1.00	0.44\ -0.10	^d	-	^d

4 [†] P<0.10 for the null hypothesis that the correlation is 0

5 * P<0.05

6 ^a The lower diagonal values shows the auto-correlations with a one year time-lag. The
 7 two auto-correlations are given as $r_1 \backslash r_2$ where time series 1 is given by the row name
 8 and time series 2 is given by the column name.

9 ^b Correlation between the elements in the auto-correlated time series.

10 ^c The Aerial counts were analysed as independent between years.

11 ^d Less than three observations.

12

13 .

14

1 **Figure 1** Description of the data from the new pellet group survey. Average number of
2 pellet groups per 100 square meters within the 32 sub-areas of the Grimsö Wildlife
3 Research Area. The four sub-regions (NE,SE,SW,NW), used in the subsequent
4 statistical analysis are also shown.

5

6 **Figure 2** Cumulative proportion of shot moose within the Grimsö Wildlife Research
7 Area estimated from the data for the years 1973-1990.

8

9 **Figure 3** Number of calves and adults shot per year within the Grimsö Wildlife
10 Research Area.

11

12 **Figure 4** Estimated survival curve of adult moose. Dashed curves show 95%-
13 confidence limits and smoothed curve corresponds to the approximation used for the
14 reconstruction.

15

16 **Figure 5** Population density (per 1000 ha) estimated from the reconstruction. The
17 population density was estimated as the total number of adults prior to the hunting
18 season divided by the size of the research area (135 km²). The reconstruction results are
19 compared to aerial counts (moose per 1000 hectares), pellet groups (per 100 m²) and
20 hunter observations (observed moose per hunter and day). In the figure, the aerial
21 counts have not been corrected for sightability.

22

23 **Figure 6** Sex ratio of adults (males per female). Estimates from the reconstruction and
24 aerial counts given as bold line and squares, respectively.

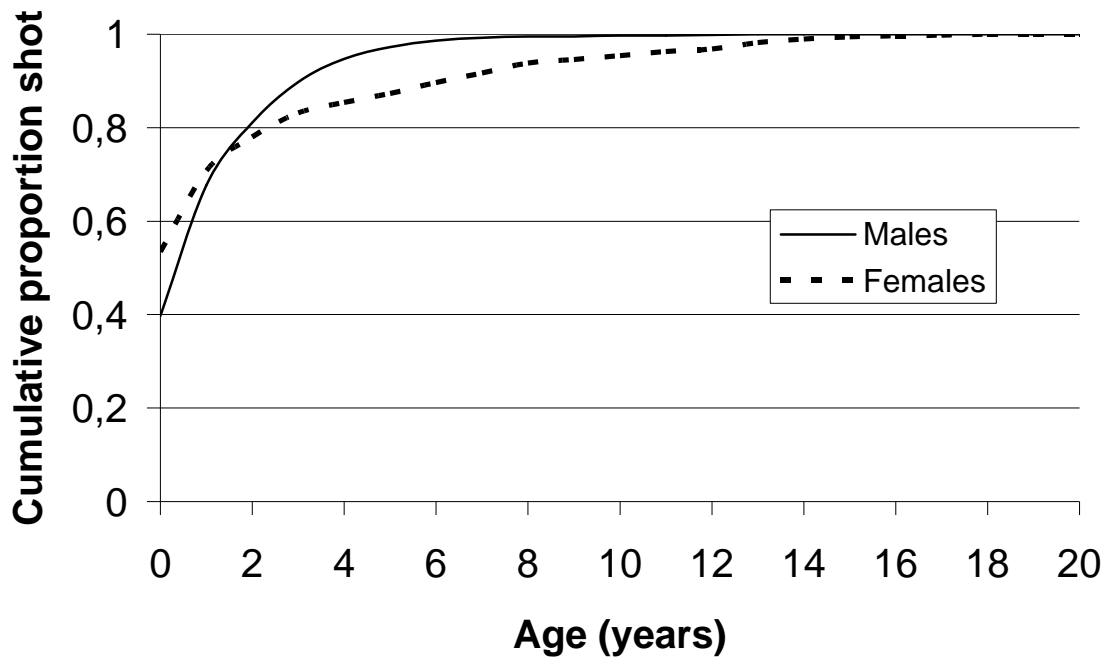
1 FIGURE 1
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QuickTime™ and a
TIFF (Uncompressed) decompressor
are needed to see this picture.

