

## Performance of hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in Norway

MAYUMI UENO,<sup>1,†</sup> ERLING J. SOLBERG,<sup>2</sup> HAYATO IJIMA,<sup>3</sup> CHRISTER M. ROLANDSEN,<sup>2</sup> AND LARS ERIK GANGSEI<sup>4</sup>

<sup>1</sup>Eastern Field Station, Institute of Environmental Sciences, Hokkaido Research Organization, 085-8588 Hokkaido, Japan

<sup>2</sup>Norwegian Institute for Nature Research (NINA), NO-7485 Trondheim, Norway

<sup>3</sup>Yamanashi Forest Research Institute, 400-0502 Yamanashi, Japan

<sup>4</sup>Faun Naturforvaltning AS, Fyresdal Næringsshage, NO-3870 Fyresdal, Norway

**Citation:** Ueno, M., E. J. Solberg, H. Iijima, C. M. Rolandsen, and L. E. Gangsei. 2014. Performance of hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in Norway. *Ecosphere* 5(2):13. <http://dx.doi.org/10.1890/ES13-00083.1>

**Abstract.** Wildlife managers are often asking for reliable information of population density across larger spatial scales. In this study, we examined the spatiotemporal relationships between moose density as estimated by cohort analysis and the density indices (1) harvest density (HD; hunter kills per km<sup>2</sup>), (2) moose seen per unit effort (SPUE), seen moose density (SMD; seen moose per km<sup>2</sup>), and density of moose-vehicle accidents (MVA density; e.g., traffic kills per km<sup>2</sup>) in 16 areas in Norway with 13–42 years of data. HD showed a close positive relationship with moose density both within and between regions. However, the temporal variation in HD was best explained as a delayed reflection of moose density and tended to overestimate its growth and decline. Conversely, SMD and SPUE were unable to predict the spatial variation in moose density with high precision, though both indices were relatively precise temporal reflectors of moose density. However, the SPUE tended to underestimate population growth, probably because of a decrease in searching efficiency with increasing moose density. Compared to the other indices, MVA density performed poor as an index of moose density within regions, and not at all among regions, but may, because of its independent source of data, be used to cross-check population trends suggested by other indices. Our study shows that the temporal trends in moose density can be surveyed over large areas by the use of cheap indices based on data collected by hunters and local managers, and supports the general assumption that the number of moose killed per km<sup>2</sup> provides a precise and isometric index of the variation in moose density at the spatial scale of our study.

**Key words:** cohort analysis; isometric index; management; monitoring; population reconstruction; precision; saturation; seen per unit effort (SPUE).

**Received** 11 March 2013; revised 18 September 2013; accepted 25 October 2013; final version received 6 January 2014; **published** 6 February 2014. Corresponding Editor: G. Chapron.

**Copyright:** © 2014 Ueno et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

† **E-mail:** ueno-mayumi@hro.or.jp

### INTRODUCTION

One of many challenges for ungulate management in the 21st century is the coordination of management over large geographical scales (Apollonio et al. 2010). The effects of local management actions can be diluted unless it is

coordinated with neighboring areas, and therefore managers are often asking for reliable information of population density across larger spatial scales. To enable this, it is important that census information is inexpensive and relatively easy to obtain. Many estimation methods, such as capture-mark-recapture (CMR) methods, can

provide accurate estimates of ungulate abundance (e.g., Buckland et al. 2000), but are rarely applicable to larger scales because they are too expensive to run on a regular basis. Monitoring based on density indices are usually less expensive and require less effort, but are yielding weaker inference (Williams et al. 2001). To provide a unified index that is both precise and cheap to support is therefore a difficult, if not an impossible task. However, some alternatives are often better than others, and by critically assessing the various alternatives, the more optimal indices for management purposes can be identified and applied.

An index of density is any measurement that is correlated with ungulate abundance (Caughley 1977). Most indices of ungulate density are based on direct counts of animals, such as drive counts, vantage point counts, transect counts and hunter observations, or they are indirectly reflecting ungulate density by the density of tracks (on snow or bare ground), fecal pellet groups or browsing marks (see review in Morellet et al. 2011). Also the annual hunting bag (e.g., Forchhammer et al. 1998, Mysterud et al. 2001, 2002, 2007, Rolandsen et al. 2011) and number of traffic kills (Rolley and Lehman 1992) have been used as density indices, in particular when these are the only statistics that cover sufficiently large areas and time periods. In common for most indices, however, is that they are not providing measures of precision, meaning that the functional way indices are related to density (or abundance) have to be evaluated (Williams et al. 2001).

The performance of density indices can be evaluated by comparing them to the real population density in a sample of populations. However, as the population abundance is seldom known, an alternative is to compare them with other independent indices or estimates of density (e.g., Skalski et al. 2007). For instance, by examining the relationship between the moose, *Alces alces*, seen per unit effort (SPUE) and moose abundance reconstructed by cohort analysis, Solberg and Sæther (1999) concluded that the SPUE may be used for monitoring the temporal variation in moose abundance (see also Rönnegård et al. 2008). For many indices, however, the relationship to abundance is at best based on a few studies and comparative merits of indices are unclear. This is unfortunate as the performance of

indices may vary substantially both within and between populations, e.g., due to varying detection probabilities (Williams et al. 2001). To fully appreciate these statistics, it is therefore important to examine their spatiotemporal relationship with independent estimates of abundance over a larger range of populations and environmental conditions.

In Norway, harvest quotas of moose are often determined based on indices of abundance calculated from harvest data (harvest density, HD), hunter moose observations (SPUE and seen moose density, SMD) and number of traffic kills (density of moose-vehicle accidents, MVA). Here, we compared these indices with moose density in 16 different populations reconstructed by cohort analysis, and assessed to what extent the different indices provide a monotonic, linear and precise reflection of moose density. Nonmonotonic or strongly non-linear indices are usually of little practical use and the same is true if the precision is low (Williams et al. 2001). Conversely, it is desirable to have an index that is scaled isometric to density, i.e., that a doubling of the index implies a doubling of density (i.e., index/density is constant). However, even non-linear indices may provide important information about population density as long as the relationship is monotonic and reasonably precise.

We hypothesized that the indices in question would be mostly linearly related to moose density, but with varying slope and precision. In particular, we predicted that SPUE and SMD would change with a rate less than isometric (or proportional) to moose density because the searching efficiency decreases with increasing population density (e.g., Hatter 2001, Solberg et al. 2006). Conversely, we predicted that HD would increase with a rate higher than in density (higher than isometric), i.e., increasing harvest rate with increasing moose density. Such density dependent harvesting has previously been reported for several Norwegian moose populations (e.g., Solberg et al. 1999, Solberg et al. 2006), and indicates that harvesting is the main mechanism regulating the population size. We also hypothesized that the relationship between indices and population density would be weaker among than within populations because of larger spatial than temporal variation in other interacting factors. Accordingly, we also included in the models

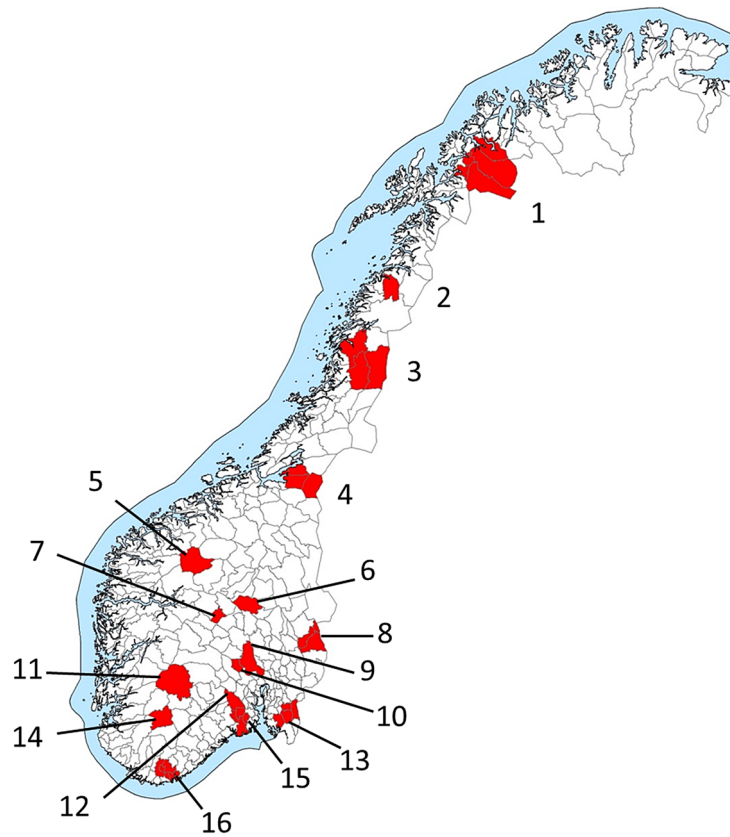


Fig. 1. Distribution of the 16 study sites in Norway. Name and location (in  $x^{\circ}.y'$  N,  $x^{\circ}.y'$  E format): 1: Troms (69.5, 19.6), 2: Beiar (66.9, 14.7), 3: Vefsndalen (67.0, 12.2), 4: Innhered (64.5, 11.9), 5: Skjåk (61.9, 8.0), 6: Gausdal (61.3, 9.9), 7: V-Slidre (61.4, 9.0), 8: Solør (69.1, 18.8) 9: Ringerike (60.3, 10.0) 10: Krødsherad (60.2, 9.7), 11: Vinje (59.6, 7.8), 12: Kongsberg (59.7, 9.6), 13: Østfold (59.3, 11.3). 14: Valle (59.3, 7.6), 15: Vestfold/Telemark (59.5, 11.4), 16: Vest-Agder (58.5, 6.9).

indices of recruitment rate and observation conditions, predicting that relatively more moose would be harvested or observed in high-productive populations or in areas with good conditions for detecting moose, respectively.

