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Variation in recruitment failure of moose (*Alces alces*) - any effects of population condition and climate?

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Biology

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Summary

1. Recruitment failure may represent an important demographic response to changes in the environment or in population size. In this study, I examined whether there was a positive relationship between recruitment rates and ovulation rates in year $t-1$ in eight Norwegian moose populations. Further, I examined how body condition and climate affected the spatiotemporal variation in recruitment rates and ovulation rates.
2. Both recruitment rates and ovulation rates exhibited spatial and temporal variation. The ovulation and twin ovulation rate in yearlings showed more temporal variation than in prime-aged adults. Furthermore, twinning rates varied more than ovulation and calving rates.
3. The number of calves per female recruited to the population was positively related to number of eggs per female the previous year. More calves per female were recorded in years with a high June temperature, smaller snow depths and larger yearling body mass, indicating that more egg cells are realised into a calf in years with good living conditions.,
4. Additionally, more calves per female were found in regions with higher number of eggs per female, cool June temperatures and low snow depths. The level of recruitment failure varied among regions, and was highest in Vestfold which is associated with low ovulation rates and body masses. This shows that prenatal or neonatal losses of offspring are likely to be an important demographic response in moose to changes in population size or in the environment.

1. Introduction

Spatiotemporal variation in vital rates is common in wildlife populations and such variation can have important consequences for population dynamics. In age-structured populations with iteroparous life histories, different vital rates may respond differently to various limiting factors (Gaillard et al., 1998). More than 30 years ago, Eberhardt (1977) proposed that an increase in population size would affect fitness components in a fixed sequence. Among vital rates, juvenile survival would first be affected, followed by fecundity of young females (age at first reproduction), then fecundity of adult females, and lastly adult survival. Several studies have supported this sequence (e.g. Fowler, 1981; Gaillard et al., 1998; Gaillard et al., 2000; Sæther & Bakke, 2000; Eberhardt, 2002; Gaillard & Yoccoz, 2003) and generalised it to include all sources of temporal variation in living conditions (Gaillard et al., 2000). This sequence is apparently due to a trade-off between the potential importance of a fitness component for changing population growth rate and its observed temporal variability: components whose variation has greatest impact on the population growth rate are expected to show less temporal variability (Gaillard et al., 2000, Gaillard & Yoccoz, 2003). Animals of different age often allocate different amounts of energy to reproduction, growth, and maintenance (Clutton-Brock, 1991; Stearns, 1992) that can lead to variation in the reproductive rates across age classes.

A number of studies have found close relationships between age-specific body mass and ovulation rate in ungulates (e.g. Albon et al., 1983; Gaillard et al., 2000) and between body mass and litter size (Sand, 1996). In moose *Alces alces*, for instance, the probability of maturation increases with the body mass of the yearling female (Sæther & Heim, 1993; Sand & Cederlund, 1996; Gaillard et al., 2000) and early age of maturation is associated with an earlier onset of production of twin calves (Sæther & Haagenrud, 1983; Sæther et al., 1996). Ungulates experiencing good living conditions may thus have both faster body growth and higher ovulation rates (Bonenfant et al., 2002; Langvatn et al., 2004; McLoughlin et al., 2008).

Both environmental conditions and population density may affect the body mass of ungulates. High population density may lead to food competition and retarded body growth (Solberg & Sæther, 1994; Gaillard et al., 1996; Solberg et al., 1999; Hjeljord & Histøl, 1999; Bonenfant et al., 2002; Bjørneraas et al., 2009) and reduced fecundity (Albon et al., 1983; Albon et al., 1987; Coulson et al., 2000). Similarly, body growth may decrease during periods of harsh climatic conditions (Sæther, 1985; Sand, 1996; Sæther et al., 1996; Solberg et al., 1999; Herfindal et al., 2006a, b; Grøtan et al., 2009). In temperate and arctic ungulate

populations where climate and food availability varies between seasons, higher body masses have also been associated with low snow depths (Cederlund et al., 1991; Loison et al., 1999; Solberg et al., 2004) and higher temperatures during winter (Clutton-Brock & Albon 1983; Sæther & Gravem, 1988). This is probably due to increased access to food and decreased energy expenditure. Similarly, summer conditions may affect body mass through variation in food quality and quantity. Cold and wet summers are associated with higher body growth in moose and red deer *Cervus elaphus*, probably because food quality increases under such conditions (Sæther, 1985; Bø & Hjeljord, 1991; Solberg & Sæther, 1994; Gaillard et al., 1996; Langvatn et al., 1996; Sæther et al., 1996; Herfindal et al., 2006b).

The moose is an important game resource in Norway, and is under intensive management to maintain a high productivity that allows high annual harvest rates (Østgård, 1987; DN, 1995). To monitor this resource, moose hunters collect data from observed and harvested moose during the hunting season each year (Solberg et al., 2006). Indexes based on moose observations has been shown to be a reliable management tool to predict the directional and quantitative change in population size in moose (Ericsson & Wallin, 1999; Solberg & Sæther, 1999). In addition, data collection of several fitness related parameters, such as age-specific body mass and reproductive measurements from reproductive organs, is an inexpensive solution to measure the viability of large populations. A common method is ovary-sectioning and estimation of the reproductive status and history of ovulation rates and calving rates from luteal scars (Langvatn, 1992; Langvatn et al., 1994). This method has been used to monitor age-specific variation in moose and red deer reproduction in the Nordic countries (Solberg et al., 2006; Solberg et al., 2009; Solberg et al., 2010b) and have also been applied to the same or other ungulate species in other countries (e.g. Simard et al., 2008; Simard et al., 2010).

The ovulation rate measures the potential rate of calf production, but not necessarily the number of calves that are actually born or recruited to the population. Not all egg cells will necessarily be fertilised and some fertilised eggs and embryos and foetuses could be reabsorbed and aborted during pregnancy. Solberg et al. (2006) indicated that the observed twinning rates were consistently lower than the twinning rates estimated from ovaries in a number of populations of moose, indicating that varying fertilisation rate, as well as prenatal (absorptions, abortion) and neonatal mortality may also be at work. These relationships may indicate that recruitment failure (i.e. prenatal or neonatal losses) may represent an important demographic response to changes in environmental conditions or in population density, as proposed by Eberhardt (1977; 2002).

The purpose of the present study was fourfold: First, I examined the spatiotemporal variations in recruitment rates and ovulation rates in different monitoring populations of moose in Norway. Analyses of spatiotemporal variation in reproductive parameters require access to long-term data from several populations (Ozgul et al., 2007). Body mass, lower jaws (for age determination) and ovaries of moose have been collected for more than 20 years in 8 regions in Norway, and from which the age-specific ovulation pattern could be estimated. For the same period, autumn calf recruitment rates (calving rates, twinning rates) could be estimated based on hunter moose observation monitoring data. According to Eberhardt (1977), I expected to record larger spatiotemporal variation in ovulation rates for yearlings than for prime-aged females. Second, by using these two sources of data, I examined to what extent there was a positive relationship between the annual age-specific ovulation or twin ovulation rates and the observed calf recruitment rates in the subsequent year within and between monitoring populations. Third, I further investigated whether these relationships were confounded by fluctuations in the age composition by adjusting the age-specific ovulation rates for variation in female age structure. This was only possible in three monitoring populations where age structure could be reconstructed using cohort analysis (e.g. Ueno et al. 2009). This also enabled me to examine to what extent the variation in recruitment rates were associated with variation in body condition and weather. Previous studies have indicated that variation in weather during gestation or just after birth can have a significant effect on the survival of the foetus or calf, respectively. Because summer temperatures have previously been found to negatively affect body growth in moose (Herfindal et al., 2006b), I particularly examined to what extent early summer temperature affected the variation in recruitment rates (see Grøtan et al. 2009). Finally, if recruitment failures are influenced by extrinsic climate variables, I expected the annual variation in ovulation rates and recruitment rates to be spatially synchronised, dependent on the distance between the different monitoring regions.

2. Material and methods

2.1 Study species

The moose is the largest member of the deer family (Cervidae) and is widely distributed in the northern parts of Europe, Asia and North-America (Franzmann, 1981). In Norway, moose are predominantly found in the boreal vegetation zone, except in the southernmost counties, which also extends into the nemoral vegetation zone (Moen, 1999). The counties with the highest population densities are currently Østfold, Akershus, Hedmark and Nord-Trøndelag (Solberg et al., 2010b). Following sex-biased harvesting, the Norwegian moose population is biased towards females, and females are also on average older than males (Solberg et al., 2006).

The moose undergoes an annual weight cycle, where it gain weight in the summer season and loses weight during winter (Haagenrud, 1993). Therefore, access to sufficient quantities of food during summer is likely to affect body condition of the moose during autumn (Sæther and Heim 1993), and in turn the probability that a female will ovulate and produce calves the subsequent spring (Solberg et al., 2006). Female yearlings usually come into rut later than older females and the rutting period tend to last longer for younger females (Solberg et al., 2006; Garel et al., 2009). The rutting period range from late September, slightly earlier in the south than in the north, to the end of October (Haagenrud, 1993; Solberg et al., 2006; Garel et al., 2009). Calves are born in May/June and weighs between 8-17 kilos (Haagenrud, 1993). Moose regularly produce twins (Franzmann, 1981) and most twins are born when the female is between 4-9 years old (Sæther, 1993). The most productive females are found in central and northern Norway where more than 70 % of the older females produce twins each year (Solberg et al., 2009).

2.2 Study areas

The study areas cover eight different regions along a north-south gradient (Fig. 1). The areas cover representative living areas for moose and include the most important regions where moose are harvested in Norway (Solberg et al., 2002; Solberg et al., 2006; Solberg et al., 2010b). In these regions, moose populations are monitored annually as part of the National Monitoring Program for Cervids (Solberg et al., 2010b). The monitoring program is funded by the Directorate for nature management (DN), and operated by the Norwegian Institute for Nature Research (NINA). The national monitoring program started in 1991, but similar data were collected in the same regions as part of other projects at DN and NINA for another 15-

20 years prior to the start (Solberg et al., 2006). In total, the program has collected data from > 70,000 moose, including ovary data from ~12,000 females.