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1 FIGURE 2

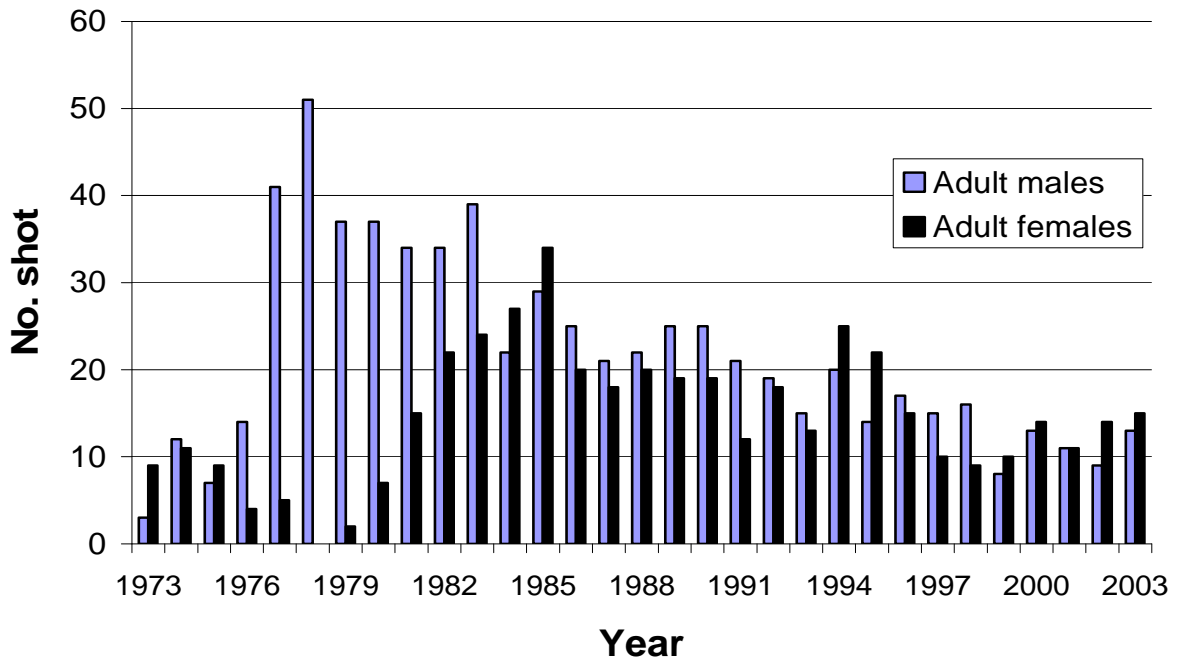
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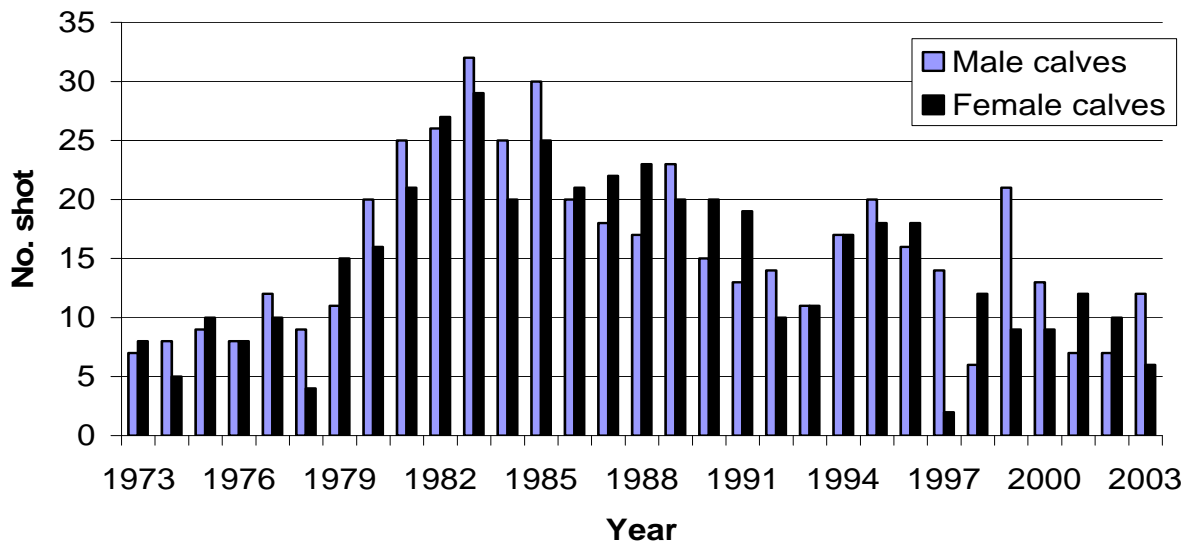
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1 FIGURE 3