## MATERIALS AND METHODS

### Study areas

Data were collected from 16 different study areas (regions) from all over the distributional range of moose in Norway (Fig. 1). Due to different starting year, the study periods for each region varied from 13 to 42 years and ended in 2008 (Table 1). All regions are found within the boreal vegetation zone, except for the southern region (16; Fig. 1) that extends into the nemoral vegetation zone (Moen 1999). The regions vary in

altitude, forest productivity, topography, moose density and extent of moose land (Table 1). Moose land includes all forests and bogs, but not open farmland (agricultural fields), lakes, urban areas and land above the tree line. The moose land in the south (16) and southeast (8, 9, 10, 12, 13, 15) are found at low to moderate altitudes and have higher than average forest productivity. Further west and north, the moose land extends to the tree line and the range of altitude and forest productivity is larger. The dominating tree species is Norway spruce, *Picea abies*, downy birch, *Betula pubescens*, and Scots pine, *Pinus sylvestris*. In the two northern regions, birch and pine constitute the main forest trees, whereas spruce and pine dominate the forests further south. For more information on the study areas,

Table 1. Overview of data from 16 study sites in Norway. Recruitment rate is estimated as the proportion of calves to all moose observed within study site.

Region	Starting year	Study period (years)	Moose land (km <sup>2</sup> )	Annual mean no.				Recruitment rate
				Moose harvested	Moose seen	Hunter-days	Moose-vehicle accidents	
1	1979	30	2983	367	4905	11224	22	0.33
2	1989	20	329	76	1364	1615	3	0.35
3	1967	42	2523	291	2609	5852	49	0.33
4	1989	20	1779	674	4459	7921	41	0.34
5	1982	27	248	43	461	682	4	0.27
6	1979	30	798	211	1031	3360	1	0.27
7	1996	13	250	99	745	1032	3	0.30
8	1987	22	1509	727	4305	9742	16	0.31
9	1986	23	1266	566	2692	6196	30	0.29
10	1988	21	293	148	1038	1143	5	0.31
11	1993	16	885	226	1338	3295	7	0.25
12	1991	18	669	331	2097	3216	13	0.28
13	1992	17	1014	462	2887	9728	27	0.37
14	1992	17	502	129	628	1128	5	0.25
15	1988	21	957	665	3225	4303	14	0.27
16	1995	14	1098	659	4656	5835	16	0.30
Mean		22	1069	355	2402	4767	16	0.30

see Sæther and Heim (1993), Solberg and Sæther (1993), Sæther et al. (1996), Gangsei (1999), Hjeljord and Histøl (1999), and Solberg et al. (2006).

#### *Harvest and hunter moose observation data*

The moose hunting season typically ranges from the last week of September to the end of October, with small variation over time and between regions. In Norway, hunting quotas are established at the municipality level. In our study, 9 of the 16 regions consist of a single municipality, while the remainder consists of 2–7 smaller neighboring municipalities. Hence, in some of the regions the quotas are set by a single authority while in others the quota is the results of several partly independent decisions. However, given the fact that moose may range beyond the size of a municipality, local wildlife authorities are asked (by the national authorities) to collaborate with neighboring municipalities when settling the quotas (or for making other management decisions).

Reporting the number, sex and age (calf, adult) of harvested moose is compulsory for Norwegian moose hunters, and the official harvest statistics is generally assumed to provide accurate estimates of the harvest. On average, 355 (ranging from 12 to 984) moose were harvested per year and region within the study period (see Table 1 for mean values within study sites). We used the

total number of harvested moose in a given year and region divided by the area (km<sup>2</sup>) of moose land as an index of moose density (MD).

Besides reporting the harvest, Norwegian moose hunters are asked to report all moose observed during the hunting season on a standardized form. Called the moose observation monitoring (Morellet et al. 2011), this system was started in a few municipalities in the late 1960s, and extended to cover the entire country during the 1980s. On a daily basis, the leader of each moose hunting team is recording the number, sex (male, female, unknown) and age (calf, adult, unknown) of all moose observed by the team members, but cancel individuals that by certainty are observed by more than one member of the team. In addition, they record the number of members that are hunting each day of the hunting season. Data are later reported to the municipality wildlife board and the national deer register ([www.hjorteviltregisteret.no/](http://www.hjorteviltregisteret.no/)), and used to generate various indices of moose population density and structure for use by the wildlife management (Morellet et al. 2011). On average, 2402 (range: 188–6709) moose were seen by the effort of 4767 hunter-days (range: 434–15045) per year and region during the study period. For average values within study sites, see Table 1. We calculated SPUE (seen per unit effort) as the total number of observed moose divided by the number of hunter-days (i.e., hunters × mean

Table 2. Annual mean of moose density, estimated by the use of cohort analysis, harvest rate (harvest density/moose density) and youngest age in oldest age group in the reconstructed populations. Regions with † are reconstructed based on females only and then rescaled to full population size by the observed sex ratio (see *Methods*).

Region	Annual mean		Youngest age in oldest age group	
	Moose density	Harvest rate	Males ( <i>p</i> )	Females ( <i>q</i> )
1†	0.45	0.31	...	9
2	0.76	0.30	4	4
3	0.43	0.26	6	9
4†	0.98	0.39	...	9
5	0.80	0.21	4	4
6	1.04	0.25	6	9
7	1.48	0.27	6	7
8	1.51	0.32	5	8
9	1.79	0.24	7	9
10	2.25	0.22	6	7
11	1.05	0.24	8	8
12	1.90	0.26	8	9
13	1.60	0.29	6	9
14	1.23	0.21	8	6
15†	2.76	0.25	...	9
16†	2.12	0.29	...	6
Mean	1.39	0.27	...	...

number of days hunting) and the observation density (seen moose density = SMD) as the number of observed moose divided by the area (km<sup>2</sup>) of moose land. In region 3, moose observations were only recorded on 56% of the entire moose land (2522 km<sup>2</sup>) during the period 1968–1986, and accordingly the number of moose observations were scaled with a smaller land area (2522 × 0.56 = 1412) for this period. This land represents the state owned forest and is relatively evenly distributed within the entire moose area.

Unfortunately, we were unable to calculate the catch per unit effort (CPUE), which is another useful index of deer abundance (e.g., Crête et al. 1981, Fryxell et al. 1988, 1991, Hatter 2001, Schmidt et al. 2005). This is because harvest data, until recently, only has been reported as the municipality sum of moose killed, and because the moose observation form was not submitted by all hunting teams. Accordingly, we were not able to scale the harvest with the total number of days hunting in most years and areas.

#### Density of moose-vehicle accidents

As a measure of MVA, we used the official

number of moose killed on roads in each year and region. All car drivers that collide with moose are obliged to report the accident to the police and municipality wildlife board, which in turn report all killed individuals to Statistics Norway (www.ssb.no). These involve moose killed on impact or moose injured in the accident and later dispatched by wildlife officials. Moose that are visually assessed by wildlife officials to be unharmed, or that are not seen after the accident, are not included. MVAs are reported for the hunting regulatory year (1 April–31 March), but assigned to the first year in the period. Most moose are killed in traffic during October–February (Solberg et al. 2009). On average, 16 (ranging from 0 to 101) moose were killed on roads per year and area (Table 1). We used the total number of MVAs divided by the area (km<sup>2</sup>) of moose land within region as an index of moose density.

#### Age- and sex-specific harvest data for cohort analysis

Data on age and sex of harvested moose were available for 13–42 years in the different regions. Sex and kill date were recorded by the hunters in the field and the lower jaws collected for age determination in the lab. Calves and most yearlings were aged by the tooth replacement pattern while age in older animals was determined by the number of annuli in the cementum of incisors. Both methods are widely used in ungulate research and are found to provide accurate estimates of age in moose (e.g., Rolandson et al. 2008). All data have been collected as part of local and regional monitoring programs for moose and are available at NINA (www.nina.no) and the management agency Faun naturforvaltning AS (www.fnat.no).

Age data are available for most males and females harvested during the study periods, but for economic reasons data have not been collected for males in four areas (Table 2). Moreover, in region 13 (Fig. 1), age determination of older moose were only conducted every second year. For years with missing data we estimated the age structure of the harvest by interpolation between neighboring years (i.e., the average between the year before and after). Such interpolations have only small effects on the precision of the reconstructed population as the age structure of

the harvest are only varying slightly between successive years (Gangsei 1999). Overall, we used 95,650 harvested moose in the cohort analyses, of which age was determined for 85,441 (90%) moose by tooth replacement patterns or sectioning. The remaining (non-aged) moose were assigned the same age structure as the aged sample.

#### *Population reconstruction by cohort analysis*

The moose density was estimated using cohort analysis, which is a retrospective reconstruction of population abundance using the age-at-death data collected over several years. This method was originally developed within the fishery sciences (e.g., Gulland 1965, Pope 1972), but has also been extensively used to reconstruct populations of ungulates, such as moose (e.g., Fryxell et al. 1988, Solberg et al. 1999, 2004, Vucetich and Peterson 2004, Ueno et al. 2009).

The standard equation of cohort analysis describes the annual transition of the number of individuals in a particular age-class subject to autumn harvesting in a pulse-like event and natural mortality throughout the year (e.g., Solberg et al. 1999). Here, we used the following equation:

$$(N_{i,t} - C_{i,t})\exp(-NM) = N_{i+1,t+1}$$

where  $N_{i,t}$  is the reconstructed number of moose at age  $i$  in year  $t$ , just prior to the autumn hunting season,  $C_{i,t}$  is the number of moose killed at age  $i$  in year  $t$ , and  $NM$  is the assumed natural mortality coefficient, i.e., mortalities excluding harvesting. Conversely, the term  $\exp(-NM)$  is the survival rate from natural causes, i.e., the survival rate becomes smaller as the coefficient gets larger. The mortality coefficient ranges from 0 to infinity, and is more mathematically convenient to use than the mortality rate (Ueno et al. 2009). In this study, we assumed  $NM$  to be 0.05, with no annual variation.