The four northern areas (Troms, Nordland, Nord-Trøndelag and Oppland) are characterized by large valleys covered with forest to the tree line at approximately 500 (Troms) – 1000 (Oppland) m.a.s.l. The four southern areas are all below the tree line and are characterized by undulating hills (Hedmark) or a broken topography (Solberg et al., 2002). Nordland, Nord-Trøndelag and Hedmark are mainly located in coniferous forests with Norway spruce *Picea abies* and Scots Pine *Pinus sylvestris* while in Troms and Oppland, Birch *Betula pubescens* are also among the dominant tree species. The forests of the three southernmost regions (Vestfold, Aust- and Vest-Agder) consist mainly of Scots Pine, Norway spruce and birch in the interior, mixed with birch, oak *Quercus robur* and to some extent beech *Fagus silvatica* along the coast (Solberg et al., 2002). In general, the moose density increases along a north- south gradient (Solberg et al., 2006).

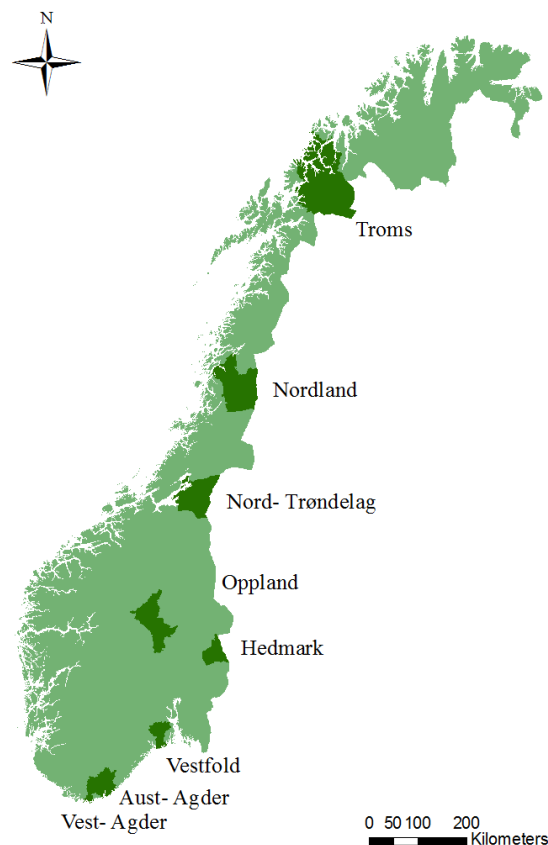


Figure 1: Location and names of the eight Norwegian study areas from which data are used in the analysis.

2.3 Age determination and ovulation data

Within the study areas, hunters recorded kill date, location, sex and carcass mass and collected ovaries and the lower jaw from harvested moose. Age was determined in the laboratory by counting the number of layers in the secondary dentin of the incisor (Haagenrud, 1978). This is considered a reliable method for estimation of age in moose (Rolandsen et al., 2008). In this study I categorised moose to five age classes: yearlings and 2.5 years, which includes most of the primiparous females (Garel et al., 2009); 3.5 year-olds, which represents the transition between immature and mature females (Sæther & Heim, 1993; Sæther et al., 1996); 4.5-10.5 year-olds, corresponding to prime-age females (most productive stage, Markgren, 1969; Sæther & Haagenrud, 1983); and ≥ 11.5 year-olds, which represent senescent females (Markgren, 1969; Sæther & Haagenrud, 1983; Ericsson & Wallin, 2001).

Ovulation rate is the proportion of moose females that ovulate in a given year, which is determined by the presence and appearance of luteal structures in the ovaries of harvested moose (Langvatn, 1992; Solberg et al, 2002, Solberg et al., 2006). Ovary-sectioning was done by removing the ovaries from the uterus and store them in formalin, and thereafter cut them into slices for ocular examination of the different luteal structures. Only females from which both ovaries were collected were used in the analysis. Ovulation was determined by the presence and number of primary corpora lutea (PCL). PCL originate from ovulated Graafian follicles after conception (Langvatn 1992; Langvatn et al., 1994) and numbers lie between 1 and 4 for both ovaries together (Solberg et al., 2006). Since moose usually give birth to 2 or less calves yearly, it is assumed that most females with more than 2 PCL have gone through a second rut. The second rut occurs normally 24 days after the first rut if the female was not fertilised (Schwartz & Hundertmark, 1993). Presence of PCL does not verify that the female is fertilised, but confirm that the female has ovulated the autumn she was killed, and consequently was sexually mature (Solberg et al., 2006).

Since the hunting period starts before the rutting season is finished in all the regions, the probability that a female had ovulated when killed increased with the time during the season. To control for this, the ovulation rates were estimated based on the development in ovulation probability with time during the hunting season within region, following the method of Garel et al. (2009). This method relates individual ovulation (yes, no) with kill date during the hunting season and estimate three parameters for a given population and age group: 1) time of ovulation, 2) the degree of synchrony and 3) the ovulation rate. The age-specific ovulation rate is given by the asymptote q in the following model:

$$p = P(T \leq t | O)P(O) = q \cdot \phi\left(\frac{t - \mu}{\sigma}\right),$$

where p is the probability that ovulation has occurred at time t , $P(O) = q$ is the probability that a particular individual would ovulate, μ corresponds to the peak of ovulation, σ corresponds to the degree of synchrony in time of ovulation and ϕ is the standard normal cumulative density function. For further description of the method see Garel et al. (2009).

I estimated the twin ovulation rate, i.e. proportion ovulating females with twin PCL, as the proportion ovulating females with twin egg cells within region, year and age category. Based on the ovulation rate and twin ovulation rate I then estimated the number of eggs per female within each age category, year and region as the ovulation rate * (1 + twin ovulation rate).

The study period was limited to the years with available ovulation rates for each age class and corresponding data for recruitment rates (see below); from 1988 to 2008, with some missing years in different regions. In Aust-Agder, data on ovulation rates were only available from 1988 and from the period 1991-1995. Likewise, in Vest-Agder, ovary data were only sampled in 1989 and in the period 1997-2005.

In addition to data obtained from individual moose, I used data on number, sex and age class (calf, adult) of moose observed during hunting, as a measure of population structure. These data are regularly collected and reported by hunters as part of the moose observation monitoring, which has been conducted in most moose hunting municipalities since the mid 1980's (Solberg et al. 2006).

From the observation data, indices of population density (moose seen per hunter-day), adult sex ratio (females seen per male), recruitment rates (calves seen per female) and the area-specific hunting pressure (moose killed of all moose seen) are normally calculated and used by the local moose management (Solberg et al., 2006). In my analysis, I used the same data to calculate the following variables: Calves per female: the total number of calves divided by the total number of yearling and adult females; Calving rate: the total number of females with a calf/calves divided by the total number of yearling and adult females; Twinning rate: the total number of females with two calves divided by the total number of females with calf/calves. Specific values were made within region and year.

2.4 Body condition variables

As a measure of body condition within region and year I used the carcass mass collected by the moose hunters. Carcass mass is body mass minus head, skin, metapodials, blood, and viscera, and constitutes on average 50 – 56% of total body mass (Wallin et al., 1996; Solberg et al., 2008; Garel et al., 2009). Here, I used the mean carcass mass of yearling females adjusted for kill date as a measure of body condition. Yearlings are independent of their mother, and have yet not started to reproduce. They are therefore assumed to provide a good measurement of the general condition for body growth in the population (Solberg et al. 2006).

2.5 Climate variables

To investigate to what extent the variations in recruitment rates are influenced by climate, I included the climatic variables: June temperature, winter temperature (December-Mars) and snow depth (December-Mars). To calculate the variables, I used gridded (1x1 km²) and downscaled monthly means of temperature and snow depth from 1988 to 2008. Only areas below the forest line were used to calculate the mean values within each region and year. All data were provided by the Norwegian Meteorological Institute (<http://met.no>).

2.6 Reconstruction of moose population age structure

To be able to estimate the potential number of calves produced per female in the population (i.e. eggs per female), I needed to control for variation in female age structure in the different populations. I therefore reconstructed the female age structure in the different regions by the use of cohort analyses and the age-at-death of the harvested moose females within population. This was done using the method of Ueno et al. (2009).

Cohort analysis is a retrospective method for population reconstruction from catch-at-age data (Hilborn & Walters, 1992). It enables calculations of the number of individuals in a particular age class by aggregating the numbers of harvested animals from that age class to the point when they reach the oldest age class (Ueno et al., 2009). A requirement is that there exists long enough time series for multiple cohorts of animals to have passed through the population. Other important assumptions are that the natural mortality rate is well-known or low and stable over time, there is no or low net migration in or out of the population and that the hunting strategy remains reasonably constant (Solberg et al., 1999; Ueno et al., 2009).

These assumptions were fulfilled in Troms, Nordland, Nord-Trøndelag and Vestfold. For these regions I could therefore estimate the population-specific number of eggs per female

each year during the study period. However, because only few ovaries ($n = 5-9$) were collected from prime-aged females in Nordland during several years, the population ovulation rates showed large random variation. I therefore decided to exclude Nordland from these analyses. In the remaining three populations, relatively large samples of ovaries were available for prime-aged females (the largest and most fecund age group) each year during the study period (Troms: $n = 16-56$, Nord-Trøndelag: $n = 12-36$, Vestfold: 20-72).

2.7 Statistical analyses

To test for spatial and temporal variations in the recruitment rates, I used a two-way ANOVA with region and years as factors with 8 and 21 levels. I checked for constancy of variance and normality of errors by visual inspection of the data. The residuals did not deviate from normality. For variations in ovulation and twin ovulation rate, I used a factorial ANOVA with year, region and age class (5 levels) as factors, with an interaction term between region and age. No significant interaction effect between age class and region were observed for twin ovulation rate, and was excluded from the final model. The temporal variation in each recruitment and ovulation variable was also assessed by calculating coefficients of variation (CV; $SD/mean$) for each year. For a pairwise comparison of CV's, I used the modified Fligner- Killeen test as described in Donnelly & Kramer (1999).

