

Age, Size, and Spatiotemporal Variation in Ovulation Patterns of a Seasonal Breeder, the Norwegian Moose (*Alces alces*)

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Submitted February 1, 2008; Accepted August 6, 2008;
Electronically published December 10, 2008

Online enhancement: appendix.

ABSTRACT: In seasonal environments, timing of reproduction is an important fitness component. However, in ungulates, our understanding of this biological process is limited. Here we analyze how age and body mass affect spatiotemporal variation in timing of ovulation of 6,178 Norwegian moose. We introduced a parametric statistical model to obtain inferences about the seasonal timing of ovulation peak, the degree of synchrony among individuals, and the proportion of individuals that ovulate. These components showed much more spatiotemporal variation than previously reported. Young (primiparous) and old (≥ 11.5 years of age) females ovulated later

than prime-aged (2.5–10.5 years of age) females. In all age classes, ovulation was delayed with decreasing body mass. Ovulation rates were lower and more variable among primiparous females than among older females. Young females required higher body mass than older females did to ovulate. The body-mass-to-ovulation relationship varied with age, showed large regional variation, and differed among years within region. These results suggest that (1) environmental and population characteristics contribute to shape seasonal variation in the breeding pattern and (2) large regional variation exists in the size-dependent age at maturity in moose. Hence, the life-history trade-off between reproduction and body growth should differ regionally in moose.

Keywords: age, body mass, ecological modeling, life-history theory, reproduction, ungulates.

Introduction

In studies of ungulates, information about age-specific vital rates, such as reproduction and survival, is strongly required to understand the population dynamics and to develop management strategies (Pojar 1981; Coulson et al. 2001). In this context, reproductive parameters are often easier to measure than survival, and the mechanisms causing individual variation in fecundity are therefore fairly well known in many mammalian populations (Sæther 1997; Gaillard et al. 2000). Whereas detailed information is available about factors structuring female reproductive output, our knowledge about the variations in ovulation patterns is still scarce. However, as variations in ovulation dates and subsequent variations in timing of birth are likely to influence the population dynamics through their effects on juvenile body mass (Albon et al. 1987; Sæther et al. 2003; Holand et al. 2006a), growth rates (Albon et al. 1987; Clutton-Brock et al. 1992; Andersen and Linnell 1997; Lindström 1999; Holand et al. 2006a), and summer (Festa-Bianchet 1988b) and winter survival (Clutton-Brock et al. 1987; Gaillard et al. 1996; Rose et al. 1998; Loison et al. 1999), variation in breeding phenology may also have strong evolutionary and management implications.

Seasonal variation in timing of breeding and synchrony

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among individuals in onset of breeding have been shown to be dependent on age and body size (Sadleir 1987). In several ungulates, a weight threshold for breeding has also been reported (Sadleir 1969; Sæther and Haagenrud 1983; Hewison 1996; Sand 1996). However, animals are expected to mature not at a fixed age or a fixed size but along an age-size trajectory (Sæther and Haagenrud 1985; Stearns and Koella 1986). Indeed, in most ungulates, fecundity is positively related to body size (Gaillard et al. 2000), growth continues after sexual maturation (e.g., Clutton-Brock et al. 1982), and phenotypic quality of offspring depends on the age and/or size of the mother (e.g., Côté and Festa-Bianchet 2001), all of which favors delayed maturity until a certain size has been attained in order to increase the overall lifetime reproductive success (Stearns 1992). Accordingly, we can expect (1) that females trade off early maturation against further growth and therefore that the age-size maturation relationship should vary between and within populations according to any factor acting on female condition (e.g., Albon et al. 1983) and offspring survival (Skogland 1989); and (2) a strong relationship between body mass and fecundity of young females; that is, young females reproduce only when they reach high body mass, given the potential cost of reproduction, whereas adults should reproduce almost irrespective of their body mass (see Sand 1996). Few studies have focused on these variations in the age-size-fecundity relationship among and within populations (Albon et al. 1983), and little is known about the role of the timing of mating in such a context (Langvatn et al. 2004).