By rewriting the above equation as:

$$N_{i,t} = N_{i+1,t+1}\exp(NM) + C_{i,t}$$

the number of moose can be reconstructed by backward calculation of the number of moose from the initial values. The initial values are moose abundance at the oldest age group, i.e.,  $\geq p$  years for males and  $\geq q$  years for females (see Table 2 for  $p$  and  $q$ ) or moose abundance for the

latest year, i.e., the year of 2008 (Fryxell et al. 1988, Solberg et al. 1999). We computed moose abundance in the older aged group from the harvest size of the oldest age group, the estimated hunting mortality, and the assumed natural mortality (Ueno et al. 2009). We estimated hunting mortality for the oldest age group by a simple linear regression of hunting mortality at age  $p+$  ( $q+$  for females) against the mortality at age  $p-1$  ( $q-1$  for females) for cohorts that have passed completely through the population (Ueno et al. 2009). The number of moose aged  $p$  ( $q$  for females) was computed by assuming a stationary stable age distribution in the oldest age class for each year (Ueno et al. 2009). Likewise, we computed the age-specific moose abundance for the final year from the harvest size and the estimated hunting mortality and assumed natural mortality (Ueno et al. 2009). The hunting mortality was assumed to be the arithmetic mean of the corresponding age-specific hunting mortality coefficients from 2005–2007. The computation of hunting mortality in the oldest age group and for the latest year is described in Appendix 1 of Ueno et al. (2009).

The cohort analysis obtains point estimates of population abundance for a given natural mortality, for which we assumed no annual variation during the study period. Although this is an unrealistic assumption, we expected only minor variation in the magnitude of natural mortality after the first 6 months in life (Gaillard et al. 2000). Indeed, most radio-telemetry studies of Norwegian moose indicate that natural mortality rates ranges from 2% to 5% for adult females and <1% to 6% for calves after the age of 6 months (Lorentsen et al. 1991, Sæther et al. 1996, Stubsjøen et al. 2000). However, natural mortality for calves may be as high as 17% in certain populations and years (Stubsjøen et al. 2000). No estimates for male natural mortality are available in Norway, but Swedish male moose are subject to about 3% natural mortality (Ericsson and Wallin 2001). Reconstructing the populations with natural mortality rates varying from 0 to 10% produced abundance estimates within  $\pm 20\%$  of the estimates in this study, but the temporal trend was the same (Ueno et al. 2010; Fig. 1). Hence, given that the natural mortality rates are not varying much among years or areas, the reconstructed population should provide a

reasonable reflection of the spatiotemporal variation in moose density.

We sorted the numbers-at-age by year to calculate the annual population abundance and converted abundance to density by dividing by the km<sup>2</sup> of moose land within study area (Table 2). For areas 1, 4, 15, 16, we only reconstructed the female part of the population. To make these estimates comparable with other regions, we divided the female density by the proportion of females observed by the moose hunters in the area. Moreover, because the population reconstruction for the last years in the time series depends heavily on the assumed hunting mortalities (Ueno et al. 2009), we skipped the last four years of the times series and only used data until 2004 in the analysis.

#### Data analysis

We modeled the relationships between indices and moose density using linear mixed effect models (Bates and Maechler 2010) with region and/or year included as random factors, and with different time lags of moose density to examine the extent to which it was a monotonic, isometric, and precise reflection of moose density. We added year as a random factor to adjust for unexplained variation caused by missing explanatory variables, including temporal autocorrelation (Rolandsen et al. 2011). For models with harvest (HD) or traffic kill (MVA density) as dependent variable, we used area as offset variable while the number of observations was scaled with area (SMD) or effort (SPUE) as offset. We also tested models with random slope, e.g., to test if the slope parameter varies among regions. Both moose density and density indices were log-transformed before use to be able to test their proportional relationship. We included one density variable at a time and selected the density with the time-lag that provided the best fit to the data.

To facilitate the interpretation of the model output we first split  $\ln(\text{moose density})$  into region-specific mean density (average of  $\ln(\text{moose density})$  within regions) and centered annual density ( $\ln(\text{annual density}) - \text{average of } \ln(\text{moose density})$ ). Accordingly, the average centered moose density will be similar (0) in all regions and vary among years within regions. By using the mean and the centered density in the

mixed effect models, we could estimate the effect of density between (spatial relationship) and within regions (temporal relationship), respectively. In general, we expected a positive temporal effect of density, but to a lesser extent a spatial effect (see *Introduction*).

Besides moose density, we included four other covariates in the models. These included (1) the proportion high-altitude area (proportion forested area above 250 m asl), (2) the proportion of bogs and (3) the proportion of deciduous trees within regions. We predicted that more moose would be seen for a given effort (i.e., SPUE) and moose density in higher altitude areas, i.e., due to less dense forest, and in areas with a higher proportion of bogs, i.e., because of a more open forest structure. Both are likely to increase the observation conditions and hence the probability to see a moose for a given density. Deciduous trees may have a similar effect because the forest becomes more transparent after leaves are shed in the autumn. In the model with harvest density we also tested for an effect of (4) recruitment rate. This measure was simply the proportion of calves observed during the hunting season, which is varying among populations (Table 1). We expected the recruitment rate to have a positive effect on harvest density since a higher proportion of the pre-harvest population can be harvested in more productive populations. In models with SMD or MVA density as dependent variable, we did not test the effects of additional covariates. Because the sample size of MVAs was very low in several study sites (Table 1), models with MVA density were weighted by the number MVAs.

The seen moose indices, harvest density and the estimated moose density are based on partly different data, but are collected by the same hunters. Accordingly, these indices may share certain (unknown) qualities that make them not entirely independent. To examine if this have seriously confounded the relationships, we also compared the hunter based indices with the variation in MVA density using a nonparametric correlation analysis. To reduce the influence of low sample sizes, we only included study sites with on average >10 MVAs per year in these analyses (Table 1).

We used the Akaike information criterion (Burnham and Anderson 2002) corrected for

small sample size ( $AIC_c$ ; Burnham and Anderson 2002) for model selection. The models with the lowest  $AIC_c$  score were considered to be the most parsimonious approximation for the information in the data (Burnham and Anderson 2002). We also considered candidate models that differed by two or less in absolute value ( $AIC_c$ ) from the best models as these are alternative good models (Burnham and Anderson 2002). Mixed effect models were fitted with maximum likelihood (ML) for model selection, whereas restricted maximum-likelihood (REML) was used to obtain un-biased parameter estimates (Pinheiro and Bates 2000). For comparison we provided the intercept and slope estimates from region-specific linear regression models.

To provide a baseline against which we could compare the more complex models, we estimated the variance components in a model including no other covariates (i.e., recruitment rate or proportion deciduous trees) but with only region included as random factor. We then estimated the fraction of explainable variation accounted for by the fixed effects in the more complex models. Following Singer (1998), we computed the proportion explainable variation explained as:  $(VC1 - VC2)/VC1$ , where VC1 and VC2 are the variance components in the baseline and the more complex model, respectively. A large proportion of variance explained would suggest that moose density is reasonably well reflected by the density index. All statistics were performed using R 2.15.1 (R Development Core Team 2011).

## RESULTS

### *Variation in moose density*

The reconstructed moose populations showed large spatiotemporal variation in density (Figs. 2–5). On average, lower densities were observed in the northern than the southern areas, ranging from about 0.43 (area 3) to 2.76 moose/km<sup>2</sup> (area 15, Table 2). With few exceptions (4, 14, 16), there were large fluctuations in moose density within areas (Figs. 2–5). The overall harvest rate was 0.27 during the study period, ranging from on average 0.21 to 0.39 between areas (Table 2).

### *Relationships between density indices, moose density and other covariates*

Harvest density was positively related to the variation in moose density within and between areas (Fig. 2, Table 3). Despite some variation in slopes among areas (i.e., random slope included in the best model), the slope of the temporal relationship between (ln)HD and (ln)moose density was on average larger than 1 (Table 3). Moreover, the temporal variation in HD was best explained by moose density in year  $t - 1$  than in year  $t$  ( $AIC_c = 125$ ) or year  $t - 2$  ( $AIC_c = 58$ ), indicating that HD is a delayed reflection of moose density (Table 3; Appendix: Fig. A1). Among areas, the variation in HD did not deviate from an isometric relationship with moose density (Table 3), and was partly related to the variation in recruitment rate (Table 3). The latter was in accordance with the prediction that more productive populations can produce a higher harvestable surplus for a given density.

Moose seen per unit effort was positively related to the variation in moose density within and between areas (Fig. 3, Table 3). The best relationship was found with the post-harvest density in year  $t$  (Table 3; Appendix: Fig. A2). Moreover, the slopes of the temporal and spatial log-log relationship were less than 1 in accordance with the prediction that the searching efficiency decreases with increasing population density (Table 3). The spatial variation in SPUE was also related to the proportion of deciduous trees in the study area, indicating that the conditions for detecting moose are better in areas where a larger part of the trees are shedding their leaves in the autumn. Also the proportion of high altitude area and proportion of bogs were positively related to the variation in SPUE, but were not included in the best model. Possibly, this was because of their relatively high correlation with the proportion of deciduous trees (proportion deciduous trees vs. high altitude area:  $r = 0.32$ , deciduous trees vs. proportion bogs:  $r = 0.43$ ).