I tested to what extent the observed annual calving rates or twinning rates was a function of varying age-specific ovulation rates or twin ovulation rates the previous year (year $t-1$). Since calving rates and twinning rates are proportions these variables were logit-transformed. I examined the variation in recruitment rates relative to the variation in ovulation rates over time by including region and age class as factors in an ANCOVA model. A positive relationship would indicate that more calves are recruited in years following high ovulation rates. Similarly, I examined the relationship between recruitment rates and ovulation rates between regions by including year and age class as factors in the models, i.e. I tested if more calves were recruited in regions associated with higher ovulation rates. Interaction effects between region and age class, and year and age class, were not significant and were excluded from the final models.

I also examined the relationship between the observed recruitment rates and the mean age-specific ovulation rates within year and region, weighting the mean for sample size within age class. Assuming that females in different age categories constitute a representative sample from the population, the latter variable is an estimate of the population ovulation rates. For

these analyses, I used ANCOVA models with either region or year as factors to test for within and between region relations, respectively.

I further made a new variable, called calves per egg, by dividing the observed calves per female on the population number of egg cells (ova) per female in year $t-1$. This variable is a measure of the number of egg cells (ova) that are realized into a calf in the autumn of the subsequent year, indicating the losses due to lack of fertilisation, as well as pre- and post-natal mortality of calves. I used a two-way ANOVA model with region and years as factors with 8 and 21 levels, to check for spatiotemporal variations. Thereafter, I tested whether calves per egg were related to female yearling weight using a simple linear regression. A measure of recruitment failure was calculated as $1 - \text{calves per egg}$ for each region.

To calculate the annual population-specific ovulation rates, twin ovulation rates and eggs per female, I multiplied the estimated age-specific rates with the female age structure within region (Troms, Nord-Trøndelag and Vestfold) and year. The relationship between the observed recruitment rates and the annual population-specific ovulation rates in year $t-1$, were then tested using ANCOVA models, with region as a factor. Similarly, I tested whether there were a relationship between recruitment rates and population-specific ovulation rates between regions by including year as a factor. Both the calving rate and twinning rate were logit-transformed. I also checked whether the log-log relationship between calves per female and number of eggs per female deviated from a slope of one by the use of linear regression.

To check whether the time series in each of the three regions were synchronized, I performed a cross-correlation analysis. Significant positive coefficients would indicate that recruitment rates or ovulation rates were synchronised between regions.

A measure of recruitment failure was calculated for each year in the three populations with age structure as the ratio between population eggs per female and observed calves per female the subsequent year; i.e. $\text{recruitment failure} = 1 - (\text{calves per female} / \text{population eggs per female})$. I then used a two-way ANOVA to check for significant differences between regions and years.

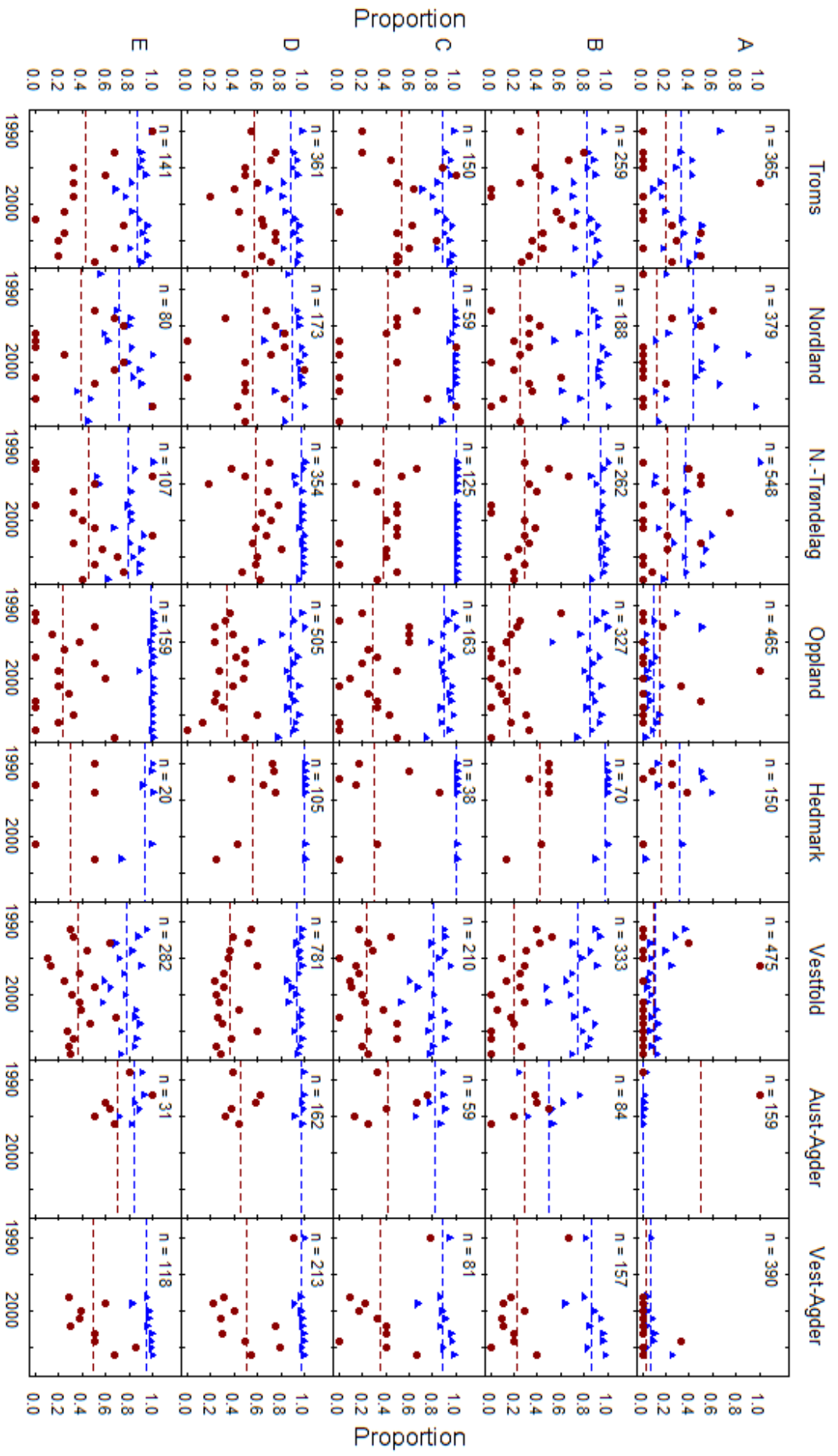
To examine if variation in yearling carcass mass or climate could explain part of the spatiotemporal variation in recruitment rates, I included yearling carcass mass and climate as covariates in the models. Model selection was done based on the Akaike Information Criteria (AIC); with second-order adjustment of the AIC (AIC_c) to correct for potential bias due to small sample sizes (Burnham & Anderson, 2002). The best models are the most parsimonious models (lowest AIC_c value) with regard to variation explained and variables included. The data were analysed using the software R 2.11.1 (R Development core team, 2010).

3. Results

3.1. Spatiotemporal variation in recruitment rates

Observed calving rates differed significantly among regions ($F_{7,505} = 110.38$, $p < 0.001$) and years ($F_{20,505} = 11.05$, $p < 0.001$; Fig. 2G). The highest mean calving rate was found in Nordland (mean \pm SE= 0.57 ± 0.01 , $n = 80$; Appendix 1), while the lowest rate was in Vestfold (mean \pm SE= 0.47 ± 0.01 , $n = 90$). Similarly, the observed twinning rates showed large spatial ($F_{7,505} = 1205.45$, $p < 0.001$; Fig. 2G) and temporal ($F_{20,505} = 17.03$, $p < 0.001$) variation. The CV of twinning rates were significantly different from the calving rates ($z = 19.64$, $p < 0.001$; Fig. 3), i.e. twinning rates showed the larger temporal variation. As expected, twinning rates were much higher in the three northern regions (Troms: mean \pm SE= 0.38 ± 0.004 , $n = 80$; Nordland: mean \pm SE= 0.39 ± 0.003 , $n = 80$; Nord-Trøndelag: mean \pm SE= 0.36 ± 0.005 , $n = 80$) than further south (Fig. 2G). The lowest twinning rate was found in Aust-Agder (mean \pm SE= 0.13 ± 0.01 , $n = 30$).

The observed number of calves per female was also highest in the northern regions (Fig. 2H). Similar to the pattern recorded for the observed calving and twinning rates, the highest mean number of observed calves per female was recorded in Nordland (mean \pm SE= 0.79 ± 0.01 , $n = 80$). The observed number of calves per female showed more temporal variation than calving rates ($z = 11.82$, $p < 0.001$; Fig. 3).



