Monitoring Population Size of Red Deer Cervus Elaphus: An Evaluation of Two Types of Census Data from Norway

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Monitoring population size of red deer *Cervus elaphus*: an evaluation of two types of census data from Norway

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Proper management of wildlife relies on metrics of population development. Typically, the best estimation techniques are too expensive for coarse-scale management. In marine fisheries, catch-per-unit effort is commonly used, but problems may arise due to changes in spatial harvest effort or in habitat use as density changes. Managers in Norway are in the early phases of implementing 'seen deer' during harvesting and 'spring counts' on farmland as a means of monitoring red deer *Cervus elaphus* populations. We provide a first evaluation of how suitable these methods are by comparing the results with population estimates obtained using cohort analysis, and by analysing the within-season variation in number of seen deer. 'Seen deer' predicted annual increases in populations fairly well. Adjusting for harvesting effort provided less good estimates, due to a proportionally larger increase in effort relative to deer population size as population size increased. The number of seen deer per day decreased rapidly at the beginning of the season, and then levelled off or increased slightly during the rut, especially on farmland. The number of seen deer increased both with the number of harvesters and hours harvested, but at a diminishing rate. The current practice of 'spring counts' was not successful in predicting population changes, probably due to a lack of replication. Indeed, date strongly affected the number of deer seen during spring counts. While 'seen deer' seems to be a very promising tool for monitoring population size of red deer, there are some limitations to the practice as implemented for moose *Alces alces* in Scandinavia due to a more complex relationship with harvesting effort. Our study highlights that the large number of hours harvesters observe wildlife can provide a useful tool for population monitoring. However, the use of such indices may vary between species and according to harvest techniques and should thus be assessed with care before implementation.

Key words: age structure, catch-per-unit effort, cohort analysis, farmland, harvest effort, population density, seen deer, spring counts

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One of the main challenges a wildlife manager faces is how to estimate population size, demography and trends. Although capture-mark-recapture methods allow accurate estimation of population sizes and uncertainties (Lebreton et al. 1992), such methods are typically too expensive for large-scale management. A number of alternative, cheaper methods have been developed, such as line transecting (Buckland et al. 1993, 2001; for ungulates see e.g. Vincent et al. 1991, Focardi et al. 2002, Koenen et al. 2002, Ward et al. 2004), pellet group counts (review in Neff 1968), thermal imaging (Wiggers & Beckerman 1993, Gill et al. 1997) or indirect methods based on performance indices such as body weight or size (Hewison et al. 1996). Catch-per-unit effort (CPUE) is a frequently used protocol in marine fisheries (e.g. Hanchet et al. 2005, Casini et al. 2005) and for important game species (Noss et al. 2005). For moose *Alces alces* management in Scandinavia, the use of 'seen moose' schemes filled in by harvesters has been very successful (Norway: Solberg & Sæther 1999, Rolandsen et al. 2003; Sweden: Ericsson & Wallin 1999, Sylvén 2000). It provides a relatively cheap and logistically feasible way of obtaining data on population trends and to some extent also on recruitment and sex ratios.

In Norway, harvest of red deer *Cervus elaphus* has increased from 2,484 in 1965 to 26,130 in 2004 (Statistics Norway 2004, see Milner et al. 2006). Red deer have therefore become a very valuable game species in Norway. Several municipalities have recently started 'seen deer' schemes similar to those for moose (Veiberg et al. 2003, Samdal et al. 2003), and most municipalities along the west coast of Norway are now about to start such registrations. However, it is not entirely clear if this will work equally well with red deer, since red deer often gather on agricultural areas in smaller or larger herds (Bonenfant et al. 2004). Clearly, if weather conditions during the harvest season to a large degree will determine whether deer use agricultural pasture, then use of 'seen deer' schemes may not be equally reliable compared to those for moose who live in forested areas and have family group as the largest social unit. As a consequence of the red deer's aggregation on agricultural pasture during early spring, several municipalities have organised spring counts (Samdal et al. 2003). As is the case with 'seen deer', no proper evaluation of the spring count method as a monitoring technique has been carried out.

Even though management plans at the population level are required in many areas of Norway (Samdal et al. 2003), hitherto no evaluation of methods suitable for population census of red deer has been performed. In our study, we compare the performance of 'seen deer' during harvesting in autumn and 'spring counts' as indices of population size and trends and compare these with population size as estimated by cohort analysis (Fryxell et al. 1988, Roseberry & Woolf 1991, Solberg et al. 1999, Gove et al. 2002). For 'seen deer' total daily number of observed and shot animals (distributed in age and sex classes) together with total number of hours harvested are noted by the harvesters (harvesting team) for each harvesting day. To ease the punching procedure managers normally pool these numbers for each harvesting field over the entire harvesting season. We therefore also provide an assessment of what factors determine how many deer are seen within a year, and how and if effort should be adjusted for. For spring counts, we determine how date of counting affects the number of deer observed.

Material and methods

Study area

Data derive from the main distribution range of red deer along the west coast of Norway. The vegetation on the west coast of Norway is mostly in the boreonemoral zone (Abrahamsen et al. 1977). Red deer are typically harvested both in the forest and on farmland. A more thorough description of the study area is given elsewhere (Mysterud et al. 2001, Mysterud et al. 2002). Data in this study derive from the municipality of Kvinnherad in the county of Hordaland within what we often refer to as population 'P1', Stryn, Sogn og Fjordane in population 'P2', Tingvoll, Møre og Romsdal in population 'P3' and Otterøy in the county of Nord-Trøndelag in population 'P4' (*cf.* Mysterud et al. 2002).