As for SPUE, SMD was positively related to the variation in moose density within and between areas (Fig. 4, Table 3). The log-log relationship did not deviate from an isometric relationship within areas, but was lower than 1 between areas (Table 3). We found no indications of time lags in the relationship between SMD and moose den-



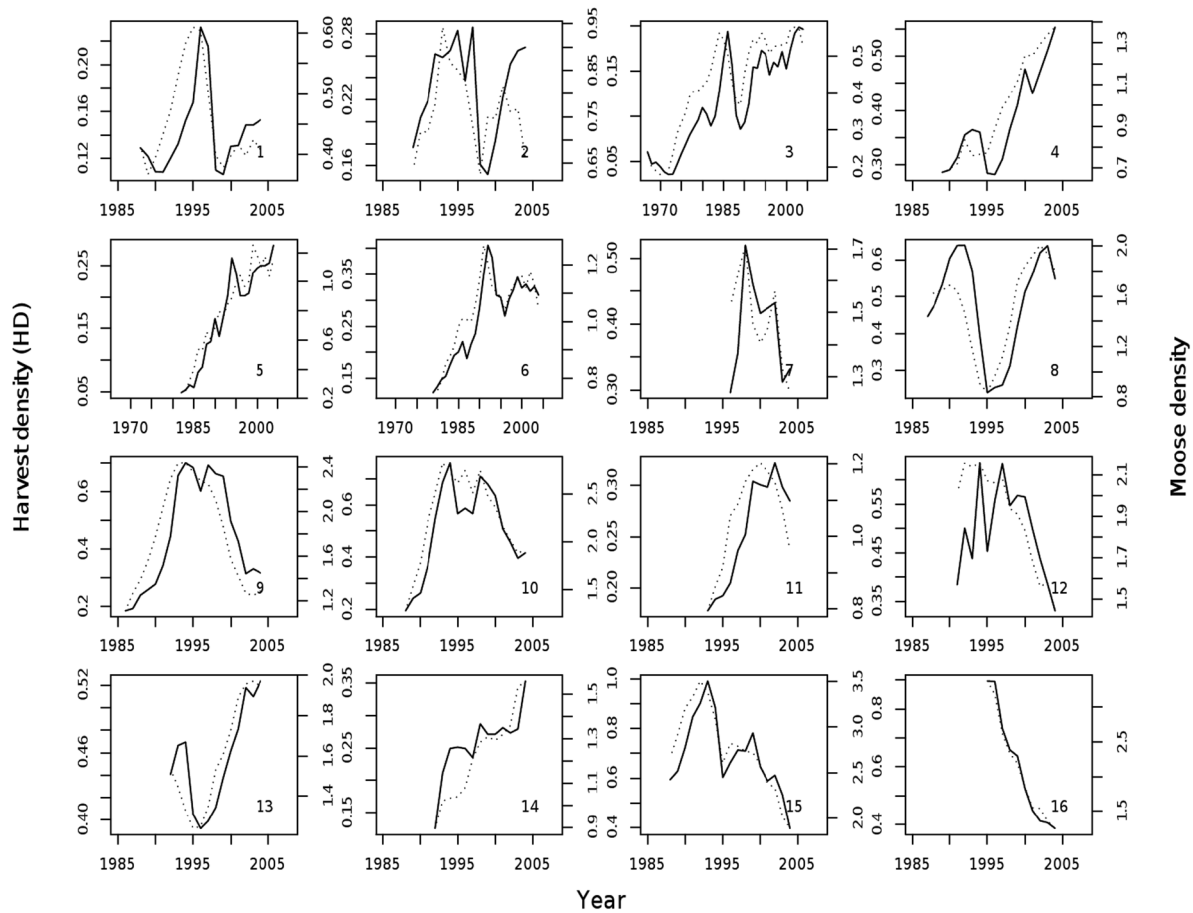


Fig. 2. Time series of harvest density (HD; solid line) and moose density (dotted line) in the period 1967–2004 for 16 study sites in Norway.

sity (Fig. 4; Appendix: Fig. A3).

Moose-vehicle accident density was positively related to moose density within areas, while moose density between areas did not enter the highest ranked model (Fig. 5, Table 3). The temporal variation in MVA density was best explained by moose density in year  $t + 1$ ; a result that most likely reflect that MVAs are collected from the hunting regulatory year (1 April–31 March), while most MVAs happen during October–February, i.e., mostly after the hunting season in year  $t$  (see *Methods* and Appendix: Fig. A4). The slope of the relationship between  $(\ln)$ MVA density and  $(\ln)$ moose density was larger than 1 within areas (Table 3). We also found in general high positive correlations between the hunter based indices and MVA density (SPUE-MVA, mean  $r_{Sp} = 0.60$ , range:

0.34–0.95, SMD-MVA, mean  $r_{Sp} = 0.56$ , range: 0.29–0.94,  $HD_{t+1}$ -MVA, mean  $r_{Sp} = 0.47$ , range: 0.05–0.93).

The region specific intercepts from the best mixed effect models (“shrinkage estimates,” Pinheiro and Bates 2000) indicate that the between spatial variation in density alone could explain a substantial part of the variation in HD (e.g., “shrinkage estimates” vary less than regression intercepts), but far less of the spatial variation in SPUE, SMD and MVA. In models including no other covariates (i.e., recruitment rate or proportion deciduous trees), mean and centered moose density explained 95% and 84% of the explainable variation in HD between (spatial) and within (temporal) areas, respectively. Hence, HD alone seems to be a good predictor of the spatiotemporal variation in moose density

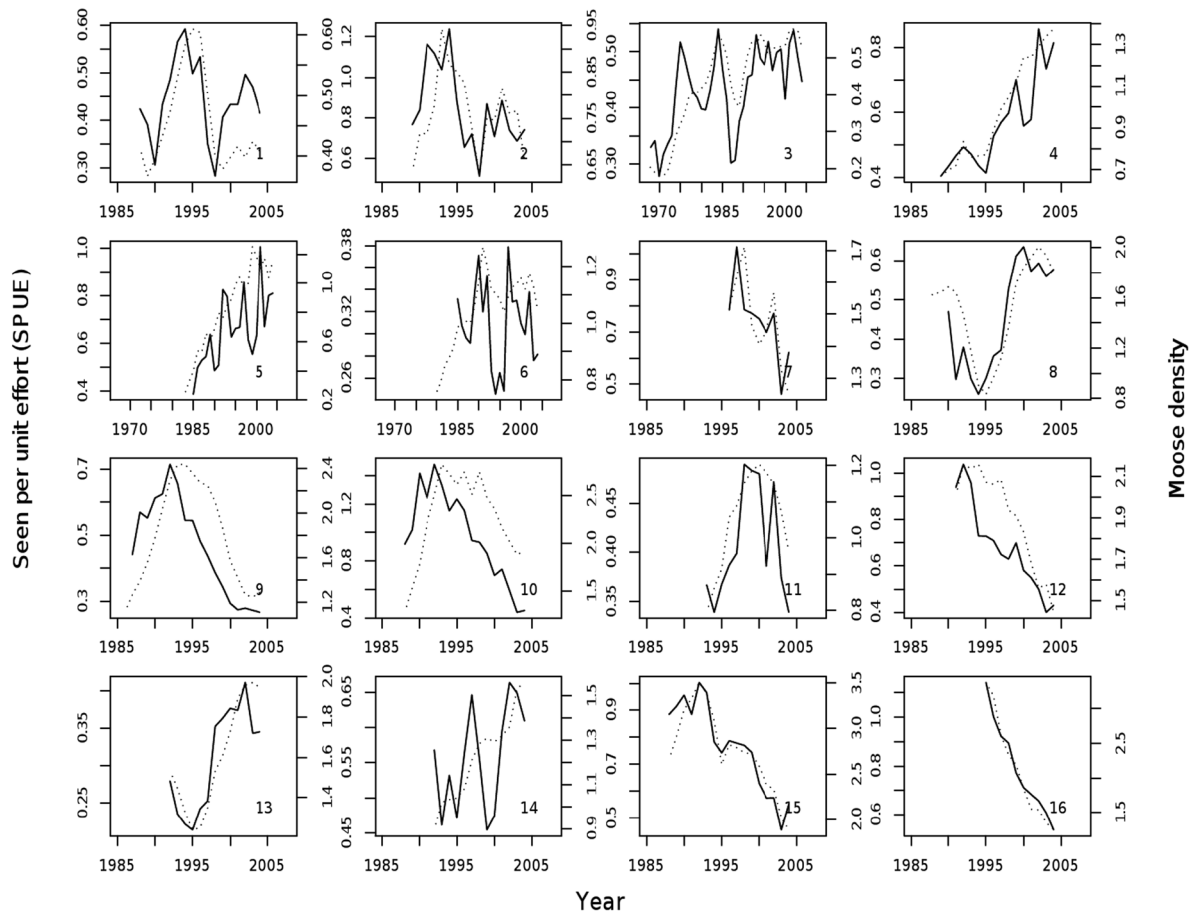


Fig. 3. Time series of seen per unit effort (SPUE; solid line) and moose density (dotted line) in the period 1967–2004 for 16 study sites in Norway.

(Appendix: Fig. A1). For other indices, substantial higher proportions of the variation were explained by moose density within areas (SMD: 62%, SPUE: 48%, MVA density: 25%) than between areas (SMD: 23%, SPUE: 17%, MVA density: –3%). These indices are therefore less useful for predicting variation in moose density between areas.