We studied the ovulation patterns in Norwegian moose (*Alces alces*), a widespread, heavily exploited species (Lav-sund et al. 2003). Several studies have examined ovulation patterns in this species, but often on the basis of small data sets (Pimlott 1959; Simkin 1965; Markgren 1969; Schladweiler and Stevens 1973; Sæther and Haagenrud 1983, 1985; Schwartz and Hundertmark 1993; Sand 1996; Sigouin et al. 1997). We also introduce a new statistical model that assumes the unobserved time of ovulation T to be a normally distributed variable. On the basis of ovary data from 6,178 moose females in six harvested populations, we inferred how the mean (μ , ovulation peak) and standard deviation (σ , ovulation synchrony) of this distribution, as well as the overall ovulation rate (q , multiplying the normal distribution), depend on spatiotemporal covariates of interest. We also discuss the usefulness of this approach in studying reproduction of seasonal breeders and assess the extent to which we obtained the same general results as previous studies from Scandinavia and North America. We specifically examined how variation in the probability of ovulation can be described by age and body mass and whether these relationships differ geographically.

Observed patterns and possible mechanisms are discussed in the light of life-history theory.

Study Areas

Moose data were collected from 29 municipalities in the counties of Vestfold ($n = 5$ municipalities), Oppland ($n = 5$), Hedmark ($n = 2$), Nord-Trøndelag ($n = 5$), Nordland ($n = 3$), and Troms ($n = 9$), Norway (fig. 1). The data collection was part of the national monitoring of cervids in Norway, which is funded by the Directorate for Nature Management and is conducted by the Norwegian Institute for Nature Research. Data cover most of the distribution range of moose in Norway, spanning a large variety of habitats along a north-south gradient (for more details, see Garel et al. 2006; Herfindal et al. 2006a). The study areas range from 58°N to 70°N, and the average altitude ranges from 50 to 840 m above sea level. All study areas are situated within the boreal vegetation zones. The study areas in Nordland, Nord-Trøndelag, and Hedmark counties are located mainly in coniferous forests that consist of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), whereas in Troms and Oppland, a large part of the study area is covered by birch (*Betula pubescens*) in addition to Scots pine and Norway spruce (Oppland only). Forests in Vestfold consist mainly of Scots pine, Norway

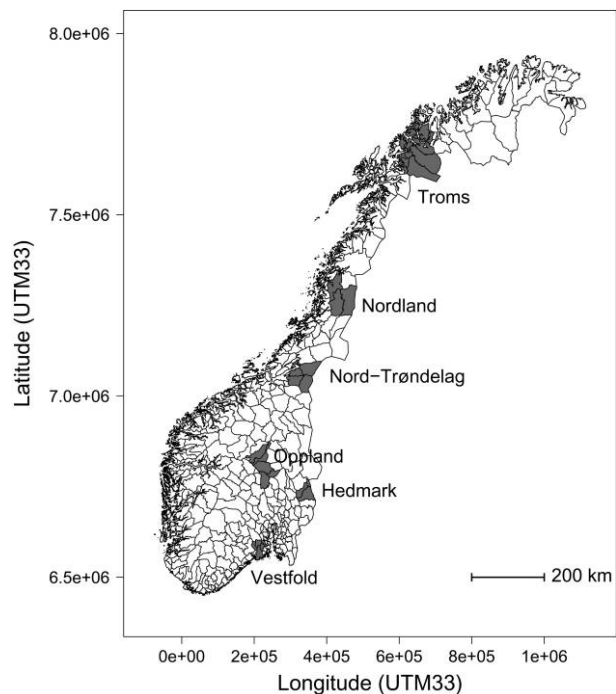


Figure 1: Location of the six Norwegian regions from which moose data were collected in 29 municipalities.

spruce, and birch in the interior and coniferous trees mixed with birch, oak (*Quercus robur*), and, to some extent, beech (*Fagus sylvatica*) along the coast.

Material and Methods

Moose Data

Hunting is controlled through licenses issued by wildlife boards in each municipality. The hunting season during the study period was from September 25 to October 1 and from October 10 to October 31 in the counties of Nord-Trøndelag, Nordland, and Troms and from October 5 to October 31 in Hedmark and Vestfold counties. In Oppland, hunting mainly occurs during the entire period September 25–October 31. In the three northern regions (fig. 1), an 8-day break in the hunting season (from October 2 to October 9) was established to protect moose during the assumed peak of rut. Since 2002, local management boards have been permitted to extend the hunting season by up to 2 weeks in November and December as well as during the previous week of protection (October 2–9). However, except for a few municipalities, most moose are still shot within the same period as the pre-2002 hunting season.