Red deer harvest data

Data analysed in this paper are given in Table 1. As part of the National Monitoring Program for Cervids funded by the Directorate for Nature Management in Norway, harvesters provide mandibles from all animals shot, together with records of sex, date and locality (municipality), and report to local wildlife boards in each municipality. Jawbones and the above-mentioned information are subsequently sent to us. We determined the age of calves, yearlings and 2-year old deer on the basis of tooth eruption patterns (Mitchell & Youngson 1969, Loe et al. 2004), whereas for older animals we determined their age on the basis of *cementum annuli* in the root of the first incisor (Reimers & Nordby 1968, Hamlin et al. 2000).

For Kvinnherad in P1, we received jawbones which were used to age deer for all years from 1991 to 2004. We had jawbones from 68.1 and 68.5% of male and female calves, 88.7 and 86.0% of male and female yearlings, and 80.3 and 85.8% of adult males and females, respectively. In addition to this, we obtained data from Statistics Norway (2004) on the total number of calves, yearlings and adults (of each sex) shot. We added the data on calves and yearlings, even though age had not been checked by us. For calves, errors made by harvesters are negligible and cases of small yearlings being reported as calves are infrequent (R. Langvatn, unpubl. data). For yearling females, some error is most likely present (small 2-year olds and large calves may be reported as yearlings), but we regard it as highly unlikely that the frequency is high enough to have any effect on our conclusions. As 39% of females and 49% of males were harvested either as calves or yearlings, we had data on age from most animals harvested from the municipality. By including data on calves and yearlings from the harvest statistics, we therefore had data on age for on average 90.3% of the harvest each year, varying between 80.3 and 94.3%.

For Stryn in P2, we had jawbones for ageing of deer for all years (1992-2004). For Stryn, we had data on 90.0% of adult males and 93.0% of adult females, and we also used information from Statistics Norway (2004) so that we had data on all calves and yearlings harvested.

'Seen deer' data

Seen deer data were collected by harvesters during the harvest season, starting on 10 September and ending either in October or continuing until 15 November. In some areas, there is a rutting break in the harvest season lasting from 26 September until 10 October (*cf.* Yoccoz et al. 2002). For each day, harvesters note the number of deer seen (including days

Table 1. Time periods for which data sets were available for analyses of different indices of population size of red deer for nine municipalities along the west coast of Norway, from the populations P1 in the south, via P2 and P3 in the middle, to P4 in the north. For Otterøy, we used harvested deer from Namsos.

	P1		P2		P3	P4
	Kvinnherad	Etne	Askvoll, Gaular, Jølster and Førde	Stryn	Tingvoll	Otterøy
Jawbones	1991-2004			1992-2004		
Population size estimated using cohort analysis	1991-2001			1992-2001		
Harvest size, quota	1965-2004		1965-2004	1965-2004	1965-2004	1965-2004
Seen deer - aggregated	1988-2003					1983-2003
Seen deer - detailed	1999-2001, 2003		1999-2002/03		1999-2004	
Spring count				1995, 1997, 1999-2001		1983-1989, 1991-2004
Spring count - detailed		1999-2002				

with no observations), the number of hours harvested, the number of harvesters and the type of habitat (farmland or forest) on a fixed diagram. Data on 'seen deer per day' for each harvesting field for the entire harvesting period were available for shorter time periods (4-6 years) from six municipalities in three different counties (see Table 1). When reported to wildlife boards in the municipalities, the data are usually aggregated. Such aggregated data, i.e. the number of seen deer per harvesting field per year (with and without adjusting for effort), were available for 1988-2003 for Kvinnherad in P1, and for 1983-2003 for Otterøy in P4.

It is intuitive to adjust the number of seen deer relative to the harvesting effort. Clearly, the more time you are out harvesting the more deer you are expected to see. There are a number of ways and reasons to adjust for harvest effort, as both number of harvesters, days and hour per day of harvesting will clearly affect estimates of seen deer irrespective of deer population density. For moose, number of seen moose per harvester day (8 hours) is the standard (Solberg & Sæther 1999). We therefore also chose to calculate number of seen deer per harvester day (but the number of hours could not be corrected for). As the harvesting season progresses, there are fewer deer around (many are shot), the remaining deer are possibly more vary (shy) as well and the number of day light hours is decreasing. In addition, with increased quotas, it may take longer time to fill them and recent years' quotas have often been more detailed (in terms of which age and sex classes could be harvested). Since effort can also be linked to population size, the solution of adjusting for effort is not as easy as one might imagine. For a given municipality, harvesting effort also has a spatial component because new areas are included as red deer harvesting ground when population sizes increase (Mysterud et al. 2000). We calculated seen deer per harvester day by first summing all seen deer for a given population (mainly at municipality scale), before dividing this by the total number of harvester days (i.e. the number of harvesters multiplied by the number of days harvested). An alternative approach could be to first calculate seen deer per harvester day for each harvesting area, and then use the average, but then equal weight would be given to small and large areas regardless of the original observation numbers.

Spring count data

Spring count data from Stryn in P2, were available from only five years (see Table 1), whereas data were available for 1983-1989 and for 1991-2003 from Otterøy in P4. In addition, data from four years of repeated spring censuses were available from Etne in P1 (see Table 1). Spring counts in Otterøy and Stryn were carried out simultaneously over the entire area at one date each year. The date, usually in April-May, was chosen according to the timing of green up. In Etne the counting was repeated at six dates per year. Observations were made from cars at pastures along fixed routes.