## DISCUSSION

Many studies have used density indices to detect trends in deer abundance or spatial variation in density, but often based on the assumptions that the relationship with density is monotonic, isometric (proportional) and precise. We examined the validity of those assumptions for four indices of moose density in 16 areas

in Norway. The results indicated that all indices were monotonically related to moose density within areas, but that they differed in degree of being isometric and precise. Harvest density showed the closest relationship with moose density both within and between areas, but the temporal variation in HD was a delayed reflection of moose density and tended to overestimate its growth and decline. Conversely, SMD and SPUE were unable to predict the spatial variation in moose density with high precision, though both observation indices were good temporal reflectors of the variation in moose density. However, the SPUE tended to underestimate the population growth, possibly because of decreasing searching efficiency with increasing density. In the following we discuss the basis of these relationships, as well as the utility of the

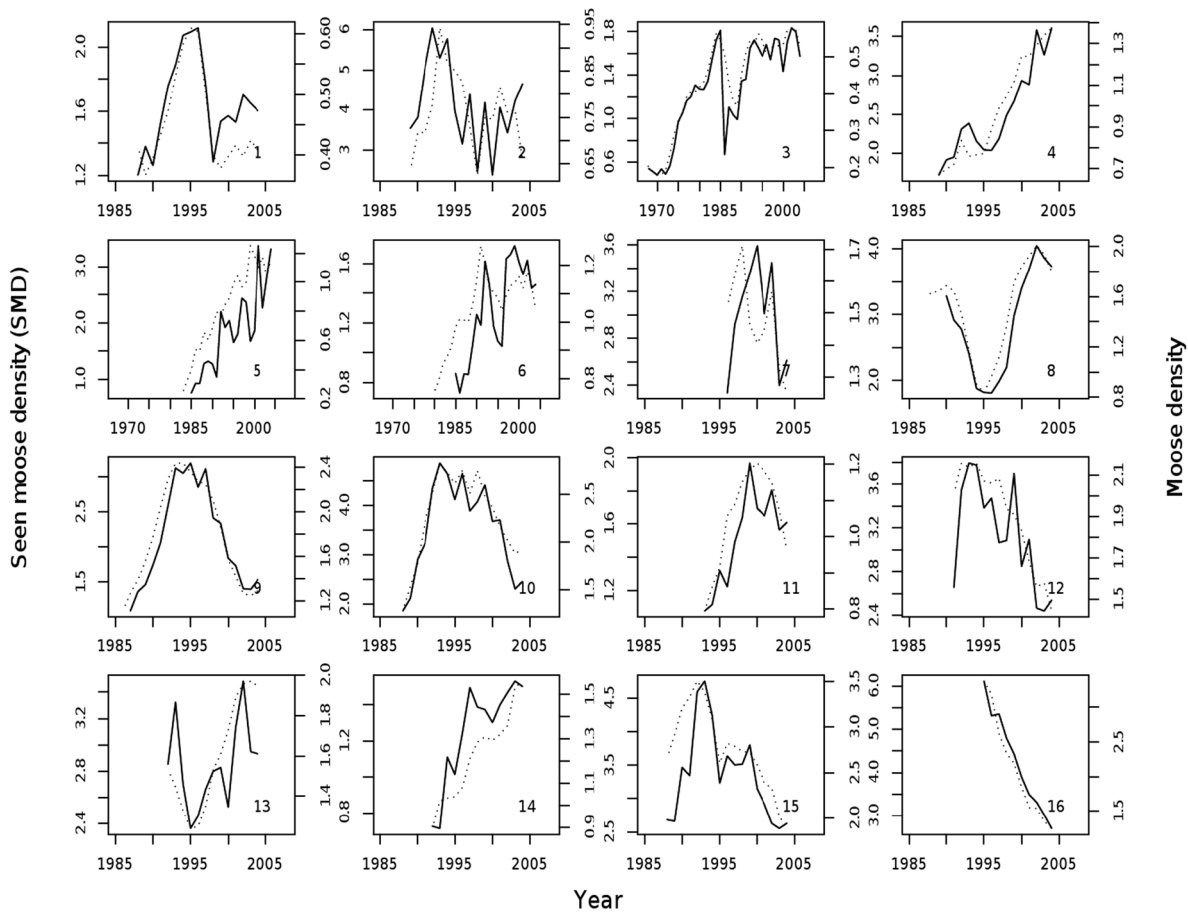


Fig. 4. Time series of seen moose density (SMD; solid line) and moose density (dotted line) in the period 1967–2004 for 16 study sites in Norway.

indices for management purposes.

The utility of hunting statistics as density indices differed depending on the spatiotemporal scale. As for comparison between areas, HD was a fairly good reflector of the variation in moose density, while SPUE and SMD failed to represent the spatial variation in moose density. However, both observation indices provided a good representation of the temporal variation in moose density within study sites, consistent with previous studies (Ericsson and Wallin 1999, Solberg and Sæther 1999, Rönnegård et al. 2008). Part of the spatial variation in SPUE was explained by the proportion of deciduous forests, which we believe can have a strong effect on the visual transparency of the forest and thus the probability of detecting a moose. Because more deciduous forests are found in the more rugged

landscape at higher altitudes and in the north, more moose may also be observed at larger distances. Still, a large part of the spatial variation in SPUE (and SMD) remained unexplained, possibly because of different hunting practices between areas (Ericsson and Wallin 1999). Conversely, most of the spatial variation in HD was explained by the variation in moose density although the model fit increased by adding an index of recruitment rate as a covariate. Many previous studies have used HD as an index of moose abundance among areas because this is the only available index at larger scales (e.g., Seiler 2005). In this study, we show that the variation in hunting rate was rather small compared to the regional variation in detectability. Hence, HD seems to provide a fair index of the spatial variation in moose density at

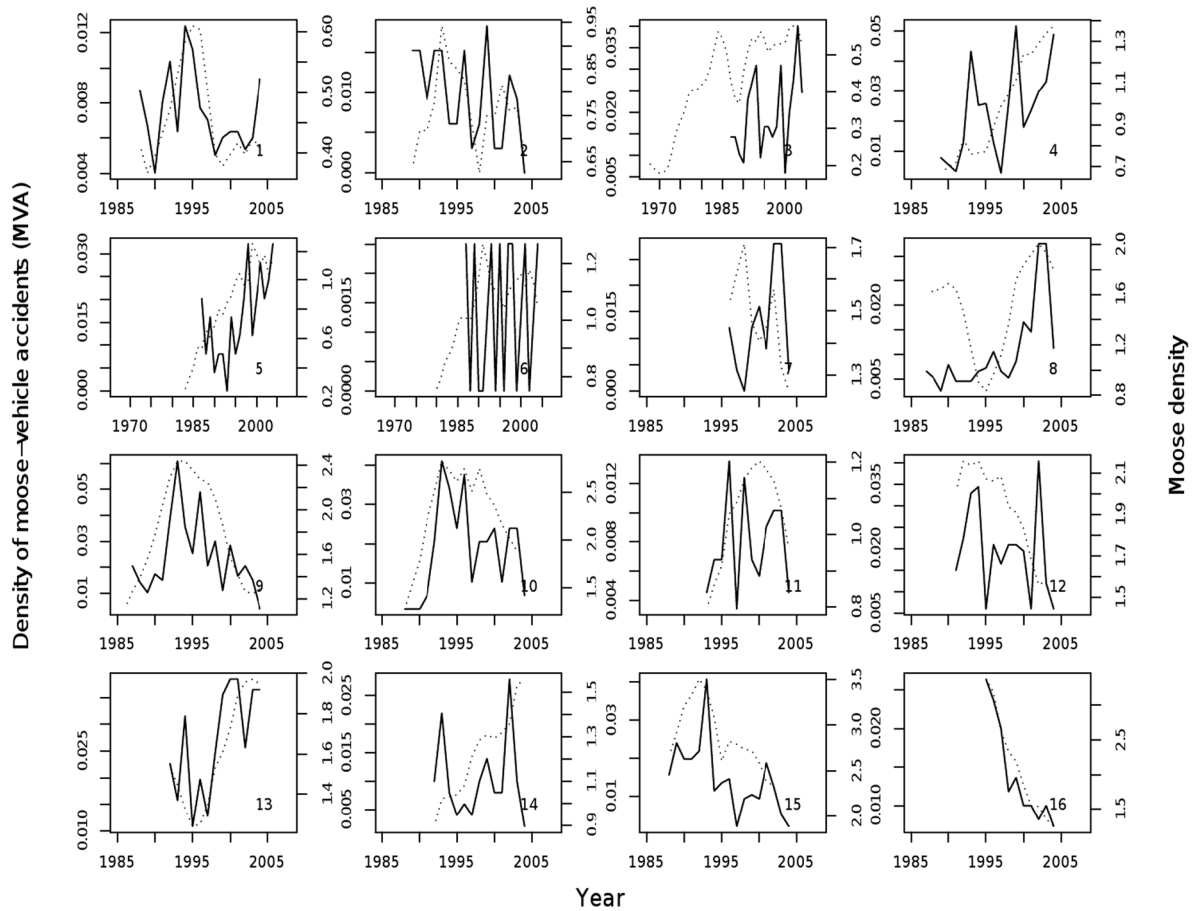


Fig. 5. Time series of the density of moose-vehicle accidents (MVA; solid line) and moose density (dotted line) in the period 1967–2004 for 16 study sites in Norway.

Table 3. Parameter estimates for the best models (according to AIC<sub>c</sub>) explaining the variation in harvest density (HD), observation density (SMD), seen per unit effort (SPUE) and density of moose-vehicle accidents (MVA).