Hunters recorded kill date, locality, sex, and carcass mass and collected the lower jawbone for age determination, as well as the uterus and ovaries. Carcass mass, which constitutes 50%–56% of total body mass, on average (Wallin et al. 1996; Solberg et al. 2008), was equal to body mass minus head, skin, metapodials, bleedable blood, and viscera and was weighed to the nearest kilogram. For yearlings, the ontogenetic development of and the pattern of tooth replacement in the lower jawbone determined age (Franzmann and Schwartz 1998), whereas for animals that were ≥ 2.5 years old, age was estimated in the laboratory by counting the number of layers in the secondary dentin of the incisor (Haagenrud 1978). We did not include female calves in the material, as most studies do not report any evidence of ovarian activity for these females (e.g., see Pimlott 1959; Simkin 1965; Markgren 1969; Schladweiler and Stevens 1973; Sæther and Haagenrud 1983; Schwartz and Hundertmark 1993). Kill date was transformed to Julian date, with September 25 as day 268 (reference day, January 1). In leap years (years with 366 days), September 25 is day 269, to account for the difference of 1 day compared with the last reproductive season.

Ovulation was determined by the presence and appearance of luteal structures in ovaries (e.g., in moose, Simkin 1965; Markgren 1969; Sæther and Haagenrud 1985; Sand 1998; in barren-ground caribou [*Rangifer tarandus groenlandicus*], Dauphiné and McClure 1974; in red deer [*Cervus elaphus*], Langvatn 1992; Langvatn et al. 1994;

in Cantabrian chamois [*Rupicapra pyrenaica parva*], Perez-Barberia et al. 1998). The ovaries were removed from the uterus, stored in formalin, and subsequently cut into slices for ocular examination of luteal structures. Only females for whom both ovaries were collected were included in the analysis. Ovulation was determined by the absence or presence of one or more primary corpora lutea, which indicate that the female had ovulated in the current rutting season (Markgren 1969; Langvatn et al. 1994). The number of corpora lutea per female usually ranges from 0 to two, but on rare occasions may reach three or four (Markgren 1969). We pooled females with one, two, three, or four corpora lutea in a single category of females who had ovulated. Thus, absence of corpora lutea was scored as 0, and presence was scored as 1.

We restricted the study period to 1991–2005, when more than 30 females with two ovaries collected were available in each region and for each age class used in the analysis (table 1). Moreover, we considered only regions for which data were available each year. We considered five age classes according to the minimum sample size and biological characteristics. We thus distinguished between yearlings and 2.5-year-olds, which includes most of the primiparous females, depending on years and regions; 3.5-year-olds, representing the transition between immature and mature females (e.g., Sæther and Heim 1993; Sæther et al. 1996); 4.5–10.5-year-olds, corresponding to prime-age females (most productive stage, Markgren 1969; Sæther and Haagenrud 1983); and ≥ 11.5 -year-olds, representing senescent individuals. In moose, there is evidence that senescence in reproduction and survival starts at the age of 10–12 years (e.g., see Markgren 1969; Sæther and Haagenrud 1983; Ericsson and Wallin 2001; Ericsson et al. 2001). Ovaries from 6,178 females were collected during the study period (table 1).

Modeling the Ovulation Patterns

We assumed that the time of ovulation T of each individual is a random variable, with expectation μ and standard

Table 1: Number of female moose with two ovaries collected, by age group, in each study region (see fig. 1), 1991–2005

Region	Age group				
	Yearling	2.5 years	3.5 years	4.5–10.5 years	≥ 11.5 years
Hedmark	148	85	40	119	34
Nordland	329	170	51	135	67
Nord-Trøndelag	391	197	89	246	80
Oppland	421	277	138	433	132
Troms	276	206	124	283	111
Vestfold	377	250	165	585	219
Total	1,942	1,185	607	1,801	643

deviation σ . In addition, we assumed that T follows a normal distribution. The use of such a normal model has a long tradition in analyses of selection and evolution of quantitative characters (Lande 1979, 1982) and can be theoretically justified by assuming that many small, unknown, independent effects are additively contributing to each observation (central-limit theorem). Let O be the event that a particular individual would ovulate and let $P(O) = q$. Then the probability that ovulation has occurred at time t is

$$p = P(T \leq t | O)P(O) = q \cdot \Phi\left(\frac{t - \mu}{\sigma}\right), \quad (1)$$

where Φ is the standard normal cumulative density function. Equation (1) specifies a sigmoid relationship between p and t leveling off at an asymptote q (ovulation rate in the following). The curve has an inflection point at $t = \mu$, corresponding in biological terms to the peak of ovulation, and a steepness determined by σ , corresponding to the degree of synchrony in time of ovulation. For $q = 1$, this model simplifies to a generalized linear model with a probit-link function.