Statistical analyses

Cohort analysis

Population reconstruction based on cohort analysis produces unbiased results if input data are unbiased and assumptions are met (Roseberry & Woolf 1991). We aimed at estimating population size at the municipality scale. This was done for each sex and subsequently summed. We made the following assumptions:

1) We adjusted the number of individuals within a specific sex and age group to account for the variable proportion of (jawbone) data retrieved each year (to match how many adults were actually harvested in the municipality). We assumed the same age structure among adults not reported, as among the majority of deer for which we had access to jawbones.
2) Cohort analysis should preferably be used together with information on natural mortality rates obtained, e.g. through marking of animals (Roseberry & Woolf 1991). Unfortunately, no data are currently available from marked deer to provide estimates of natural survival rates for the population in Kvinnherad or Stryn. Thus, we used estimates on natural mortality obtained by Langvatn & Loison (1999) for the Snillfjord population in P3 further north, i.e. annual mean natural mortality being 20% for male and female yearlings, 13% for 2-year-old males and 8% for 2-year-old females, and 7% for adults (> 2 years old) of both sexes. As this population is situated north of the Kvinnherad and Stryn subpopulations, these estimates are likely somewhat high. If estimates of natural mortality are too high, this would lead to overestimation of the population size, and to underestimation of the harvest pressure. However, for our purpose this is not a problem, as we are interested mainly in changes from one year to the next.

3) It is recommended that data be included from age classes up to an age where only 1% of a cohort is still alive in the population (Solberg et al. 1999). This cut-off was seven years of age for males and 11 years of age for females. Thus, we could complete cohorts from 1991-1997 for males and 1991-1994 for females. To be able to estimate population size for a longer period, we had to assume that each age class contributed the same proportion of data as for the last four years.

For each sex, we did the following matrix operations to estimate population size:

[Age structure] / [Survival] / [Sample]

where 'Age structure' is the annual age structure as estimated from jawbones, 'Survival' the age dependent natural survival (to account for natural mortality), and 'Sample' the annual age dependent proportion of animals (jawbones) sampled from the total harvest (to account for variable sampling between years). Our population estimate was then the sum of males and females alive for a given year before harvesting.

Establishing time series of 'seen deer'

One problem connected with the establishing of time series of seen deer is the often large spatial variation in the number of seen deer. For example, in Kvinnherad, adding harvesting field increased the explained variance in the order of 10% to around 40-50%. In total, we registered 142 harvesting fields over the entire period. Ideally, one would expect 16 observations from each harvesting field given the length of the time series (1988-2003), but the observed average was only 7.85 observations. This suggests that harvesting fields had either changed in size or numbers, or that some harvesting fields for some reason had not reported the number of seen deer. Thus, fitting only a categorical term for year would possibly lead to bias since the number of fields is different between years. Data for $\geq$ 10 years were available from 53 fields. There was also a temporal trend in the number of harvesting fields, increasing from 43 in 1988 to 106 in 2002. However, in 1995 it was only 25 fields. This suggests that the variation in the number of harvesting fields from which observations were reported was not only a trend towards more harvesting fields, but also a matter of sampling. Naturally, there was a very close correlation between total number of seen deer per year and the number of harvesting fields ($r = 0.949$). We therefore tried several models, with and without adjusting for number of fields and to restrict to those fields only from which data were available for most years.

Comparing time series

There are two reasons why we are mainly interested in parameter estimation rather than in significance testing. First, the time series were fairly short (10-11 years; five years for spring counts in Stryn), and it is not likely that significant results would be found unless correlations are very high. Second, we assessed autocorrelation for time series without missing values in the middle (thus excluding spring counts in Stryn). When autocorrelation is high, this will inflate confidence intervals. Although it is possible to adjust for this, we rather report autocorrelation and are more concerned with growth rates that were much less autocorrelated than population size. We thus compared models using the Akaike Information Criterion (AIC; Burnham & Anderson 1998, Johnson & Omland 2004), having a 1st order and 2nd order term. The small-sample correction $AIC_c = AIC+2K(K+1)/(N-K+1)$, where N is the number of observations and K is the number of regression coefficients including intercept, was applied when $N/K < 40$. If time series were very short, we also report the Pearson correlation. Even though these time series are counts, log-transformation generally decreased the fit, and we therefore focus mainly on the non-transformed data that also are easier to assess for managers.

Detailed data on 'seen deer' and repeated spring counts

The detailed 'seen deer' data derive from a small number of years. We were interested in using these data to see how number of seen deer varied with date, habitat (farmland vs forest), number of harvesters and number of hours harvested as well as their interactions. In all models, we adjusted for the harvesting field ('vald'). We log-transformed the number of seen deer (+1), since it is a counting process.

We started using additive models (AM) to assess non-linear relationships (Hastie & Tibshirani 1990). In the following model selection, we tried polynomial terms and log-transformations if relevant. We used the Akaike Information Criterion (AIC; Burnham & Anderson 1998, Johnson & Omland 2004). The model with the lowest AIC value is the most parsimonious model; i.e. the best compromise between explaining most of the variation and simultaneously using as few parameters as possible. The detailed strategy of model selection and parameter estimates for all factors in all models can be obtained from the authors upon request.

Results

Kvinnherad: Seen deer evaluation

The population size in Kvinnherad in P1, as estimated using cohort analysis increased from 2,339 deer in 1991 to 4,254 in 2001 (Fig. 1A), which gives an average growth rate (r) of 6% that was also fairly stable (variation between -0.8 and +8.7%). There was a parallel increase in the number of harvested and seen deer (see Fig. 1C), and thus a close correlation between these variables and the population size increase (Fig. 2). The steady population increase led to a high autocorrelation in the time series (see Fig. 2). When analysing growth rates, autocorrelation was low. There was also correlation between growth rate of population size and growth rates of seen deer and harvest. No correlation was found between population size and number of animals shot per harvester day.