Model	$\hat{A}$	1 SE	Random intercept for region	Random intercept for year	Random slope of centered moose density
Harvest density					
Intercept	-2.110	0.277	X		X
Mean (ln)moose density <sub>t-1</sub>	0.976	0.059			
Centered (ln)moose density <sub>t-1</sub>	1.177	0.085			
Mean recruitment rate	2.631	0.905			
Seen per unit effort					
Intercept	-0.902	0.168	X		X
Mean (ln)postharvest moose density	0.700	0.099			
Centered (ln)postharvest moose density	0.823	0.078			
Mean proportion of deciduous trees	0.812	0.312			
Observation density					
Intercept	0.687	0.097	X	X	
Mean (ln)moose density	0.488	0.171			
Centered (ln)moose density	0.982	0.040			
Moose-vehicle accident density					
Intercept	-4.279	0.033	X	X	
Centered (ln)moose density <sub>t+1</sub>	1.300	0.036			

the spatial scale of our study sites.

Despite of being a rather precise index of moose density, the rate of increase in HD was larger than that in moose density within study sites, a fact we believe is due to density dependent harvesting. In the almost absence of large carnivores, such as wolves (*Canis lupus*) and bears (*Ursus arctos*), Norwegian moose populations are mostly regulated (controlled) by harvesting (Solberg et al. 1999, 2006). Accordingly, the rate of increase in number of permits is usually higher than the rate of increase in density, particularly when the population is approaching historically high densities for the area (Solberg et al. 1999). In accordance with the strong impact of hunting on the moose population dynamics, we also found HD to be a time delayed reflection of moose density. This is a common observation in predator-prey systems, where the predator is the main driver of the prey dynamics (Anderson and May 1978, Hanski et al. 2001), and has also been shown in systems where humans are the main predator (e.g., Ferguson and Messier 1996, Solberg et al. 1999). Because managers and hunters are often unable to respond instantaneously to changes in prey abundance, harvesting can induce large fluctuations in the population size (Fryxell et al. 2010). Such fluctuations are apparent in several of the 16 study sites, in particular in the first part of the time series, at a stage when the use of the seen moose indices was still in its infancy (Solberg and Sæther 1999). As the use of seen moose indices increases, we expect to see stronger compensatory responses by managers, and fewer unintended large fluctuations in population size.

Contrary to HD, the SPUE increased with a rate less than proportional with moose density, which has also been reported by others (Ericsson and Wallin 1999, Solberg and Sæther 1999). On average, the SPUE increased by 80% for every doubling of the population (Table 3), a pattern that did not differ between increasing or decreasing populations (Fig. 3). A similar pattern was observed by Hatter (2001) between the catch per unit effort (CPUE) and abundance in declining populations of black tailed deer (*Odocoileus hemionus columbianus*) and moose. He suggested that this could be due to increased concentration of hunting in high density areas and/or decreased participation of less experienced hunters as

population density decline, a phenomenon often referred to as saturation effects in the fisheries science (Gaertner and Dreyfus-Leon 2004). Similar changes could also have occurred in our study populations, leading to a decline in searching efficiency as population size increased. The fact that SMD—which is not scaled with hunting effort—increased proportionally with moose density (Table 3), support such an explanation.

We also suspect that the searching efficiency have been affected by varying handling time. Moose hunting in Norway is typically performed by a team of hunters harvesting several moose during the season (e.g., 0–46 kills per team in the study areas in 2008, mean = 4.25), and where most members are also participating in the process of transporting, skinning and butchering the carcass. As a consequence, more of the hunting day is likely to be used for handling the kill than searching for moose as population density and hunting success increase (Solberg et al. 2006). A similar mechanism was also suggested by Myrsetrud et al. (2007) to explain the weak relationship between seen red deer per hunter-day and red deer density in Norway. As a possible remedy, both moose and red deer hunters in Norway are now asked to record not only the number of hunter-days, but also the number of hours actually searching as a measure of hunting effort ([www.hjorteviltregisteret.no](http://www.hjorteviltregisteret.no)).

The MVA density was the only index examined based on data not collected during the hunting season, and may as such provide a valuable corrective to the lack of independence among the other indices. Indeed, as also the age-at-death data used for reconstructing population density are collected by hunters, we acknowledge that the hunter based indices (mainly HD and SMD) and moose density may not be entirely independent (i.e., a common source of data). It was therefore reassuring to find mainly positive temporal relationships between MVA density and moose density and between the hunter-based indices and MVA density in most study sites. Also previous studies have found the number of MVAs to correlate positively with SPUE and the annual harvest within area (e.g., Seiler 2005, Solberg et al. 2009, Rolandsen et al. 2011), as well as with the moose harvest among areas (Solberg et al. 2009, Rolandsen et al. 2011).

Compared to the other indices, however, MVA density performed relatively poor as an index of moose density within areas, and not at all with moose density among areas. Most likely this has to do with the additional influence of other factors on the number of MVAs (Andersen et al. 1991, Seiler 2005, Rolandsen et al. 2011) combined with the low annual number of traffic kills recorded in several study sites (mean  $n = 18$ ). Although testing for other interacting factors is beyond the scope of this study, we particularly suspect that varying snow conditions (Andersen et al. 1991, Rolandsen et al. 2011) and traffic intensity (cars per km per year) (Seiler 2005, Rolandsen et al. 2011) affected the pattern. Moreover, in our study the spatial scale of several areas are likely to be too small to encompass the annual migration distances of moose (see, e.g., Bunnefeld et al. 2011). Thus, density estimates for the hunting season (Cohort analysis, HD, SMD and SPUE) may not always correspond well with density estimates originating from data collected over the whole year, such as MVA density. In support for this, Rolandsen et al. (2011) found an isometric relationship between MVA and HD at a larger spatial scale after controlling for factors related to climate and traffic intensity.

#### *Conclusions and management implications*

There was no perfect density index to reflect the temporal and spatial variation in moose density, although some indices performed better than others. First, HD seems to provide a fair index of the spatial differences in moose density at the spatial scale of our study sites, while SMD and SPUE were largely influenced by region-specific detectability. However, although HD also traced temporal variation in moose density within populations, HD is more of a product than a source of census information (Myrsterud et al. 2007) and may therefore respond with large fluctuations if by chance the growth in hunting quota should deviate much from the population growth rate. This may happen even in tightly managed populations, where large changes in the harvest pressure often are needed to achieve management goals. Large changes in the harvest pressure are almost bound to create a time delay in the response of the harvest to a change in density, and for that reason alone we advise

managers to never use harvest density as the only source of information to set the annual quota.

Unlike HD, SPUE and SMD have the benefit of being directly synchronized with the pre- or post-harvest moose density. However, although SMD were more precise than the SPUE, it is not scaled with hunting effort. Accordingly, we suspect that SMD, like the HD, may show large deflections when the number of permits is large relative to the population size. Under such conditions, hunters are likely to hunt for more days and thus see more moose, with the result that both the HD and SMD become disproportionately high. This is less of a problem for SPUE, which is scaled with effort. In contrast, the SPUE did not change proportionally with moose density and therefore cannot be used for estimating the rate of growth in moose populations unless the relationship between SPUE and density is known. From a management perspective, we cannot therefore advise the single use of any of the indices, but suggest that management decisions should be based on a collectively assessment of the development in all indices. In that process the management could also take advantage of other correlates of moose density, such as the MVA. Because this index is based on data not collected during the hunting season, it is a valuable corrective for cross-checking the temporal population trends suggested by the hunter-based indices. MVA may be particularly valuable if the management can also control for temporal variation in climatic (e.g., snow depth) and road specific variables (e.g., Rolandsen et al. 2011).

Because of the substantial traffic and commercial forest costs associated with high moose density, it is generally accepted that Norwegian moose populations should be regulated at moderate densities by harvesting. To enable that, regional managers need reliable information of population trends, but at a monetary cost compatible with the income from the annual hunting fee. Aerial surveys and pellet group counts have been conducted in several areas at irregular intervals, but these methods are usually found too expensive to run on a regular basis. As an alternative, indices based on moose observation data are cheap, and may provide as precise estimates as aerial surveys (Rønnegård et al. 2008). Although similar conclusions have been

drawn in other studies (Rönnegård et al. 2008), the novelty of our study is to demonstrate that the same positive pattern appears across large environmental gradients and in regions of different spatial scales.

## ACKNOWLEDGMENTS

This work was funded by the Norwegian Research Council (Japan–Norway Researcher Mobility Program 2009, Miljø 2015, 184036), the Directorate for Nature Management, the Norwegian Institute for Nature Research, Faun Naturforvaltning and the Japanese Society for Promoting Sciences. We also thank all hunters and regional managers for collecting basic data, and technicians at Faun and NINA for processing (age determination) and managing the huge number of data.