Our interest was in how age, region, year, and body mass influence the expected time of ovulation μ , the degree of synchrony σ , and the ovulation rate q . In general, we assumed that μ , $\ln \sigma$, and $\text{logit } q$ are determined by linear predictors, that is, functions of covariates linear in the model parameters. For instance, for the best model (model 1; see “Results”; table 2), we can write these linear predictors in a so-called symbolic notation (e.g., see McCullagh and Nelder 1989, p. 56):

$$\mu = \text{age} + \text{region} + \text{year} + \text{mass}, \quad (2)$$

$$\text{logit } q = \text{age} \times \text{mass} + \text{region} \times \text{mass} + \text{year}, \quad (3)$$

$$\ln \sigma = \text{region} + \text{year}, \quad (4)$$

where age, region, and year are factors (categorical variables) and mass is a continuous covariate. The logit- and log-links in equations (3) and (4) ensure that $0 < q < 1$ and that $\sigma > 0$. The use of a log-link for σ means that different covariates act multiplicatively by increasing the standard deviation of ovulation times T by a factor of, say, 10%.

Statistical Procedures

To avoid overparameterization of the model, the constraint that the effect size for the first level of a factor (or interaction terms) should be equal to 0 was introduced. To compute maximum likelihood estimates of each model, a

Table 2: Modeling variations in ovulation peak μ , ovulation rate q , and ovulation synchrony σ in female moose ($n = 6,178$)

Effect, model variation	Model	
	1	2
μ :		
Age	×	×
Region	×	×
Year	×	×
BM	×	×
Age × region		
Age × BM		
Region × BM		
q :		
Age	×	×
Region	×	×
Year	×	×
BM	×	×
Age × region		
Age × BM	×	×
Region × BM	×	×
σ :		
Age		
Region	×	×
Year	×	×
BM		×
Age × region		
Age × BM		
Region × BM		
No. parameters	79	80
ΔAIC_c	.00	3.28
$\text{AIC}_c w$.41	.08

Note: Only models with a change in Akaike Information Criterion with second-order adjustment $\Delta\text{AIC}_c < 4$ compared with the best model (lowest AIC_c , 5,218.2; model 1) are reported (Burnham and Anderson 1998). × = term included; BM = body mass effect.

function computing the log-likelihood function was implemented in R, version 2.6.0 (R Development Core Team 2007), and was maximized numerically using the optim function (quasi-Newton method; Venables and Ripley 2002).

To deal with the problems of convergence (e.g., local maxima) during the optimization process, we (1) examined the eigenvalues of the Hessian matrix evaluated at the maximum log-likelihood estimate of the parameter vector; that is, all eigenvalues being negative indicated that the log-likelihood had reached a maximum; and (2) used different sets of starting values to be more confident that we had actually found the global maximum.

Because reproductive patterns in ungulates are known to be strongly dependent on body mass and age (e.g., Sadleir 1969; Hewison 1996; Sand 1996; Hewison and Gaillard 2001), we included these variables in the models.

We also accounted for spatiotemporal variations in reproductive patterns (region as a factor with six levels and year as a factor with 15 levels). Before taking into account any two-way interactions (higher-order interactions were excluded because of sample sizes), we first tested for the additive effects of the main effects and then constrained the set of models being tested by systematically including main effects that were present in the best additive models ($\Delta AIC_c < 11$; table A1 in the online edition of the *American Naturalist*). We did not account for interactions between year and other factors because of the low within-year sample sizes. Year was mainly included in the analysis to account for annual variation in ovulation and thereby to minimize bias in parameter estimates.

Model selection was based on the Akaike Information Criterion (AIC), with second-order adjustment of the AIC (AIC_c) to correct for small-sample bias (Burnham and Anderson 1998). This criterion is based on the principle of parsimony and is well adapted for multiple comparisons between nonnested models (Burnham and Anderson 1998). The most parsimonious models (i.e., lowest AIC_c) were selected as the best models. We also computed Akaike weights ($AIC_c w$) to compare the relative performance of models in addition to the absolute AIC_c values (Burnham and Anderson 2001). Weights can be interpreted as the probability ($\sum_{i=1}^n AIC_c w_i = 1$) that a model i is the best model, given the data and the set of n candidate models. The strength of evidence in favor of one model over the others was obtained by dividing their Akaike weights ($AIC_c w_{ratio}$).