The best fit for seen deer models was obtained when restricting the data set to harvesting fields with > 10 observations per year, and by incorporating field either as a fixed or random term. Measures using absolute number of seen deer outperformed seen deer adjusted for effort, which may seem surprising. However, the number of harvesters (l.s. mean = 1.605, SE = 0.135, T = 11.930, P < 0.001) and hours harvested increased over time (l.s. mean = 0.630, SE = 0.052, T = 12.048, P < 0.001), as population size increased. Therefore, the ratio of seen deer relative to effort did actually decrease (see Fig. 1C). Indeed, the estimate for total number of seen deer as a function of population size decreased from 0.0109 (± 0.0030) to 0.0046 (± 0.0025) when adding the number of harvester days to the model.

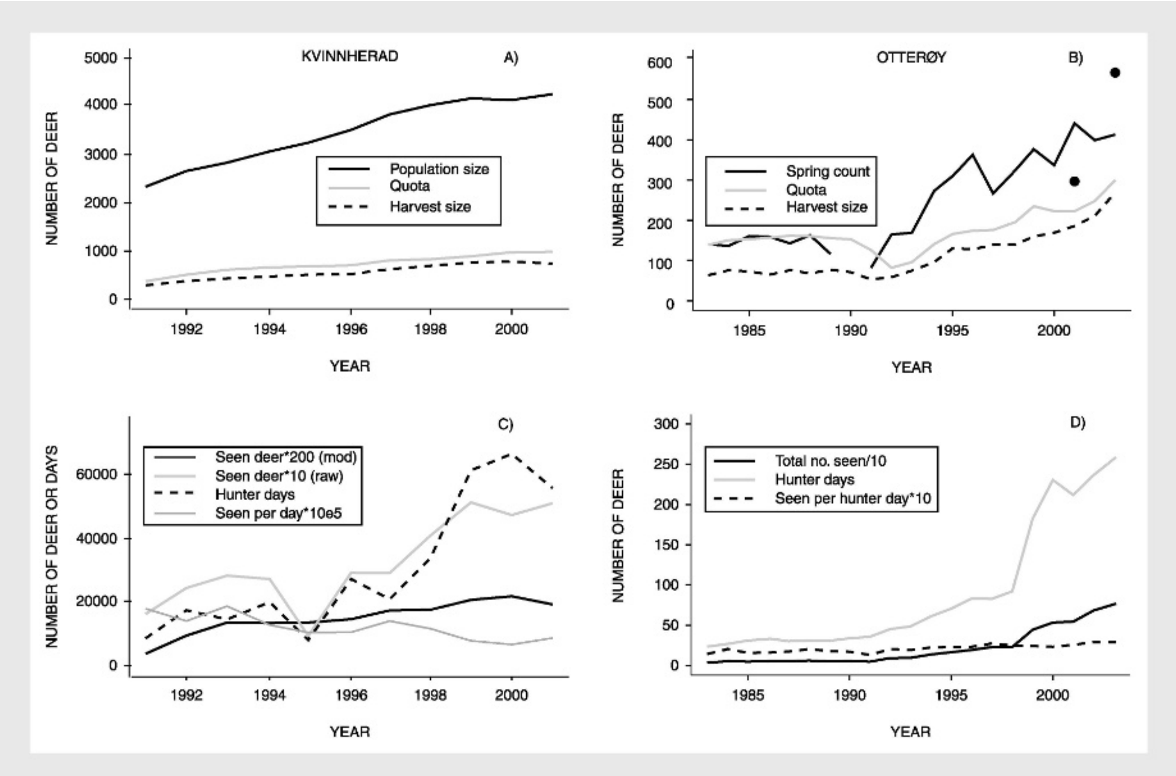

Figure 1. Development of the red deer population as estimated with cohort analysis and harvest (quota and size; A), and number of seen deer (as estimated with a model [mod] or the raw data [raw]), harvester effort and number of seen deer per day over the period 1991-2001 (C) in Kvinnherad in P1. Development of the red deer harvest (quota and size) and spring counts (B) and number of seen deer and harvester effort over the period 1983-2003 (D) on the island of Otterøy in P4. The two dark points in B) are from a repeated spring count, thus showing the huge variation between counts. Note that the lines for hunter days and number of seen deer cross each other in C).