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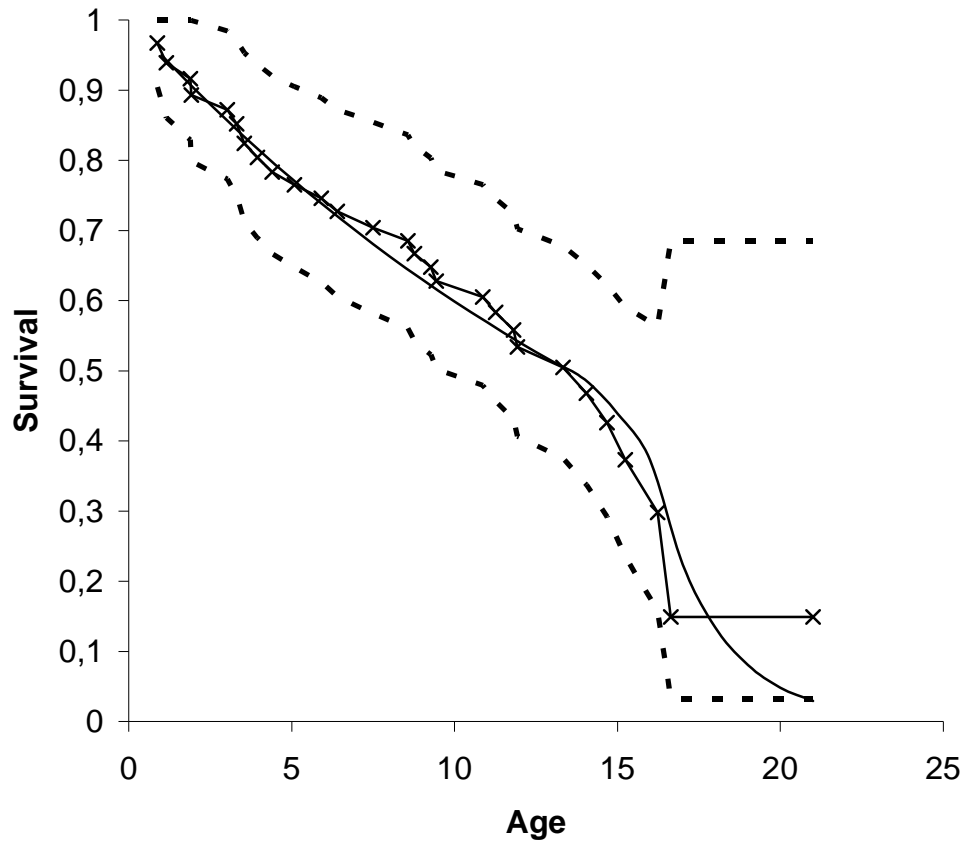