For the selected model, we computed the maximum likelihood estimates (MLEs) of the parameters (including differences between, for instance, region-specific coefficients). Confidence intervals (CIs; 2.5% and 97.5% quantiles) were computed by simulating 1,000 bootstrap replicates from the fitted models. Approximate tests of hypotheses were based on whether these CIs included a 0 value. Means were also computed from these bootstrap replicates to assess the extent to which MLEs were biased.

When individual body mass is included in the model, the number of observations within each sample unit becomes equal to 1. This precludes assessment of goodness of fit (Agresti 2002). We therefore excluded body mass and fitted a model with only an age effect ($\ln L_{model} = -2,817.9$). We then computed the log-likelihood of the full model on the basis of data aggregated at the level of age and day number ($n = 190$) as

$$\ln L_{full} = \sum_{i=1}^5 \sum_{j=268}^{305} \log [\pi_{ij}^{nf_{ij}} \times (1 - \pi_{ij})^{n_{ij} - nf_{ij}}] = -2,722.7, \quad (5)$$

where nf_{ij} is the number of females having ovulated, n_{ij} is the total number of females, and π_{ij} is the observed proportion of ovulating females (i.e., nf_{ij}/n_{ij}) for a given age i and day number j . By comparing the deviance of the age model ($2[\ln L_{full} - \ln L_{model}] = 190.4$) with a χ^2 distribution at $n - p$ degrees of freedom ($190 - 15 = 175$, $P = .20$), where p is the number of parameters in the age model, we concluded that a model with only an age effect fitted the data well. Therefore, we were confident that the more complicated models (e.g., those including region and year effects) fitted the data appropriately (see Langvatn et al. 2004 for a similar approach). Furthermore, we fitted a model including the two-way interaction between age and region to assess the goodness of fit between this simple model and the observed ovulation probabilities (see fig. 2).

Results

Among the set of best models ($\Delta AIC_c < 4$; Burnham and Anderson 1998; table 2), both the mean ovulation date μ and the ovulation rate q were dependent on age, area, year, and body mass, whereas the synchrony in ovulation σ showed mostly variation among regions as well as variation among years. We chose to keep model 1 (table 2; see eqq. [2]–[4] in “Material and Methods”), which did not consider any effect of body mass on σ . This model had by far the strongest support from the data (it was >5 times better supported than the second-best model, $AIC_c w_{ratio} = 0.41/0.08$). Residuals of this model (see fig. A1 in the online edition of the *American Naturalist*) did not display any particular pattern and were included in the 95% CI (see Gelman and Hill 2007), indicating that the model assumptions were correct (see also goodness-of-fit test in “Material and Methods” and fig. 3 to assess bias in coefficient estimates). In the following, we applied treatment contrasts (McCullagh and Nelder 1989) to explore the effects of independent variables, with the yearling, Oppland, and 1991 levels of age, region, and year factors, respectively, as control groups.

The adjusted coefficient of determination ($R_{l,adj}^2$; see Liao and McGee 2003 for computation) was equal to 0.40, meaning that 40% of the variation in the data was explained by including age, region, year, and body mass effects in the model, that is, without including any environmental variables or density effects. In table 3, predicted probabilities were averaged at the level of region and age, that is, assuming that body mass and sampling design were balanced among years, whatever the region and age categories. Such a procedure gave us a first overview of the ovulation pattern in Norwegian female moose. With the exception of the Vestfold county population, ovulation occurred from the end of September to early October and was highly synchronized, with 95% of the ovulations tak-