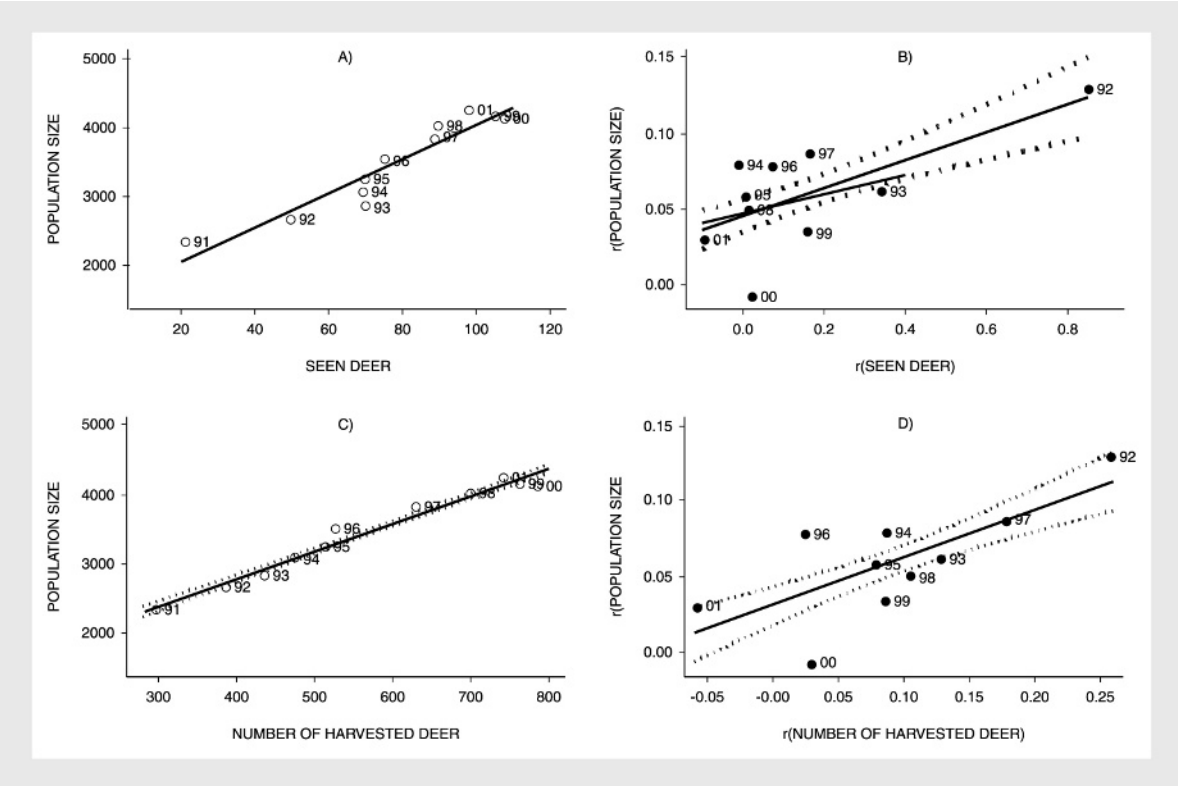

Figure 2. Relationship between population size and number of seen deer (A-B) and harvest size (C-D) in Kvinnherad in P1. Note that the thin full line in B) is the fitted line when excluding year 1992. A) and C) show absolute values, whereas B) and D) show annual growth rates. Dashed lines indicate 95% confidence intervals.

Stryn and Otterøy: spring count evaluation

Stryn in P2

The population size in Stryn increased from 2,002 deer in 1986, peaking at 2,857 deer in 1997 and decreasing to 2,566 in 2001, which gives an average growth rate of 2.8% varying between -7.9 and +11.8%. There was a close correlation between population size and number of harvested deer, as well as between growth rate of the two variables (T = 2.263, P = 0.058). When entered into the same model, growth rate of harvested deer (T = 2.108, P = 0.080) was a better predictor of population growth rate than growth rate of quota (T = -0.697, P = 0.512). When restricting data to the five years with good counting conditions (1995, 1997, 1999, 2000 and 2001) only a weak, non-significant correlation between spring counts and population size was found (r = 0.564, P = 0.322). Adjusting for the fact that the two areas were missing (assuming that the proportional difference between the areas was similar), the correlation more or less disappeared (r = 0.187, P = 0.763). When using data from all areas, and adjusting for size of area, no correlation was found (r = -0.246, P = 0.690).

Otterøy in P4

The harvest size was correlated with both the number of seen deer in autumn and spring counts (see Fig. 1B,D and Fig. 3), and the number of seen deer was also correlated with spring counts. Much of this correlation was due to a trend in the time series. The time series of harvest size and the number of seen deer per day were positively autocorrelated (lag 1), whereas the time series on annual growth rate of harvest size (r = 0.150) and seen deer (r = -0.434) were not. As the number of deer counted during spring was not available for 1990, we did not estimate autocorrelation. The correlation between growth in harvest and growth in seen deer was small (r = 0.377), and it was absent in the relationship between growth in harvest and growth in spring count (r = 0.041). In two years repeated sampling was done, and there was a huge variation between the two subsequent counts (see Fig. 1B).