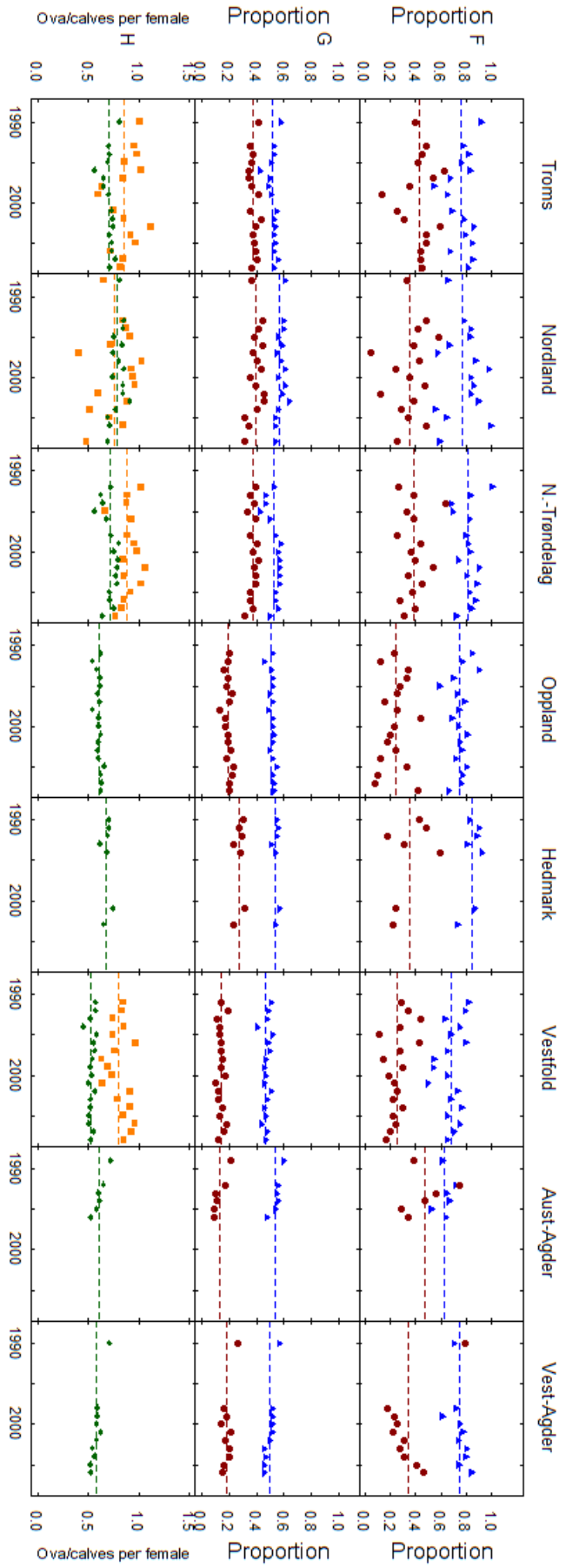


Figure 2: Spatiotemporal variation in parameter values. **A-F:** Ovulation rate (blue triangle) and twin ovulation rate (red circle) in year $t-1$ in each region from 1988-2008 for age class 1 (one year old) **(A)**, age class 2 **(B)**, age class 3 **(C)**, age class 4 (4-10 years old) **(D)**, age class 5 (>10 years old) **(E)**, and the mean of all age classes, weighted for sample size **(F)**. **G:** Observed calving rate (blue triangle) and twinning rate (red circle) in each region from 1988-2008. **H:** Observed calves per female (green circle) and population eggs per female adjusted for age structure (orange square) in each region from 1989-2008. Dashed lines indicate the mean values within region. n = number of female moose with 2 ovaries, collected within each age class and region.

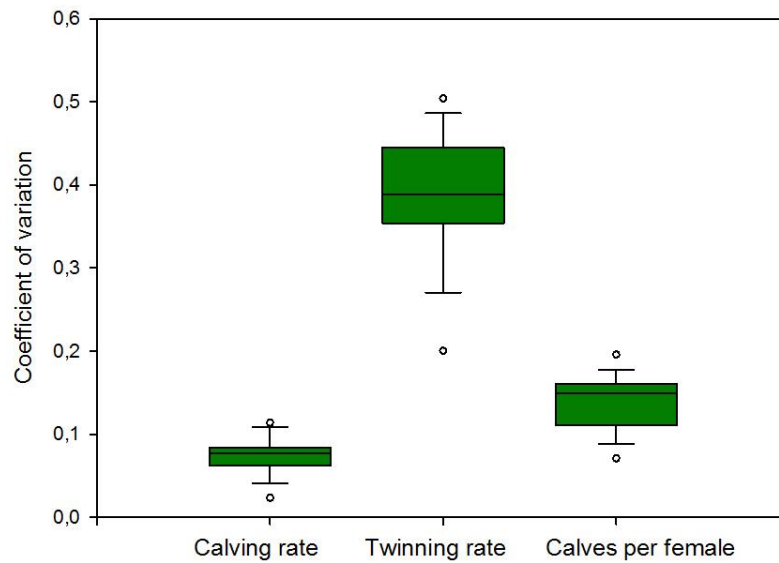


Figure 3: Coefficient of variation for observed calving rate, twinning rate and calves per female for all regions. Each box-plot shows the median (black line) of coefficients of variation, the interquartile (25%-75%) range, 1.5 times this range (brackets), and outliers (circle).

3.2 Age and spatiotemporal variation in ovulation rates

Ovulation rates varied significantly among age classes ($F_{4,473} = 659.57$, $p < 0.001$; Fig. 2A-E), years ($F_{20,473} = 8.82$, $p < 0.001$) and regions ($F_{7,473} = 35.33$, $p < 0.001$). In addition, there was an interaction effect between age class and region ($F_{28,473} = 15.98$, $p < 0.001$), which was strongly influenced by larger difference in ovulation rates between young and prime-aged females in the southern than in the northern regions.

The mean age of harvested females varied from 3.47 in Nordland to 5.15 in Vestfold over the study period, and was relatively constant over years (Appendix 4). The ovulation rates increased with increasing age up to age class 4 (4-10 years old) in all regions (Appendix 2). The largest increase was from yearlings to 2-year olds (a 60 % increase; Fig. 2A-E). In age class 4, which represents the prime-aged females, over 90 % showed signs of ovulation. Generally, a larger proportion of females ovulated in the north than in the south. An exception was Hedmark (mean±SE= 0.84±0.05, n= 34), which had the highest mean ovulation rate, 21 % higher than in Aust-Agder (mean±SE= 0.63±0.07, n= 30; Fig. 2F). The proportion of females that ovulated as yearlings showed significantly more temporal variation than prime-aged females in age class 4, as indicated by their CV ($z = 8.97$, $p < 0.001$; Fig. 4).

There twin ovulation rate varied significantly among the different age classes ($F_{4,473} = 31.63$, $p < 0.001$; Fig. 2A-E), years ($F_{20,473} = 1.61$, $p = 0.046$) and regions ($F_{7,473} = 4.60$, $p < 0.001$). 15 % of yearlings showed twin ovulation, compared to an average of 49 % of in age

class 4 (Fig. 2B). In the three northern areas, 58% of females in age class 4 showed twin ovulation, compared to 44% in Vestfold and Vest-Agder. The mean twin ovulation rate was highest in Aust-Agder (mean±SE= 0.48±0.05, n= 25; Fig. 2F), followed by Troms (mean±SE= 0.43±0.03, n= 74; Appendix 3), whereas the lowest mean twin ovulation was found in Oppland (mean±SE = 0.24±0.02, n= 86). The twin ovulation rates varied significantly more than the ovulation rates, as indicated by their higher coefficient of variation (yearlings: $z= 2.40$, $p= 0.016$; adults: $z= 7.97$, $p< 0.001$; Fig. 4). Similarly, the CV for twin ovulation rates in yearlings were more variable than for adults ($z= 2.30$, $p= 0.021$; Fig. 4).

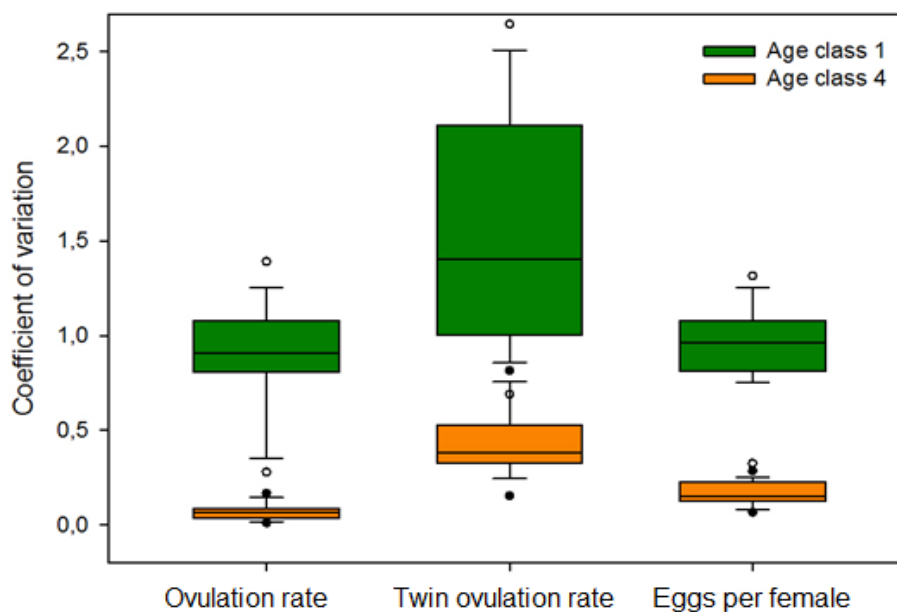


Figure 4: Coefficient of variation for ovulation rate, twin ovulation rate and eggs per female in age class 1 (green) and age class 4 (orange) for all regions. Each box-plot shows the median (black line) coefficient of variation, the interquartile (25%-75%) range, 1.5 times this range (brackets), and outliers (age class 1: black circles; age class 4; white circles).

3.3 Relationship between observed recruitment rates and ovulation rates

There was a positive relationship between the observed calving rate in a given year and the age-specific ovulation rate the previous year ($\beta= 0.14\pm 0.04$, $t= 3.55$, $p< 0.001$; Table 1), when controlling for region and age class (i.e. the temporal model). Hence, more females were observed in company with calves in years following years with high ovulation rates. For a given ovulation rate and age class, the calving rate tended to be highest in Nordland, Hedmark and Aust-Agder and lowest in Vest-Agder and Vestfold (Table 1).

Table 1: Parameter estimates (\pm standard error) from a linear model for annual calving rate against ovulation rate in year $t-1$, controlling for region and age category. Intercept represent Troms at age class 1. Calving rates were logit- transformed. $N= 533$. $R^2= 0.53$.