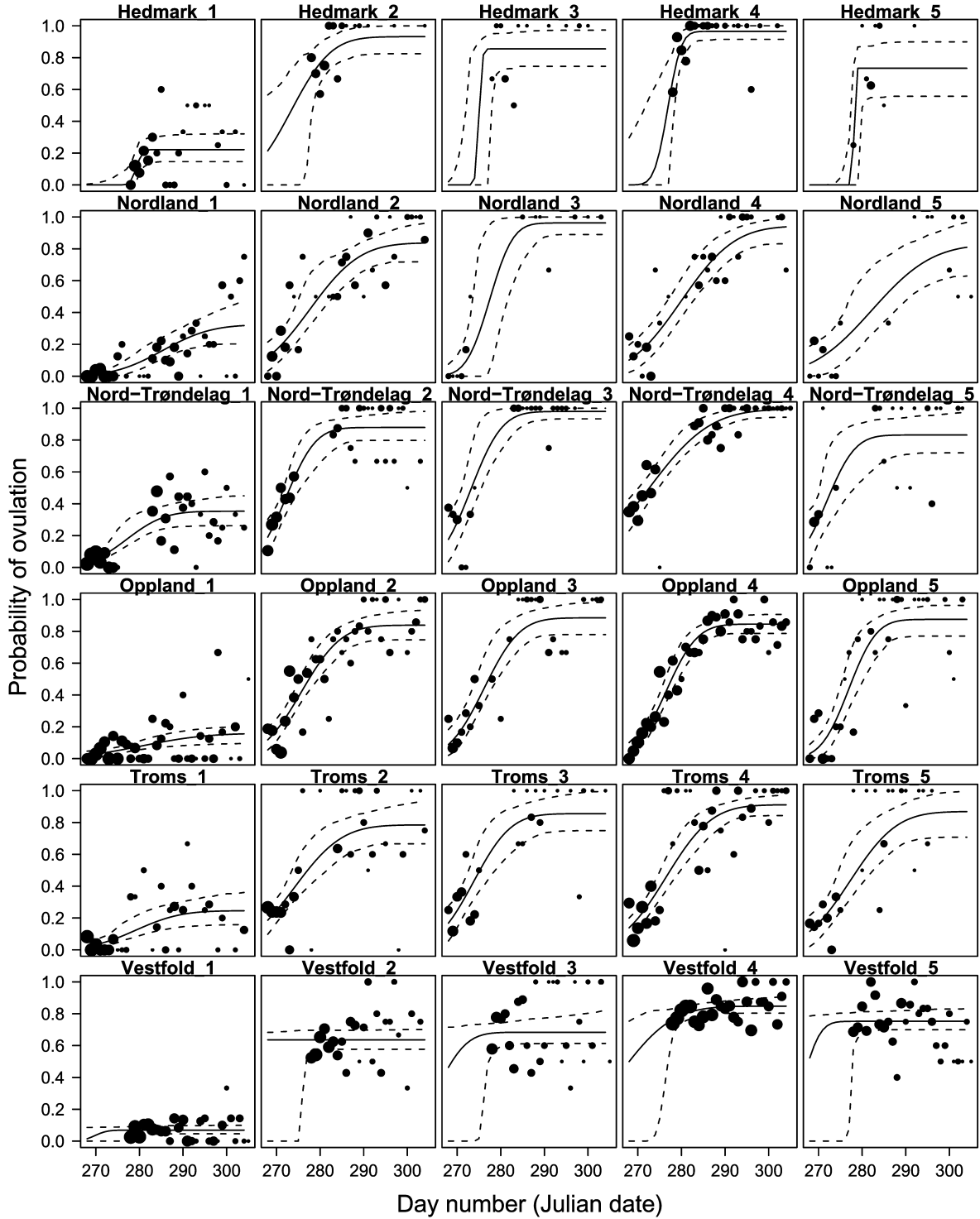


Figure 2: Ovulation pattern in female moose according to age group (1 = yearling, 2 = 2.5 years, 3 = 3.5 years, 4 = 4.5–10.5 years, and 5 = ≥ 11.5 years) and region (see fig. 1). Circles represent the observed ovulation rates, the size being proportional to the sample size (ranging from 1 to 50). Solid lines are based on maximum likelihood estimates of a model where ovulation peak μ , ovulation rate q , and ovulation synchrony σ are age and region dependent. Dashed lines represent bootstrap 95% confidence intervals (1,000 replications). Day 268 corresponds to September 25.