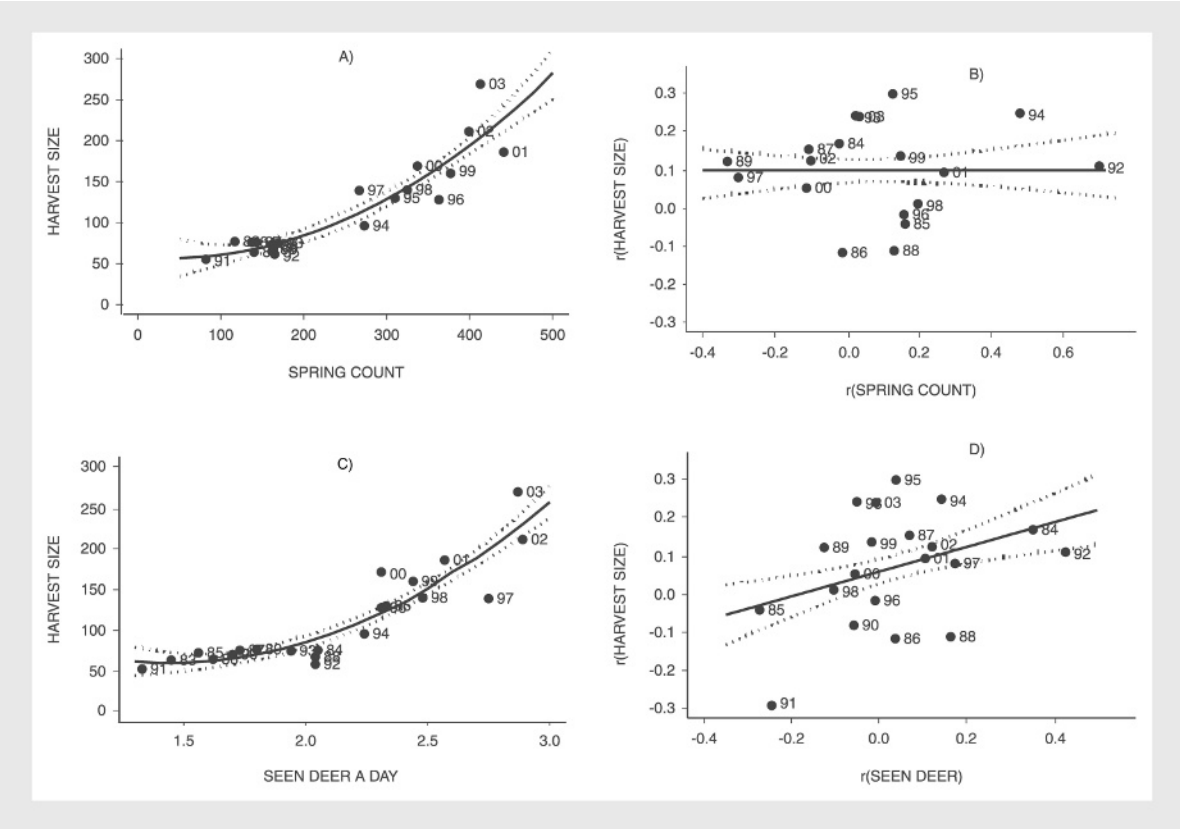

Figure 3. Relationship between harvest size and spring counts (A-B) and number of seen deer during harvesting (C-D) over the period 1983-2003 on the island of Otterøy in P4. A) and C) show absolute values, whereas B) and D) show annual growth rates. Dashed lines indicate 95% confidence intervals.

Factors affecting within-year variation in 'seen deer'

As the number of harvesting fields was excessive (40-70 per municipality), we do not present the full models in this paper, but rather the harvesting field with most data was used in plotting.

Kvinnherad in P1

The total number of seen deer (ln+1) decreased slightly with date (Fig. 4A), increased with the number of harvesters, but at a slightly decelerating rate, so the log (number of harvesters) provided a better fit. More animals were seen on farmland than in the forest. The number of seen deer was similar for 1-3 hours of harvesting, and then increased markedly and reached a stable plateau at about 9-12 hours of harvesting per day. There was interaction between habitat and year, but the number of seen deer was always higher in farmland habitat. Similarly, the effect of date varied between years, though it was always negative. The interaction between habitat and date entered the model, but was not significant. The variance explained by this model was 48.8%, and decreased to only 16.4% when removing the spatial factor (i.e. harvesting field), demonstrating the huge impact of spatial variation in density.

Førde, Jølster, Askvoll and Gaular in P2

Model selection of the number of seen deer (ln+1) in the four municipalities in Sogn og Fjordane resulted in models explaining fairly similar amounts of variance (Førde: $r^2 = 0.308$; Jølster: $r^2 = 0.380$; Askvoll: $r^2 = 0.421$; Gaular: $r^2 = 0.413$).

The relationships between number of seen deer and habitat, year and date were rather complex, including up to a 5th order term for date. In Jølster, only the habitat*date interaction improved the model. In the other models, including also year*date and year*habitat and year*habitat*date improved the models as measured by the AIC. In Figure 4, we have plotted the simplest (Jølster) and the more complex (Førde) patterns. When plotting the complex patterns, it turned out that similar to