	Estimate \pm SE	t value	P-value
Intercept	0.024 \pm 0.020	1.21	0.229
Ovulation rate	0.140 \pm 0.039	3.55	<0.001
Nordland	0.264 \pm 0.020	11.46	<0.001
Nord-Trøndelag	0.041 \pm 0.020	1.05	0.294
Oppland	-0.009 \pm 0.019	-1.74	0.082
Hedmark	0.097 \pm 0.026	2.87	0.004
Vestfold	-0.158 \pm 0.019	-9.43	<0.001
Aust-Agder	0.139 \pm 0.027	4.27	<0.001
Vest-Agder	-0.077 \pm 0.022	-4.51	<0.001
Age class 2	-0.059 \pm 0.029	-2.88	0.004
Age class 3	-0.070 \pm 0.031	-3.00	0.003
Age class 4	-0.073 \pm 0.032	-3.02	0.003
Age class 5	-0.065 \pm 0.030	-3.00	0.003

Also the observed twinning rate tended to be positively related to the twin ovulation rate the year before when controlling for region and age class, but this relationship was not significant ($\beta= 0.04\pm 0.04$, $t= 0.91$, $p= 0.37$; Table 2). However, there was a significant effect of region, indicating that less twins were recruited per female for a given twin ovulation rate and age class in Vestfold, Aust- Agder and Vest-Agder than in regions further north (Table 2).

Table 2: Parameter estimates (\pm standard error) for the relationship between twinning rate and twin ovulation rate in year $t-1$, controlling for region and age class. Intercept represent Troms at age class 1. Twinning rates were logit-transformed. $N= 517$. $R^2= 0.91$.

	Estimate \pm SE	t value	P value
Intercept	-0.511 \pm 0.029	-17.78	<0.001
Twin ovulation rate	0.036 \pm 0.036	1.01	0.314
Nordland	-0.445 \pm 0.030	2.16	0.031
Nord-Trøndelag	-0.536 \pm 0.029	-0.84	0.404
Oppland	-1.451 \pm 0.030	-31.63	<0.001
Hedmark	-0.979 \pm 0.039	-12.13	<0.001
Vestfold	-1.825 \pm 0.029	-44.63	<0.001
Aust-Agder	-1.956 \pm 0.042	-34.31	<0.001
Vest-Agder	-1.527 \pm 0.034	-29.98	<0.001
Age class 2	-0.527 \pm 0.027	-0.61	0.543
Age class 3	-0.532 \pm 0.027	-0.76	0.449
Age class 4	-0.530 \pm 0.029	-0.67	0.501
Age class 5	-0.494 \pm 0.028	-0.59	0.556

In the model with age class and year included as factors (i.e. the spatial model), the relationship between calving rate and ovulation rate was positive ($\beta = 0.31 \pm 0.05$, $t = 6.17$, $p < 0.001$). Likewise, I found a positive spatial relationship between observed twinning rate and twin ovulation rate ($\beta = 0.54 \pm 0.12$, $t = 4.65$, $p < 0.001$). Thus, higher calving rates and twinning rates were present in regions with higher ovulation rates and twin ovulation rates, respectively.

Accordingly, annual variation in calving rates was significantly related to mean age-specific ovulation rates (estimate of population-specific ovulation rate) in year $t-1$ ($\beta = 0.31 \pm 0.14$, $t = 2.24$, $p = 0.024$). Moose in Vestfold (intercept \pm SE = -0.35 ± 0.04 ; $p = 0.031$) showed significantly lower calving rates than Troms (intercept \pm SE = -0.18 ± 0.11) for a given ovulation rate. A similar positive relationship was found among regions ($\beta = 0.69 \pm 0.18$, $t = 3.93$, $p < 0.001$), controlling for year.

The temporal relationship between observed twinning rate and the mean twin ovulation rate were not significant ($\beta = 0.17 \pm 0.15$, $t = 1.10$, $p = 0.28$). However, a positive relationship existed between regions ($\beta = 1.57 \pm 0.48$, $t = 3.26$, $p = 0.002$), indicating that higher twinning rates were observed in regions with higher twin ovulation rates.

A positive relationship was present between the observed calves per female and the mean number of eggs produced per female in year $t-1$ ($\beta = 0.07 \pm 0.03$, $t = 2.40$, $p = 0.018$), controlling for region. The slope of this relationship was significantly lower than 1 on the log-log scale ($\beta = 0.10$, 95% CI = 0.01-0.19, $p = 0.024$), indicating that the proportion of eggs realized into a calf was lower following years with a high mean number of eggs per female. Moreover, although the slopes were similar in all regions, females in Vestfold (intercept \pm SE = 0.47 ± 0.02 ; $p < 0.001$), Vest-Agder (intercept \pm SE = 0.51 ± 0.02 ; $p < 0.001$) and Aust-Agder (intercept \pm SE = 0.55 ± 0.03 ; $p = 0.001$) produced a smaller number of calves for a given number of eggs per female than did females in Troms (intercept \pm SE = 0.63 ± 0.03). A larger number of calves per female was also observed in regions with a larger mean number of eggs produced per female ($\beta = 0.29 \pm 0.05$, $t = 5.47$, $p < 0.001$).

The mean number of calves recruited per egg ovulated, an index of recruitment failure, differed between regions ($F_{7,79} = 4.60$, $p < 0.001$) and years ($F_{20,79} = 1.96$, $p = 0.019$). In general, the level of recruitment failure was higher in Vest-Agder (43 %), Hedmark (40 %) and Vestfold (38 %) compared to Nordland (20 %), Troms (33 %) and Aust-Agder (33 %). No significant relationship was found between calves per egg and mean yearling body mass in the different regions ($F_{1,102} = 0.57$, $p = 0.45$).

3.4 Patterns in recruitment rates controlling for age structure

In the three populations with reconstructed age structure, I found a positive temporal relationship between the observed calving rate and the population ovulation rate in year $t-1$ ($\beta=0.36\pm0.29$, $t=1.24$, $p=0.22$; Fig. 5), but this relationship was not significant. However, for a given ovulation rate, moose in Vestfold had a significantly lower calving rate ($p<0.001$) than moose in Troms and Nord-Trøndelag. When controlling for year, the relationship between observed calving rate and population ovulation rate was not significant ($\beta=-0.15\pm0.51$, $t=0.29$, $p=0.78$).

No significant relationship was present between the observed annual twinning rate and the population twin ovulation rate ($\beta=-0.09\pm0.28$, $t=-0.32$, $p=0.75$; Fig. 6), controlling for region. However, in Vestfold moose females had significantly lower twinning rates ($p<0.001$) than in the two northern regions for a given twin ovulation rate. The twinning rate was positively related to the twin ovulation rate between regions ($\beta=5.24\pm1.25$, $t=4.20$, $p<0.001$).

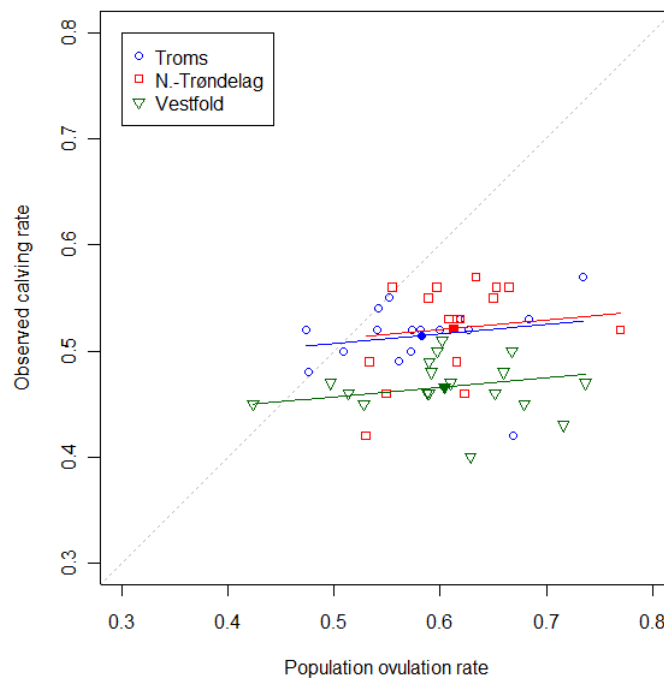


Figure 5: The relationship between observed calving rate and population ovulation rate in year $t-1$ in Troms, Nord-Trøndelag and Vestfold with linear regression lines. Grey dashed line indicates the 1:1 relationship between observed calving rate and population ovulation rate. Filled symbols are the mean values within each region.

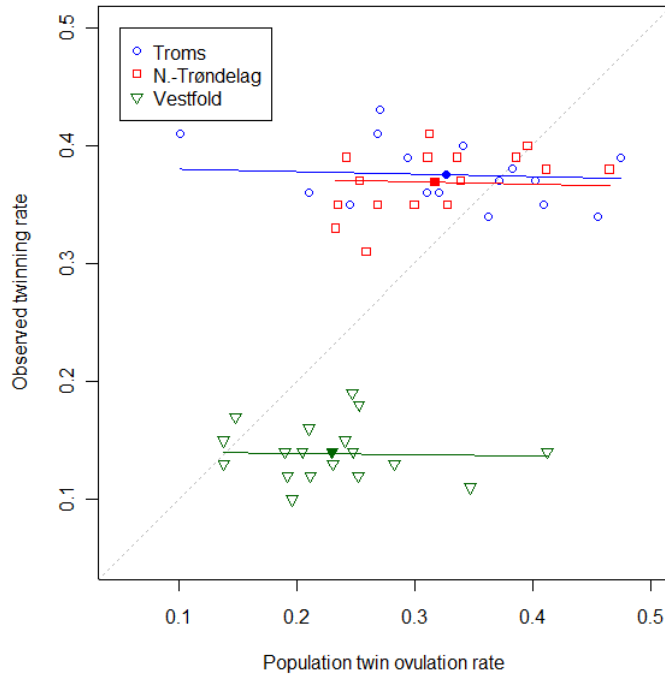


Figure 6: The relationship between observed twinning rate and population twin ovulation rate in year $t-1$ in Troms, Nord-Trøndelag and Vestfold with linear regression lines. Grey dashed line indicates the 1:1 relationship between observed twinning rate and population twin ovulation rate. Filled symbols are the mean values within each region.