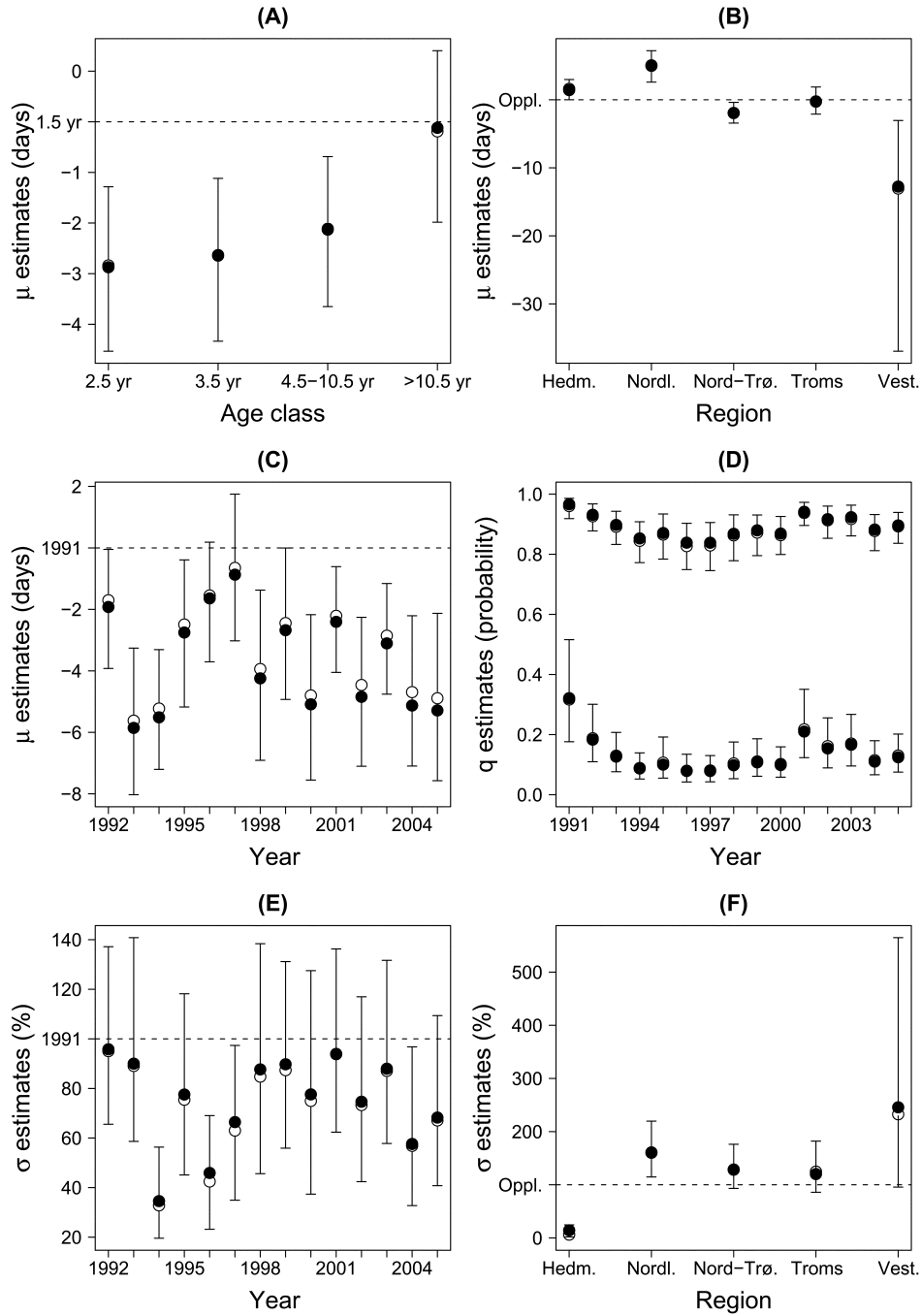


Figure 3: Coefficient estimates (bootstrap estimates with 1,000 replicates and 95% confidence intervals; *open circles*) for the best model (see table 2) with respect to additive effects of (A) age, (B) region, and (C) year on ovulation peak μ ; (D) year on ovulation rate q ; and (E) year and (F) region on ovulation synchrony σ . Given the constraint that the effect size for the first level of a factor is equal to 0 (see “Material and Methods”), the levels yearling (1.5 yr), Oppland, and 1991 correspond to the intercept (*dashed lines*) with which other coefficients are compared. Because logit and log scales are used in model parameterization for q and σ , respectively (see “Material and Methods”), effects were linear only on these scales. For q (D), we made predictions (back-transformed values) for yearlings and prime-age females (bottom and top, respectively) in Oppland and for average body mass in such categories. For σ (E and F), because we used a log scale, the effect sizes correspond to proportional changes on original scale, meaning, for example, that σ was 70% lower in 1994 than in 1991. Filled circles represent the maximum-likelihood estimates (MLEs) of each coefficient in the model (or predictions from MLEs for q in D), showing that coefficient estimates were almost unbiased or very slightly biased when compared with bootstrap estimates (mean values). For location of study areas, see figure 1.