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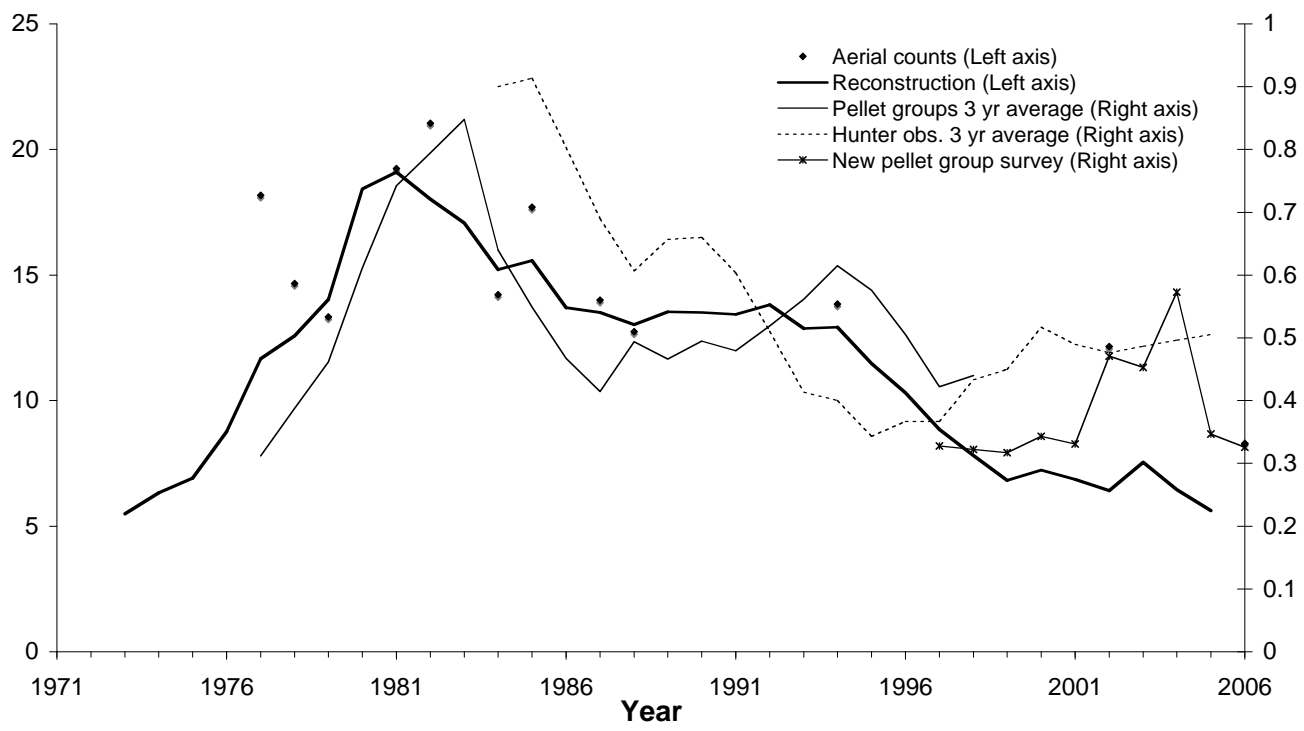
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1 FIGURE 4
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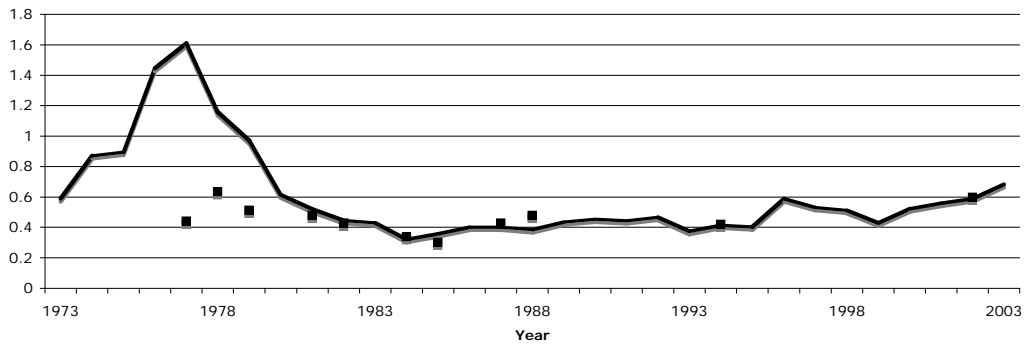
1 FIGURE 5
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1 FIGURE 6

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