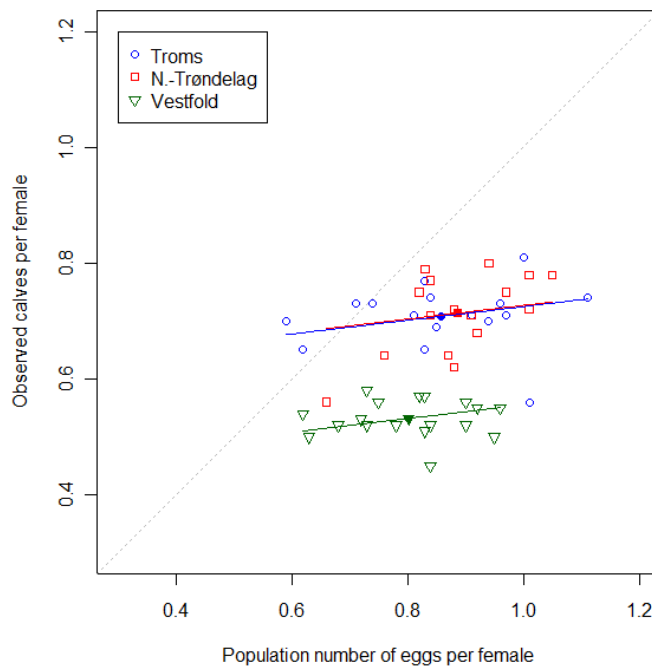


Figure 7: The relationship between observed calves per female and population number of eggs per female in year $t-1$ in Troms, Nord-Trøndelag and Vestfold with linear regression lines. Grey dashed line indicates the 1:1 relationship between mean calves seen per female and population number of eggs per female. Filled symbols are the mean values within each region.

The annual observed calves per female tended to increase with the number of eggs per female in the population the year before ($\beta = 0.12 \pm 0.06$, $t = 1.80$, $p = 0.079$; Fig. 7). For a given number of eggs per female, females in Vestfold produced significantly less calves than females in Troms and Nord-Trøndelag ($p < 0.001$). Additionally, the number of calves per female increased with the number of eggs per female when controlling for year ($\beta = 0.50 \pm 0.17$, $t = 2.94$, $p = 0.006$). The slope of the relationship between observed calves per female and population eggs per female deviated from a 1:1 relationship ($\beta = 0.14$, $p = 0.10$, 95% CI = 0.03-0.31) on a log-log scale. When including yearling body mass and climate variables in the analysis, the best model to explain temporal variation in number of calves per female included the population number of eggs per female, yearling body mass, June temperature and snow depth (Table 3). Thus for a given year, significantly more calves per female were recruited following years with a large number of eggs per female, large yearling body mass), high June temperatures and low snow depths. The second best model included yearling body mass, June temperature and snow depth, but this model was two times less supported than the best model ($\Delta AIC_{cW_{ratio}}$ of model 1 compared to model 2 = 2.18; Appendix 5).

Considering spatial differences in calves per female, the best model included the population number of eggs per female, June temperature and snow depth. More calves per female were found in regions with higher number of eggs per female ($\beta = 0.29 \pm 0.11$, $t = 2.59$, $p = 0.015$), lower June temperatures ($\beta = -0.04 \pm 0.01$, $t = -6.04$, $p < 0.001$) and lower snow depths ($\beta = -0.01 \pm 0.01$, $t = 2.12$, $p = 0.043$). The second best model, including population number of eggs per female and June temperature, was one time less supported than the best model ($\Delta AIC_{cW_{ratio}}$ of model 1 compared to model 2 = 1.25; Appendix 6).

Table 3: Parameter estimates from the most parsimonious multiple linear regression based on AIC_c -values explaining temporal variation in observed number of calves per female. $N = 50$. $R^2 = 0.85$.

	Estimate \pm SE	t value	P value
Eggs per female	0.116 \pm 0.058	2.00	0.051
Yearling body mass	0.004 \pm 0.001	2.93	0.005
June temperature	0.010 \pm 0.004	2.44	0.019
Snow depth	-0.011 \pm 0.004	-2.61	0.013

3.5 Recruitment failure

The recruitment failure varied between regions ($F_{2,29} = 14.79$, $p < 0.001$) and years ($F_{18,29} = 1.96$, $p = 0.052$). The highest recruitment failure was found in Vestfold, where 33 % of egg cells were not realised in a calf the subsequent year (Fig. 8). In Nord-Trøndelag there was a 19 % failure, while in Troms 15 % of eggs were not being realised in a calf the subsequent year.

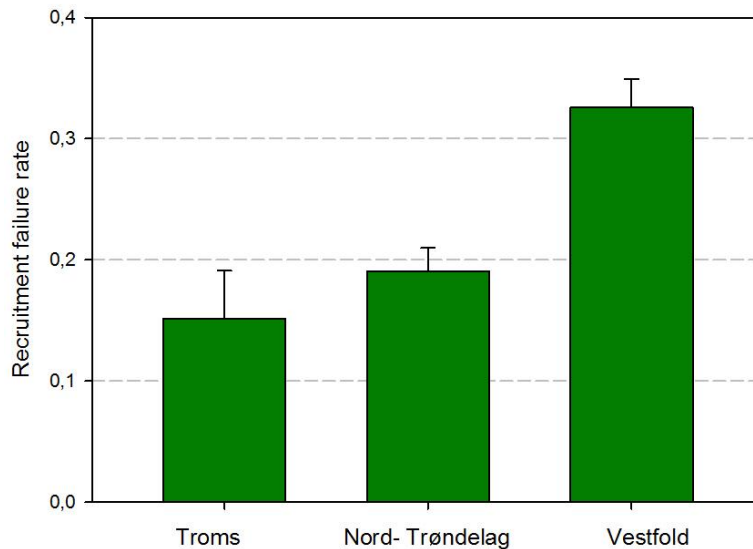


Figure 8: Mean recruitment failure rate in Troms, Nord-Trøndelag and Vestfold. Bars indicate one standard error.

3.6 Spatial synchrony in recruitment rates and ovulation rates

Despite the temporal effect of several climate variables, the cross-correlation analysis did not reveal any spatial synchrony in the time series of recruitment rates or ovulation rates between the 3 regions (e.g. number of eggs per female in Troms and Vestfold: $r = 0.42$, $p = 0.12$; Appendix 7).

4. Discussion

My results show that both recruitment rates and ovulation rates vary among regions and years (Fig. 2). Furthermore, twinning rates was more variable than ovulation and calving rates (Fig. 3-4). Similarly, young moose showed larger variation in ovulation rates and twin ovulation rates than adult moose (Fig. 4). Finally, there was a positive spatiotemporal covariation between the number of eggs per female and the number of calves per female recruited to the population in the following year (Fig. 7). However, the temporal relationships were weak and mainly caused by the positive relationship between the ovulation rates and the subsequent calving rates (Fig. 5), whereas the twinning rates from ovaries and moose observations were uncorrelated (Fig. 6). The weak relationships indicate that the levels of recruitment failure vary between years, partly due to temporal variation in climate and body condition (Table 3; Appendix 5). This indicates that more egg cells are realised into a calf in years with good living conditions. Moreover, higher recruitment failures in Vestfold (Fig. 8), where ovulation rates and body masses are low compared to populations further north, further indicates that recruitment failure occurs most frequently in populations with poor living conditions.

4.1 Effects of hunting selectivity

This study is based on data collected by hunters from different regions in Norway. I therefore examined whether biased sampling affected the results. In a previous study, Solberg et al. (2006) showed that the observed calves per female showed similar annual variation as the mean ovulation rate of harvested females, but indicated also that varying degrees of hunting selectivity could have some impact. In my case, hunting selectivity can have affected the results in two different ways.

Firstly, the observed calves seen per female are not only affected by the proportion ovulated eggs that are turned into a calf in the autumn, but is also affected by the hunting pressure on calves and adult females during the hunting season. In most populations more calves than adult females are harvested, which in turn reduces the number of calves per females observed during the hunting season. In a mathematical and graphical model, Solberg et al. (2006) showed how biased harvesting is likely to affect the ratio of calves and female estimated from observations collected during the entire hunting season. Using this model, I found that the observed calves per female may have been 17 % lower than the pre-harvest number of calves per female in Troms and 13 % lower in Vestfold. In these regions, the harvest of calves per female is only slightly higher than the observed calves per female and

thus has only a small impact on the observation rates. In Nord-Trøndelag, however, where the relative harvest rates of calves to females is much higher, the observed number of calves per female may have underestimated the pre-harvest ratio of calves and females by as much as 43 %. If so, the estimated rate of recruitment failure should actually be below zero in Nord-Trøndelag, i.e. each female is recruiting more calves than the number of eggs she produced the year before.

The second effect of hunting selectivity is acting on the sample of adult females harvested. Because hunters may be inclined to shoot females not accompanied by a calf or calves, the less fecund females may be more likely to enter the sample (Nilsen & Solberg, 2006). Accordingly, the ovulation rates and twin ovulation rates estimated from the hunting sample is likely to underestimate the rates in the different age classes and in the entire population. This effect will partly counteract the effects of biased harvesting on the observed calves per female and in turn the recruitment failure. Most likely the effect will be small in Nord-Trøndelag, where many highly fecund females lose their calf/calves during the hunting season and get themselves killed. This is less likely to happen in Troms and Vestfold, and therefore the ovulation rates are probably underestimated. Because the level of hunting selectivity is rather similar in these two populations, however, the relative difference in rate of recruitment failure is likely to be similar.

The accuracy of observed recruitment rates, will in addition to hunting selectivity, be influenced by observation conditions and moose behavior. However, previous studies have shown that hunter observations reflect variation in reproductive rates reasonably well (Ericsson & Wallin, 1999; Solberg & Sæther, 1999). In a recent study, Solberg et al. (2010a) found a close relationship between variation in observed recruitment rates and rates estimated from radiocollared individuals. Indeed, based on their results even the effects of hunting selectivity seem to have minor effects on the observed rates, despite a large proportion calves in the harvest. I therefore believe that the observed recruitment rates provide a reasonably good estimate of the similar rates in the population.