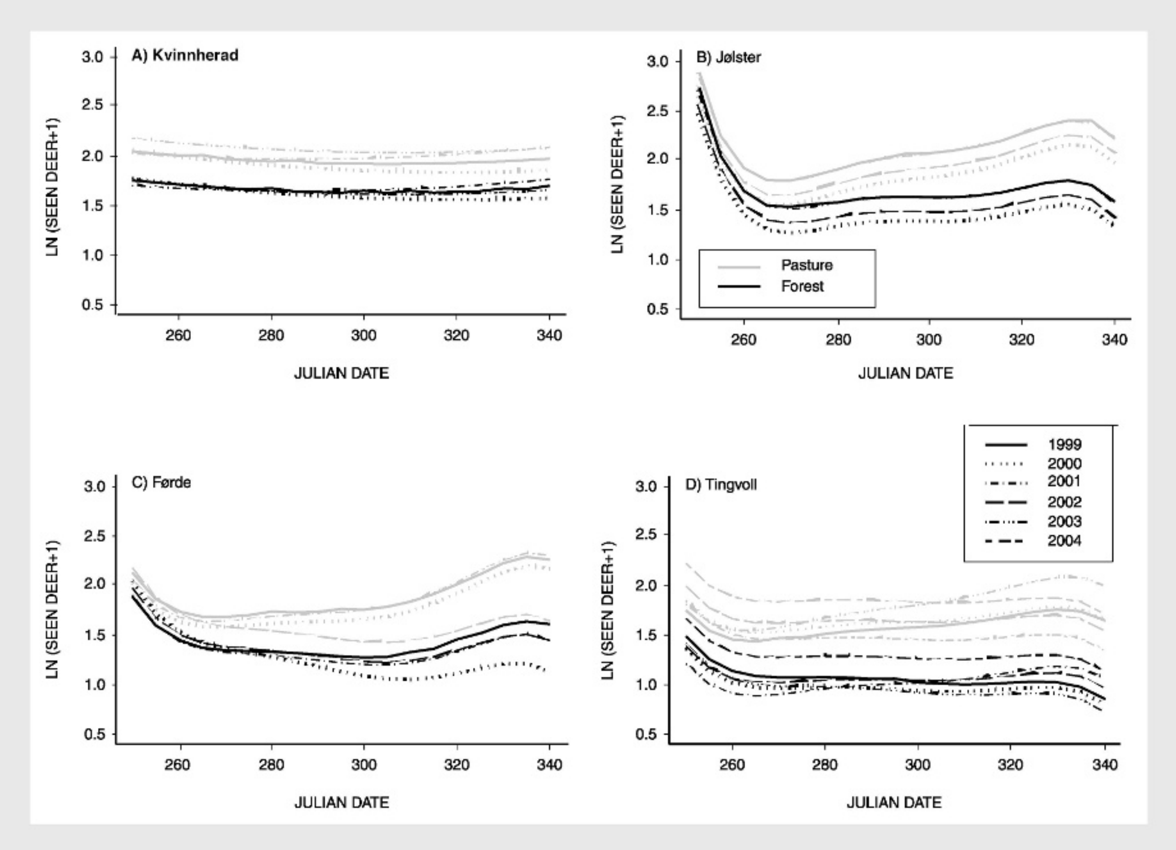

Figure 4. Variation in the number (ln+1) of 'seen deer' over the harvesting period in the habitats farmland (grey lines) and forest (black lines) in Kvinnherad (A) in P1, Jølster (B) and Førde (C) in P2 and Tingvoll in P3 (D) based on the model selected with the AIC. Note that for Tingvoll, years with an increase in number of seen deer on farmland during the harvesting season typically have a similar decrease in the number seen in the forest.

Kvinnherad the main difference was also here between habitat and habitat*date. Indeed, for Gaular few terms were even significant. Excluding non-significant terms, the main pattern remained a decrease in the number of seen deer to begin with, with farmland typically having a higher estimate, and as October progressed, more and more deer were seen in farmland, while the number was fairly stable in forest habitat.

Number of seen deer increased linearly with the number of harvesters in Førde and Askvoll and log-linearly in Jølster and Gaular, i.e. the number of seen deer increased with number of harvesters, but at a diminishing rate in the latter two municipalities.

Number of seen deer also increased with the number of hours of harvesting, but the detailed relationship varied somewhat between municipalities, being log-linear in Førde and Askvoll, being a 2nd order polynomial in Jølster and a 3rd order polynomial in Gaular. There was a close to linear increase in the number of seen deer for up to 9-10 harvesting hours in Jølster and up to 12-13 harvesting hours in Gaular. In general, the number of seen deer increased markedly with the number of harvesting hours, but at a slightly diminishing rate as the number of hours increased.

Tingvoll in P3

The total number of seen deer showed a rather complex relationship with date and also interacted with habitat (see Fig. 4). In the forest, the number of seen deer decreased from the start of harvesting towards the beginning of October, and was fairly stable towards mid-October, before decreasing linearly with date towards the end of the harvesting period (see Fig. 4). On farmland, the number of animals decreased from the beginning of the harvesting season towards 1 October and then increased with time for the rest of the harvesting season. There was no

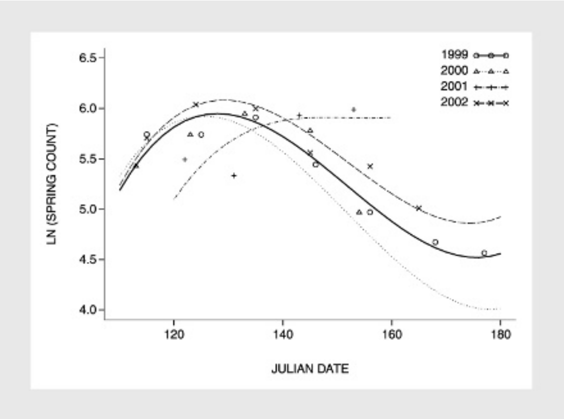

Figure 5. Variation in the number (ln) of deer seen during repeated spring counts in Etne in P1 in the years 1999-2002.

main effect of habitat, but number of deer observed on farmland vs forest differed markedly between years. The number of seen deer increased with the number of harvesters, but at a decreasing rate as the numbers of harvesters increased also in Tingvoll, and the number of seen deer increased with harvesting hours per day. The variance explained by this model was only 12.9%. When adding harvesting field to the model as a categorical covariate, the variance explained increased to 41.2%, but this had little impact upon the other factors.

Factors affecting within-year variation in 'spring counts'

The spring counts for Etne (in P1) showed a strong effect of observation date on the number of deer counted. This pattern was fairly consistent among years. In three out of four years the number of deer seen during spring counts peaked around 10 May (Fig. 5). For the last year (2001), numbers peaked some 20 days later (see Fig. 5). Data were, however, limited.

Discussion

Reliable metrics of the development of wildlife populations are one important key to successful management. Most municipalities along the west coast of Norway are in the phase of implementing 'seen deer' schemes, and many are using 'spring counts' in practical management (Samdal et al. 2003). A first evaluation to determine whether 'seen deer' and 'spring count' gives reliable information about population development is thus of prime importance to management. Catch-per-unit effort and similar metrics are fairly easy to obtain, but they may also be influenced by prey behaviour such as habitat use (Eros et al. 2005). Our results suggest that the 'seen deer' method seemed to perform very well, both capturing the trend as well as the year-to-year growth in the population, even though also strong effect of deer habitat use was evident in detailed analysis. In contrast spring counts seemed to be unreliable. This is likely due to virtually no within-year replication of counts.