## LITERATURE CITED

- Andersen, R., B. Wiseth, P. H. Pedersen, and V. Jaren. 1991. Moose-train collisions: effects of environmental conditions. *Alces* 27:79–84.
- Anderson, R. M. and R. M. May. 1978. Regulation and stability of host-parasite population interactions. *Journal of Animal Ecology* 47:219–247.
- Apollonio, M., R. Andersen, and R. Putman. 2010. European ungulates and their management in the 21st century. Cambridge University Press, Cambridge, UK.
- Bates, D., and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-35 <http://CRAN.R-project.org/package=lme4>
- Buckland, S. T., I. B. J. Goudie, and D. L. Borchers. 2000. Wildlife Population Assessment: Past Developments and Future Directions. *Biometrics* 56:1–12.
- Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80:466–476.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach second edition. Springer, New York, New York, USA.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, New York, USA.
- Crête, M., R. J. Taylor, and P. A. Jordan. 1981. Optimization of moose harvest in southwestern Quebec. *Journal of Wildlife Management* 45:598–611.
- Ericsson, G. and K. Wallin. 1999. Hunter observations as an index of moose *Alces alces* population parameters. *Wildlife Biology* 5:177–185.
- Ericsson, G. and K. Wallin. 2001. Age-specific moose (*Alces alces*) mortality in a predator free environment: evidence for senescence in females. *Écoscience* 8:157–163.
- Ferguson, S. H. and F. Messier. 1996. Can human predation of moose cause population cycles? *Alces* 32:149–161.
- Forchhammer, M. C., N. C. Stenseth, E. Post, and R. Langvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. *The Royal Society of London B* 265:341–350.
- Fryxell, J. M., D. J. T. Hussell, A. B. Lambert, and P. C. Smith. 1991. Time lags and population fluctuations in White-tailed deer. *Journal of Wildlife Management* 55:377–385.
- Fryxell, J. M., W. E. Mercer, and R. B. Gellately. 1988. Population dynamics of Newfoundland moose using cohort analysis. *Journal of Wildlife Management* 52:14–21.
- Fryxell, J. M., C. Packer, K. McCann, E. J. Solberg, and B.-E. Sæther. 2010. Resource management cycles and the sustainability of harvested wildlife populations. *Science* 328:903–906.
- Gaertner, D. and M. Dreyfus-Leon. 2004. Analysis of non-linear relationships between catch per unit effort and abundance in a tuna purse-seine fishery simulated with artificial neural networks. *ICES Journal of Marine Sciences* 61:812–820.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Reviews in Ecology and Systematics* 31:367–393.
- Gangsei, L. 1999. Er alle elgar like lette å observere? Evaluering av sett-elg metodikk ut frå samanlikning med modellpopulajsonar bygd på kohortanalyse. Hovedoppgåve ved Institutt for biologi og naturforvaltning. Norwegian University of Life Sciences, Ås, Norway. (In Norwegian.)
- Gulland, J. A. 1965. Estimation of mortality rates. Annex to the Northeast Arctic working group report. International Council for the Exploration of the Sea C.M. Doc. 3. Hamburg.
- Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. Small-rodent dynamics and predation. *Ecology* 82:1505–1520.
- Hatter, I. W. 2001. An assessment of catch per unit effort to estimate rate of change in deer and moose populations. *Alces* 37:71–77.
- Hjeljord, O. and T. Histøl. 1999. Range-body mass interactions of a northern ungulate—a test of hypothesis. *Oecologia* 119:326–339.
- Lorentsen, Ø., B. Wiseth, K. Einvik, and P. H. Pedersen. 1991. Elg i Nord-Trøndelag—Resultater fra elgundersøkelsene 1987–1990 om vandringsmønster, brunst, kalvinger og dødelighet. Fylkesmannen i Nord-Trøndelag. Report 1. (In Norwegian.)
- Moen, A. 1999. National atlas of Norway: vegetation. Norwegian Mapping Authority, Hønefoss, Norway.

- Morellet, N., F. Klein, E. J. Solberg, and R. Andersen. 2011. The census and management of populations of ungulates in Europe. Pages 106–143 in R. J. Putman, M. Apollonio, and R. Andersen, editors. *Ungulate management in Europe: problems and practices*. Cambridge University Press, Cambridge, UK.
- Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2002. Large-scale habitat variability, delayed density effects and red deer populations in Norway. *Journal of Animal Ecology* 71:569–580.
- Mysterud, A., E. L. Meisingset, V. Veiberg, R. Langvatn, E. J. Solberg, L. E. Loe, and N. C. Stenseth. 2007. Monitoring population size of red deer *Cervus elaphus*: an evaluation of two types of census data from Norway. *Wildlife Biology* 13:285–298.
- Mysterud, A., N. G. Yoccoz, N. C. Stenseth, and R. Langvatn. 2001. Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Royal Society of London B* 268:911–919.
- Pinheiro, J. C., and D. Bates. 2000. *Mixed-effects models in S and S-PLUS*. Springer Verlag, New York, New York, USA.
- Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. *Research Bulletin of the International Commission for the Northwest Atlantic Fisheries* 9:65–74.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rolandson, C. M., E. J. Solberg, M. Heim, F. Holmstrøm, M. I. Solem, and B. E. Sæther. 2008. Accuracy and repeatability of moose (*Alces alces*) age as estimated from dental cement layers. *European Journal of Wildlife Research* 54:6–14.
- Rolandson, C. M., E. J. Solberg, I. Herfindal, B. van Moorter, and B. E. Sæther. 2011. Large-scale spatiotemporal variation in road mortality of moose: Is it all about population density? *Ecosphere* 2:113.
- Rolley, R. E. and L. E. Lehman. 1992. Relationships among raccoon road-kill surveys, harvests, and traffic. *Wildlife Society Bulletin* 20:313–318.
- Rönnegård, L., H. Sand, H. Andren, J. Mansson, and A. Pehrson. 2008. Evaluation of four methods used to estimate population density of moose *Alces alces*. *Wildlife Biology* 14:358–371.
- Sæther, B. E., R. Andersen, O. Hjeljord, and M. Heim. 1996. Ecological correlates of regional variation in life history of the moose *Alces alces*. *Ecology* 77:1493–1500.
- Sæther, B. E., and M. Heim. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. *Journal of Animal Ecology* 62:482–489.
- Schmidt, J. L., J. M. Ver Hoef, J. A. K. Maier, and R. T. Bowyer. 2005. Catch per unit effort for moose: A new approach using Weibull regression. *Journal of Wildlife Management*. 69:1112–1124.
- Seiler, A. 2005. Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology* 42:371–382.
- Singer, J. D. 1998. Using SAS PROC MIXED to fit multilevel models, hierarchical models, and individual growth models. *Journal of Educational and Behavioral Statistics* 24:323–355.
- Skalski, J. R., R. L. Townsend, and B. A. Gilbert. 2007. Calibrating statistical population reconstruction models using catch-effort and index data. *Journal of Wildlife Management* 71:1309–1316.
- Solberg, E. J., A. Loison, J.-M. Gaillard, and M. Heim. 2004. Lasting effects of conditions at birth on moose body mass. *Ecography* 27:677–687.
- Solberg, E. J., C. M. Rolandson, M. Heim, V. Grøtan, M. Garel, B.-E. Sæther, E. B. Nilsen, G. Austrheim, and I. Herfindal. 2006. Moose in Norway: An analysis of material collected by moose hunters 1966–2004. NINA Report 125. (In Norwegian with English abstract.)
- Solberg, E. J., C. M. Rolandson, I. Herfindal, and M. Heim. 2009. Moose and deer-vehicle accidents in Norway during the period 1970–2007. NINA Report 463. (In Norwegian with English abstract.)
- Solberg, E. J., and B. E. Sæther. 1993. Fluctuating asymmetry in the antlers of moose (*Alces Alces*): Does it signal male quality? *Royal Society of London B* 254:251–255.
- Solberg, E. J., and B. E. Sæther. 1999. Hunter observations of moose *Alces alces* as a management tool. *Wildlife Biology* 5:107–117.
- Solberg, E. J., B. E. Sæther, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology* 68:186–204.
- Stubsjøen, T., B. E. Sæther, E. J. Solberg, M. Heim, and C. M. Rolandson. 2000. Moose (*Alces alces*) survival in three populations in northern Norway. *Canadian Journal of Zoology* 78:1822–1830.
- Ueno, M., K. Kaji, and T. Saitoh. 2010. Culling versus density effects in management of a deer population. *Journal of Wildlife Management* 74:1472–1483.
- Ueno, M., T. Matsuishi, E. J. Solberg, and T. Saitoh. 2009. Application of cohort analysis to large terrestrial mammal harvest data. *Mammal Study* 34:65–76.
- Vucetich, J. A., and R. O. Peterson. 2004. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society of London B* 271:183–189.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. *Analysis and management of animal populations*. Academic Press, San Diego, California, USA.



SUPPLEMENTAL MATERIAL

APPENDIX

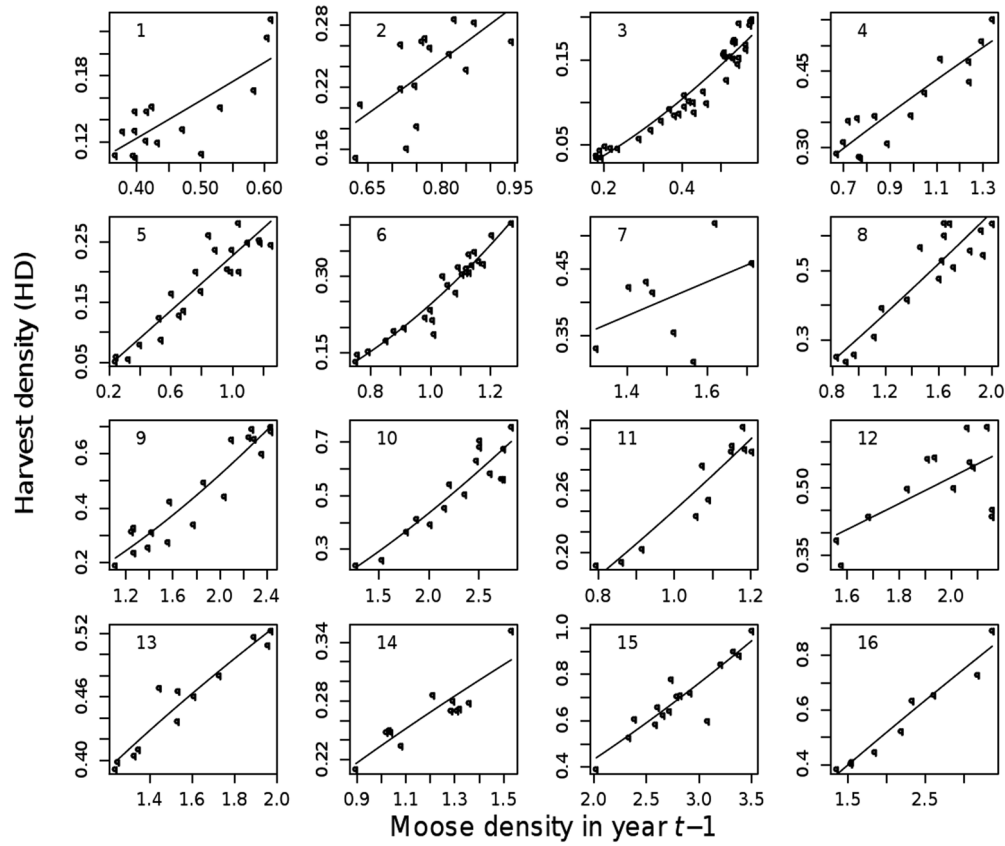


Fig. A1. Relationships between harvest density (HD) and moose density in year  $t - 1$  in 16 study sites in Norway. Trend lines estimated by linear regression.