4.2 Effects of age structure

Another factor that might have influenced my results is spatiotemporal variation in age structure. Because age-distributions among females in different parts of Norway (Solberg et al., 2006) and age-specific reproduction (Sæther and Haagenrud, 1983) show large variation, the variation in calves per female could be influenced by both varying age of females and

varying calf production within age classes. Temporal variation in age structure might appear as a result of varying mortality rates (e.g. hunting) and yearly variation in recruitment rates. For instance, strong cohorts can affect the calf production positively in consecutive years when these age classes reach prime-age (Solberg et al., 1999; Solberg et al., 2006). The effect of age structure on recruitment rates is well known from theoretical models (e.g. Caswell, 2001) and hence can confound relationships between observed recruitment rates and age-specific ovulation rates.

To examine these age-dependent effects I adjusted the ovulation rates for variation in female age structure in three populations. However, because the cohort analysis assumes no annual variation in cohort-specific natural mortality and a closed population (no emigration or net immigration during the study period), the estimated age structure is unlikely to be entirely unbiased. Indeed, even relatively modest variation in natural mortality rate may affect the age structure between years because the error accumulates across age classes in a cohort. Such error variance in the age structure has probably contributed to the relatively weak temporal relationship between observed recruitment rates and previous ovulation rates in my study. However, given the generally high and stable survival rates in moose (Stubsjøen et al. 2000) as in other large ungulates (Sæther 1997; Gaillard et al. 19998), I find it unlikely that biased age structure is the main reason for the large variation in ovulation rates observed between regions. This suggests that neither hunting selectivity, sampling biases nor varying age structure can account for the overall relationship between ovulation rates and recruitment rates.

4.3 Spatiotemporal variation in ovulation rates and observed recruitment rates

I observed a larger temporal variation in ovulation rate and twin ovulation rate for yearlings than for prime-aged adults (Fig. 4), in support of Eberhardt's hypothesis (Eberhardt, 1977). One explanation for this may be that young females experience higher costs of reproduction compared to older females (Clutton-Brock, 1991). Accordingly, fecundity of young females in ungulates has been shown more sensitive to harsh environmental conditions, high population density and food limitation (Gaillard et al. 2000), making reproductive patterns of young highly variable. Fertility of prime-aged females shows higher resilience to both density-dependent and density-independent factors (Boer, 1992; Gaillard et al., 2000).

Allocation of energy to reproduction in moose may be affected by two characteristics:
1) body growth continues after sexual maturity and can be reduced by an early maturity

(Sæther & Haagenrud, 1985; Sand 1998), and 2) maternal condition may be important for the phenotypic quality of offspring (Solberg et al., 2007), litter size (twin production, Franzmann & Schwartz, 1985; Sand, 1996) and lifetime reproductive success. Reproducing at a small body size will likely impose a relatively larger risk on future fecundity for yearlings, than older females, because of a trade-off mechanism for early maturation against further growth (Stearns, 1992; Sand, 1996).

The same mechanism may explain why the age- specific twin ovulation rates showed higher temporal variation than the ovulation rates and why the observed twinning rates was varying more than the observed calving rates (Fig. 3-4). Twin calves usually have smaller body mass than single calves (Sæther & Heim, 1993), but the difference is small compared to the reproductive costs of having two calves. Accordingly, females rearing twins usually lose more mass than females rearing only one calf (Sand, 1996). This relates to Lacks (1947) early theories of variable clutch sizes in birds and a trade-off between number and quality of offspring (Lloyd, 1987; Stearns, 1992). Twinning rates have also earlier been shown to be the most variable component of fecundity in moose (Boer, 1992).

4.4 Determinants of varying recruitment rates

The positive relationship between ovulation rates and recruitment rates the following year suggests that variation in ovulation rates predicts calf production the following year within and between populations. However, the predictive power of this relationship was quite low. One reason for the low precision may be differences among years and regions in the prenatal and neonatal mortality of calves. This was also supported by the final model, which, besides the effect of previous year's ovulation rates, also included an effect of climate and body mass on the temporal variation in autumn recruitment rates (Table 3). A larger number of calves per female were found in years with larger yearling body masses, lower snow depths and a higher June temperature. Larger body masses indicate good conditions for body growth the current year, which may act positive on the survival rate of calves during summer. Likewise, low snow depth during winter is likely to make the living conditions easier for moose during pregnancy. Deep snow increases the energetic expenditure during locomotion, restricts access to food, and may in turn reduce the body condition and recruitment rate of moose (Mech et al., 1987; Hjeljord & Histøl, 1999, but see Solberg et al. 1999). Both Sæther (1985) and Sæther & Gravem (1988) found negative effects of snow depths on moose body mass in southern- and central Norway. A reduced female body condition could therefore result in

higher rates of recruitment failure. In Troms in mid 1990s, high population density and harsh winters were associated with a high level of prenatal and neonatal mortality (Solberg et al., 2006). Similarly, in other ungulates, large foetal loss or perinatal mortality follows severe winters (e.g. Gaillard et al. 2000; Solberg et al., 2001; Garrott et al., 2003). For example, reduced female body condition during winters with deep snow and ice crust formation in Svalbard reindeer *Rangifer tarandus platyrhynchos* were followed by low recruitment rates, probably due to foetus absorption, abortion and neonatal mortality (Reimers, 1982; Solberg et al., 2001).

The temporal effect of June temperature on the variation in calves per female was positive and not negative as expected. There is considerable evidence from studies on moose that cool summer temperatures have a positive effect on body growth (Sæther 1985; Sæther et al., 1996; Solberg et al., 1999; Herfindal et al. 2006b) and reproduction in the following year (e.g. Solberg et al., 1999; but see Grøtan et al. 2009), probably due to negative effects of temperatures on the growing season which gives higher quality of feeding plants (Bliss, 1962; Klein 1970). However, the effects of summer temperatures can depend on where in Norway the population is located (Grøtan et al., 2009), and although the conditions for body growth may increase during years with a cool early summer, the survival conditions for calves may not. Indeed, a cool early summer may also involve energetic costs associated with thermoregulation, particularly for infants (Gaillard et al. 2000), and risk hazards associated with flooding rivers (Sæther & Heim, 1993). Similarly, Grøtan et al. (2009) found that recruitment rates of Norwegian moose were positively affected by temperature during early summer in northern Norway, although without simultaneously controlling for variation in ovulation rates.

Regarding spatial variation in calves per female, only snow depth and June temperature was shown to have a significant effect in the model, after accounting for the number of eggs per female. More calves per female were produced in populations with lower snow depth and cooler early summers. The negative effect of summer temperature was as expected, i.e. if we assume that better summer feeding conditions makes females better able to care for their calf/calves. However, as summer temperatures decrease from south to north, this effect may also be related to other variables that change with latitude, such as population density and body mass. Indeed, body mass was not included in the spatial model, possibly because of the close spatial correlation between yearling body mass and June temperature ($r = -0.43$, appendix 8).

4.5 Recruitment failure and spatial variation in body condition

Based on the populations with reconstructed age structure, it is apparent that the level of recruitment failure can be substantial and vary significant between regions (Fig. 8). The rate of recruitment failure was highest in Vestfold (33 %) and lowest in Troms (15 %) and Nord-Trøndelag (19 %). For comparison, Testa and Adams (1998) found that 15 % of ovulations failed to result in a detectable embryo in Alaska moose, and that additional losses occurred between early gestation and birth. Similarly, Crichton (1992) found an 8 % loss of ova through embryonic mortality or fertilisation failure in Canada, while Markgren (1969) found a 10-15 % in utero loss of embryos in moose in Sweden. Thus, given that my measurement also includes neonatal and summer mortality of calves, the failure rate observed in Troms and Nord-Trøndelag appear to be quite normal or low. In Vestfold, however, the failure rates seem to be extraordinary high. In this area, as in most of Norway, large carnivores are almost absent (Swenson et al., 2005; Wabakken et al., 2010) and accordingly the failure rate is unlikely to be the result of predation. However, body masses of moose have decreased substantially in these areas during the last 20 years following very high population densities in the late 1980's and early 1990's (Solberg et al., 2006).

A possible explanation for the pattern observed is thus that the rates of foetus loss and perinatal mortality are higher in these populations due to the poor living conditions. Both pregnancy and lactation is expensive in terms of energy (Clutton-Brock, 1991) and accordingly females in poor condition may more often lose their foetus (abortion) or calf/calves prior to recruitment. Particularly, it is difficult to recruit two calves when the living conditions deteriorates (e.g. Franzmann & Schwartz, 1985; Boer, 1992), and this may explain why it is mainly the difference between twin ovulation rates and observed twinning rate that generates the larger recruitment failure in Vestfold. An alternative explanation may be that parasites or diseases affect the body condition and recruitment rates negatively. A study of moose population decline in northwestern Minnesota indicated that parasitism and infectious disease were the most prevalent proximate cause of mortality (Murray et al., 2006). However, these explanations are not mutually exclusive. It would be expected that those females that are in poor condition also would be more susceptible to parasites and diseases. When co-occurring, the effects of parasites and/or diseases and malnutrition could interact so that the individual condition is further compromised (e.g. Murray et al., 1997; Stien et al., 2002).

4.6 Management implications

Differences in recruitment rates are determined by the variation in ovulation rates, fertilisation rates and the subsequent survival of embryos, foetuses and calves. My results indicate that more recruitment failures occur in regions and years associated with low body condition.

In Norway, the ovulation rates are used to monitor population vitality based on the assumption that ovulation reflects calf production. However, as indicated in my study the ovulation rates are only telling part of the story as varying proportions of ovulated egg cells are realised in a calf in different years and regions. Ovulation rates may therefore have small applied interest from a monitoring perspective, in particular as they are time-consuming and costly to collect and analyse. However, because the failure rate is also influenced by underlying biases and hunting selectivity, further studies should be conducted to solve these problems before collection of ovaries potentially are phased out.

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6. Appendix:

Appendix 1:

Mean observed calving rate, twinning rate and calves seen per female \pm standard error in each region. Number of years with data within each region is shown in brackets.