The most surprising and novel result of our study was that adjusting the number of seen deer per harvester effort led to an index that performed less well than just using number of seen deer (in a model). This is counterintuitive, as our detailed analysis showed that, as would be expected, more deer are seen with an increase in both number of harvesters and number of days harvesting. However, proportionally harvesters see less deer with increasing density (see Fig. 1A,D). This was most pronounced in Kvinnherad (see Fig. 1), while adjusting for effort on Otterøy (see Figs. 1 and 3) nevertheless provided fair estimates. It is thus urgent to attain a better understanding of the functional response, i.e. why seen deer per hour change as population density increases. There is more variation in the way red deer are harvested compared to moose. A typical harvester day may start and end with stalking or posting on farmland at dawn and dusk; this is often done also in the middle of the week when people work during daytime. In the middle of the day in weekends there is more harvesting in teams, as for moose. The more harvesters that participate the more marginal posts are used, leading to a decrease in the rate of deer observation with an increase in the number of harvesters participating. In marine fisheries, it has also been shown that fishing strategies differ depending on density, affecting the use of catch-per-unit estimates (e.g. Hanchet et al. 2005). It may be that with increased red deer quotas, harvesters are forced to harvest more in teams to be able to shoot a higher number of deer, but at the cost of effectiveness per harvester. This outcome of the current 'seen deer' scheme differs between red deer and moose, and there is a need to find a way to solve this. Clearly, to not adjust for effort is not satisfactory, even though this performed fairly well with the current data sets. One may consider using data only from the first week of harvesting, when most deer are seen and most harvesters are out.

However, deer may migrate during the harvesting season and harvesting strategies differ between areas, making any spatial subset less reliable if stable harvesting fields are a biased sample. Data for assessing this in more detail is currently unavailable. Thus, more information on both numerical and functional responses of human harvesters would be of great value.

Spatial variation in density or effort may cause problems to catch-per-unit effort metrics (von Szalay & Somerton 2005), for example if harvesters target effort to local hotspots, so that declines are underestimated (Bell et al. 2005). Taking spatial variation into account was also extremely important for 'seen deer' to be reliable. There are large differences in the size of local harvesting units and likely also in local density of deer, as strong spatial structure is typical in red deer populations (Coulson et al. 1997). Due to these large size differences and structures, counting all deer seen per municipality, and then dividing by number of harvester days (i.e. giving more weight to large areas), gave a different picture than first adjusting for effort for each harvesting area, and then using the average (i.e. giving equal weight to large and small areas). It may be better to concentrate the monitoring to some 10-20 stable harvesting teams within each municipality, given they are representative (see above). Using a model to predict number of seen deer, taking into account spatial variation, increased predictive ability by some 10%.

We strongly urge managers to start implementing 'seen deer' to obtain independent measures of population size and trends. Even though the number of harvested deer correlates well with population growth in our study, some of the dependency between number of harvested deer, seen deer and spring counts occurs as a consequence of managers using the census information as a background for setting quotas. Indeed, the strong correlation between growth in population size and growth of harvest was due partly to changes in quota. There are clearly limits to using 'seen deer' as an overall measure of population density. Through comparing very detailed data on 'seen deer' from shorter periods (4-6 years of data), we found rather large spatial variation in the factors causing variation in the number of deer observed. 'Seen deer' data are therefore mainly useful within a certain management unit, such as municipality scale in Norway. Similarly, there is large variation in 'seen moose' between regions, partly due to differences in harvesting practices and habitat characteristics (Ericsson & Wallin 1999, Rolandsen et al. 2003).

A major proportion of the agricultural fields along the west coast of Norway are used for making winter fodder for domestic animals, and they provide a very important food resource for red deer affecting their condition positively (Albon & Langvatn 1992, Mysterud et al. 2002). During spring, red deer frequently aggregate in large herds on these fields, before departing for their summer range. As there is some mortality to red deer during harsh winters (Loison & Langvatn 1998, Loison et al. 1999), counting during spring can possibly be a better estimate for setting quotas for next autumns harvest. The time series of spring count for Stryn was available only for five years, but showed no correlation at all with population size. Part of this is likely due to the fact that a very low proportion of the population was counted. In Stryn, only 24% of the population was counted, on average. Counts thus likely reflect more habitat selection related to weather than an increase or decrease in abundance of red deer. For Otterøy, data were available for a longer period, but we could only compare with seen deer and harvested deer data and not with population size estimates. Given that seen deer and harvested deer are fair correlates of population size as seen for Kvinnherad (see Fig. 2), it seems quite clear that the current 'snap shot spring count' management scheme, i.e. to count on only one day with good conditions, is not very useful. Indeed, date of counting will in itself produce large variation, as was seen for the repeated counts in Etne in P1 (see Fig. 5). Extensive replication is likely a reason for 'seen deer' measures during autumn to work so well. Similarly, calf per hind ratios were not successful as a metric for recruitment in France (Bonenfant et al. 2005), which may also be related to the very low number of replications. To obtain equally reliable estimates from spring counts, better planning and repeated counting are needed. It is premature to conclude that spring counts are of no use; it is the current practice that is less reliable. With access to more detailed spatial data that are replicated in time, bootstrap techniques can be used to assess the uncertainty in the estimates (Efron & Tibshirani 1993). Over time, this will also yield better insight into under what weather conditions deer are more frequently using fields. Although studies suggest that meadows are of prime importance for deer condition (Mysterud et al. 2002), we currently lack an individual based evaluation of how often deer use agricultural pastures, and how much of the population is using fields at a given time.

In much of Europe, the red deer populations have increased substantially over the last decades (Milner et al. 2006), as is also the case for many other cervid populations in Europe and the US (Gill 1990, McShea & Underwood 1997). Current management problems range from those related to traffic accidents (Mysterud 2004) and damage to crops and forestry, to more general biodiversity issues related to overgrazing (Gordon et al. 2004, Mysterud 2006). Management goals have therefore gradually changed from generally aiming at population increase to a wish for population reduction or stabilising, and this has led to an urgent need for methods enabling monitoring of population development at broad scales. Our study highlights the great potential of using the huge amount of time harvesters nevertheless spend in observing wildlife as a means to reach a useful and affordable tool for population monitoring in wildlife management. However, our study also reveals some pitfalls with such an approach related to the fact that the applicability of such indices may vary between species of cervids and due to harvesting techniques. We thus advice detailed assessment before implementation of such tools in national monitoring schemes.

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