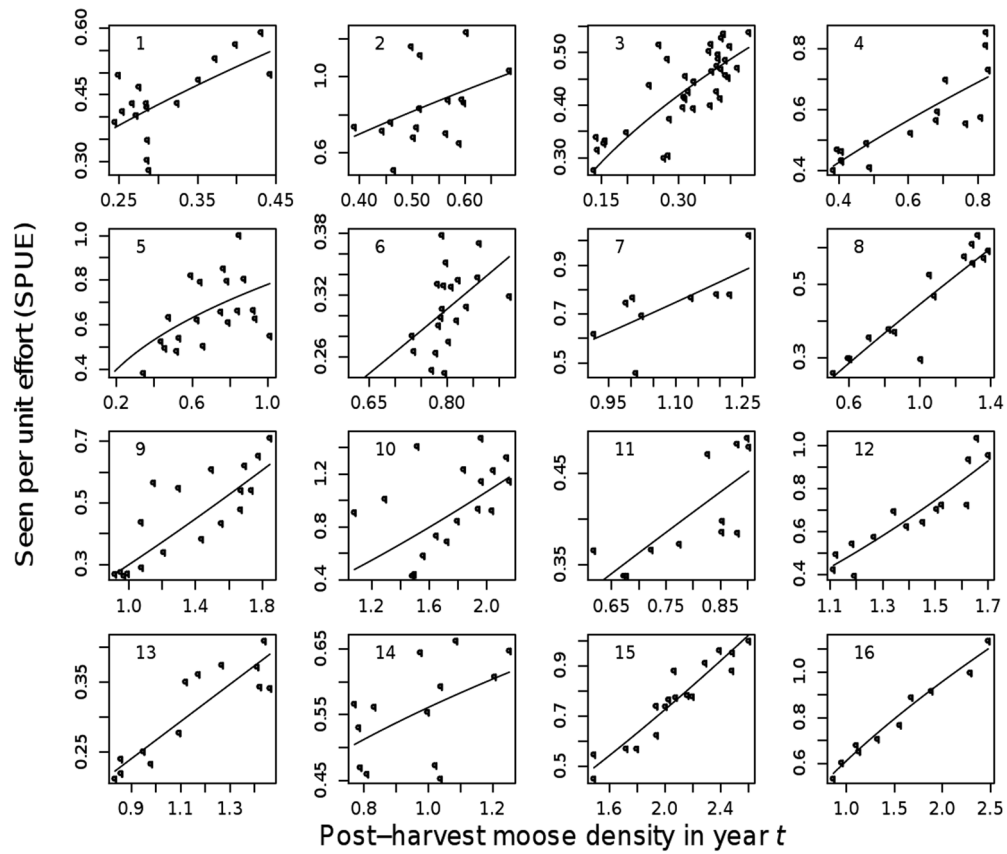


Fig. A2. Relationships between mouse seen per unit effort (SPUE) and post-harvest mouse density in 16 study sites in Norway. Trend lines estimated by linear regression.

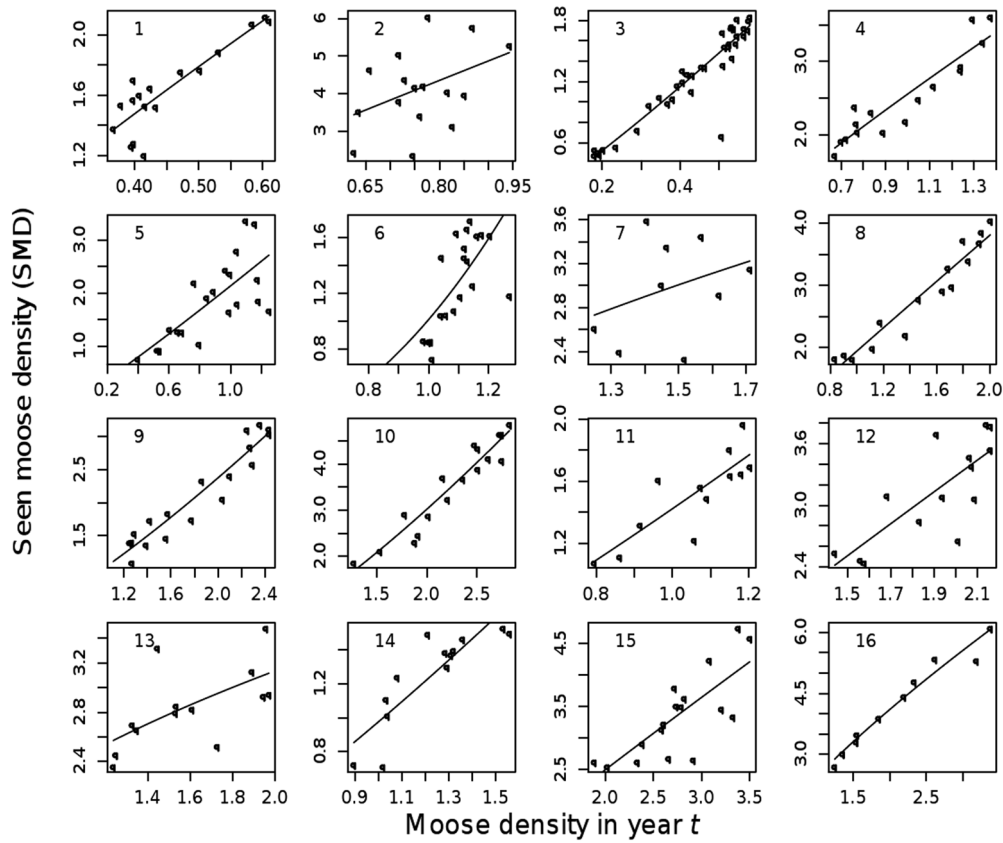


Fig. A3. Relationships between seen moose density (SMD) and moose density in 16 study sites in Norway. Trend lines estimated by linear regression.

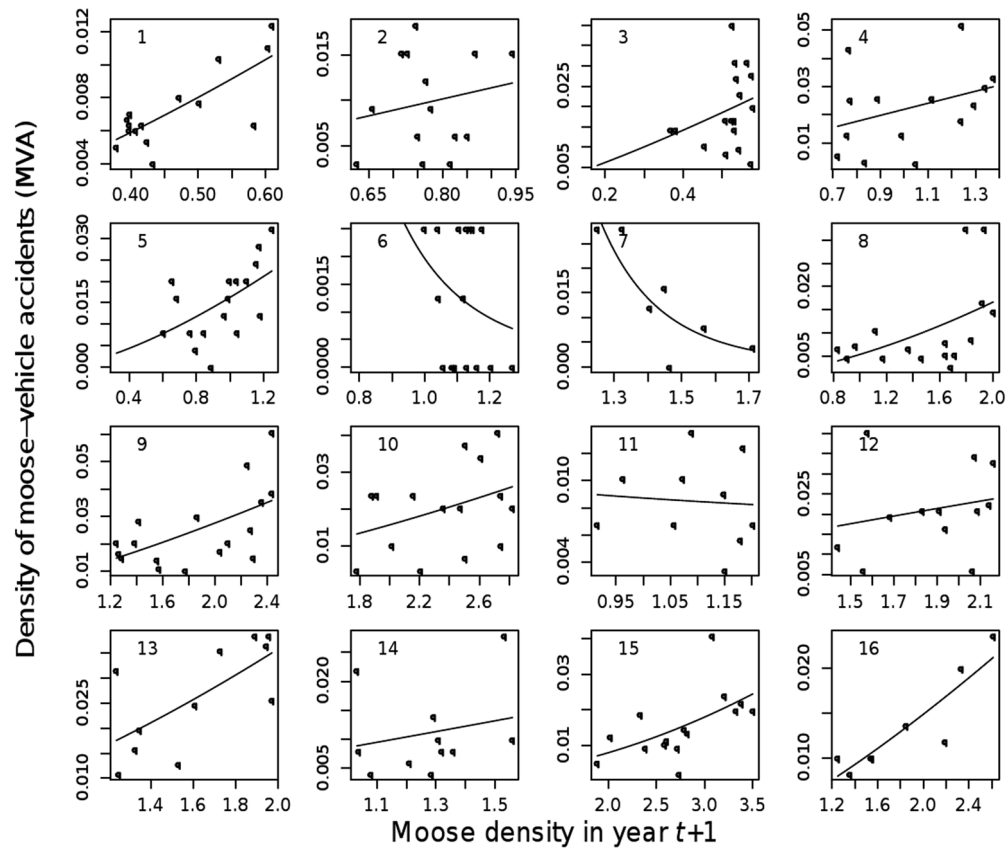


Fig. A4. Relationships between density of moose-vehicle accidents per km<sup>2</sup> (MVA) and moose density in year  $t + 1$  in 16 study sites in Norway. Trend lines estimated by linear regression.