Regions:	Calving rate	Twinning rate	Calves per female
Troms	0.51 \pm 0.004 (16)	0.38 \pm 0.003 (16)	0.71 \pm 0.01 (16)
Nordland	0.57 \pm 0.003 (16)	0.39 \pm 0.01 (16)	0.79 \pm 0.01 (16)
Nord-Trøndelag	0.52 \pm 0.01 (16)	0.37 \pm 0.003 (16)	0.71 \pm 0.01 (16)
Oppland	0.51 \pm 0.002 (18)	0.19 \pm 0.002 (18)	0.60 \pm 0.003 (18)
Hedmark	0.54 \pm 0.003 (7)	0.27 \pm 0.01 (7)	0.68 \pm 0.01 (7)
Vestfold	0.47 \pm 0.003 (18)	0.14 \pm 0.002 (18)	0.53 \pm 0.003 (18)
Aust-Agder	0.54 \pm 0.01 (6)	0.13 \pm 0.01 (6)	0.61 \pm 0.01 (6)
Vest-Agder	0.49 \pm 0.01 (10)	0.18 \pm 0.01 (10)	0.58 \pm 0.01 (10)

Appendix 2:

Mean ovulation rate \pm standard error in each region and age class. Number of years with data within each region is shown in brackets.

Region:	Age class:				
	1	2	3	4	5
Troms	0.33 \pm 0.04 (16)	0.82 \pm 0.03 (16)	0.89 \pm 0.02 (16)	0.89 \pm 0.02 (16)	0.87 \pm 0.02 (16)
Nordland	0.43 \pm 0.07 (16)	0.83 \pm 0.04 (16)	0.97 \pm 0.01 (16)	0.90 \pm 0.02 (16)	0.72 \pm 0.05 (16)
N.-Trøndelag	0.36 \pm 0.06 (16)	0.94 \pm 0.01 (16)	1.00 \pm 0.00 (16)	0.97 \pm 0.01 (16)	0.79 \pm 0.03 (16)
Oppland	0.10 \pm 0.03 (18)	0.85 \pm 0.02 (18)	0.91 \pm 0.02 (18)	0.88 \pm 0.02 (18)	0.99 \pm 0.01 (18)
Hedmark	0.31 \pm 0.09 (7)	0.98 \pm 0.01 (7)	1.00 \pm 0.00 (7)	1.00 \pm 0.01 (7)	0.94 \pm 0.04 (6)
Vestfold	0.12 \pm 0.02 (18)	0.75 \pm 0.03 (18)	0.81 \pm 0.03 (18)	0.94 \pm 0.00 (18)	0.78 \pm 0.02 (18)
Aust-Agder	0.01 \pm 0.04 (6)	0.49 \pm 0.08 (6)	0.82 \pm 0.04 (6)	0.97 \pm 0.01 (6)	0.84 \pm 0.03 (6)
Vest-Agder	0.07 \pm 0.02 (10)	0.86 \pm 0.03 (10)	0.89 \pm 0.03 (10)	0.97 \pm 0.00 (10)	0.95 \pm 0.02 (9)

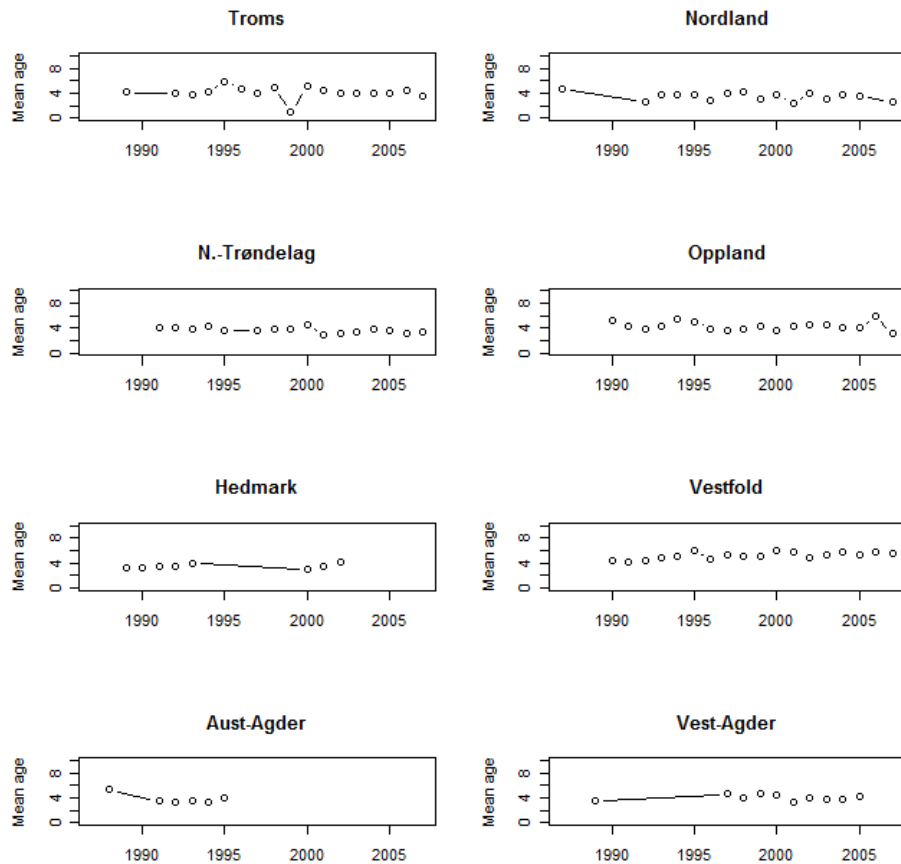
Appendix 3:

Mean twin ovulation rate \pm standard error in each region and age class. Number of years with data within each region is shown in brackets.

Region:	Age class:				
	1	2	3	4	5
Troms	0.20 \pm 0.08 (14)	0.40 \pm 0.06 (16)	0.53 \pm 0.07 (14)	0.58 \pm 0.04 (16)	0.43 \pm 0.07 (14)
Nordland	0.13 \pm 0.06 (12)	0.25 \pm 0.04 (15)	0.42 \pm 0.10 (14)	0.56 \pm 0.07 (16)	0.39 \pm 0.10 (13)
N.-Trøndelag	0.21 \pm 0.06 (16)	0.29 \pm 0.04 (16)	0.38 \pm 0.05 (16)	0.59 \pm 0.04 (16)	0.46 \pm 0.08 (16)
Oppland	0.14 \pm 0.08 (14)	0.16 \pm 0.04 (18)	0.29 \pm 0.05 (18)	0.34 \pm 0.04 (18)	0.24 \pm 0.05 (18)
Hedmark	0.16 \pm 0.06 (6)	0.41 \pm 0.05 (7)	0.30 \pm 0.12 (7)	0.56 \pm 0.08 (7)	0.30 \pm 0.12 (5)
Vestfold	0.09 \pm 0.07 (15)	0.20 \pm 0.04 (18)	0.23 \pm 0.04 (18)	0.37 \pm 0.03 (18)	0.36 \pm 0.04 (18)
Aust-Agder	0,50 \pm 0,50 (2)	0,30 \pm 0,09 (5)	0,42 \pm 0,10 (6)	0,46 \pm 0,05 (6)	0,70 \pm 0,07 (6)
Vest-Agder	0,04 \pm 0,04 (9)	0,23 \pm 0,06 (10)	0,35 \pm 0,08 (10)	0,50 \pm 0,08 (10)	0,50 \pm 0,06 (9)

Appendix 4:

Yearly variation in mean age from 1988-2008.



Appendix 5:

The AIC_c - based ranking of models explaining the temporal variation in calves per female using multiple linear regression. Variables included in the models are indicated by an X. ΔAIC_c refers to the difference between the best model (model 1) and the candidate model. Only models with $\Delta AIC_c < 2$ are presented.

Model	Eggs per female	Yearling BM	June °C	Winter °C	Snow depth	Region	AIC_c	ΔAIC_c	AIC_c weight
1	X	X	X		X	X	-161.38	0.00	0.37
2		X	X		X	X	-159.76	1.61	0.17

Appendix 6:

The AIC_c - based ranking of models explaining the spatial variation in calves per female using multiple linear regression. Variables included in the models are indicated by an X. ΔAIC_c refers to the difference between the best model (model 1) and the candidate model. Only models with $\Delta AIC_c < 2$ are presented.

Model	Eggs per female	Yearling BM	June °C	Winter °C	Snow depth	Region	AIC_c	ΔAIC_c	AIC_c weight
1	X		X		X	X	-68.79	0.00	0.34
2	X		X			X	-68.33	0.46	0.27

Appendix 7:

Cross-correlation between the time-series of population number of eggs per female (above the diagonal) and calves per female (underneath the diagonal) for the different regions. None of the correlations were significant at $p < 0.05$.

	Troms	Nord- Trøndelag	Vestfold
Troms	-	0.03	0.42
Nord- Trøndelag	0.31	-	0.19
Vestfold	-0.29	-0.06	-

Cross-correlation between the time-series of population ovulation rate (above the diagonal) and calving rate (underneath the diagonal) for the different regions. None of the correlations were significant at $p < 0.05$.

	Troms	Nord- Trøndelag	Vestfold
Troms	-	0.00	0.13
Nord- Trøndelag	0.29	-	0.02
Vestfold	-0.26	-0.11	-

Cross-correlation between the time-series of population twin ovulation rate (above the diagonal) and twinning rate (underneath the diagonal) for the different regions. None of the correlations were significant at $p < 0.05$.

	Troms	Nord- Trøndelag	Vestfold
Troms	-	-0.08	0.23
Nord- Trøndelag	0.21	-	0.18
Vestfold	0.21	0.03	-

Appendix 8:

Pearson's product- moment correlation coefficients with associated p values (underneath the diagonal) between yearling body mass, June temperature, Winter temperature (December-Mars) and snow depth (December-Mars).

	Yearling body mass	June temperature	Winter temperature	Snow depth
Yearling body mass	-	-0.43	-0.23	0.21
June temperature	<0.001	-	0.54	-0.67
Winter temperature	0.002	<0.001	-	-0.58
Snow depth	0.006	<0.001	<0.001	-