Table 3: Individual predictions (plus 95% confidence intervals) of ovulation peak μ (date), ovulation synchrony σ (days), and ovulation rate q (probability) from maximum likelihood estimates of the best model (see table 2)

Parameter, age group	Region					
	Hedmark	Nordland	Nord-Trøndelag	Oppland	Troms	Vestfold
μ :						
Yearling	10/7 (10/4–10/11)	10/11 (10/8–10/14)	10/4 (10/1–10/7)	10/6 (10/3–10/10)	10/5 (10/2–10/9)	9/24 (9/21–9/27)
2.5 Years	10/3 (10/1–10/6)	10/7 (10/4–10/11)	9/30 (9/27–10/4)	10/2 (9/29–10/6)	10/1 (9/29–10/4)	9/20 (9/17–9/23)
3.5 Years	10/4 (9/30–10/8)	10/7 (10/4–10/11)	9/30 (9/27–10/4)	10/3 (9/29–10/6)	10/1 (9/28–10/5)	9/20 (9/17–9/23)
4.5–10.5 years	10/4 (9/30–10/8)	10/7 (10/5–10/10)	9/30 (9/27–10/4)	10/3 (9/30–10/7)	10/1 (9/28–10/5)	9/20 (9/17–9/23)
≥ 11.5 years	10/5 (10/2–10/9)	10/9 (10/6–10/12)	10/2 (9/30–10/6)	10/5 (10/2–10/9)	10/3 (10/1–10/7)	9/22 (9/19–9/25)
σ :						
Yearling	1 (0–1)	9 (4–12)	7 (3–9)	6 (3–7)	7 (3–9)	15 (6–18)
2.5 Years	1 (0–1)	9 (4–11)	7 (3–10)	6 (3–7)	6 (3–9)	15 (6–18)
3.5 Years	1 (1–1)	9 (4–12)	7 (3–10)	6 (3–7)	6 (3–9)	15 (6–18)
4.5–10.5 years	1 (0–1)	9 (4–11)	7 (3–10)	6 (3–7)	6 (3–9)	14 (6–18)
≥ 11.5 years	1 (0–1)	9 (4–11)	7 (3–9)	6 (3–7)	6 (3–9)	14 (6–18)
q :						
Yearling	.27 (.09–.60)	.29 (.07–.66)	.34 (.05–.76)	.16 (.03–.56)	.28 (.06–.61)	.07 (.00–.50)
2.5 Years	.85 (.72–.96)	.88 (.74–.96)	.92 (.78–.98)	.80 (.61–.96)	.79 (.67–.90)	.72 (.28–.97)
3.5 Years	.89 (.78–.95)	.93 (.80–.98)	.95 (.86–.99)	.86 (.68–.97)	.87 (.76–.95)	.79 (.26–.99)
4.5–10.5 years	.89 (.82–.97)	.94 (.90–.98)	.96 (.90–.99)	.89 (.79–.97)	.85 (.78–.93)	.87 (.58–.99)
≥ 11.5 years	.85 (.75–.92)	.93 (.83–.97)	.94 (.83–.99)	.85 (.70–.97)	.83 (.72–.92)	.80 (.36–.99)

Note: For location of study areas, see figure 1. Predicted values of μ , σ , and q were computed for each animal according to the best model. We then took the mean value and 2.5% and 97.5% quantiles (95% CI) at the level of age and region.

ing place in less than 10 days (table 3). The ovulation rate was lower and more variable in yearlings than in any other age class. Furthermore, it peaked at prime age and did not show any strong evidence of senescence among females ≥ 11.5 years of age. Ovulation rates also varied among regions, especially for yearling females, with a very low ovulation rate for this female category in Vestfold (table 3).

According to the best model, the ovulation peak occurred later in yearling females than in females 2.5–10.5 years of age (fig. 3A), whereas there was no difference between yearlings and females ≥ 11.5 years of age (for a given body mass). In comparison with prime-age females (4.5–10.5 years old), the oldest females also reached their ovulation peak later ($P = .004$), so that yearlings and the oldest females displayed a similar pattern.

We observed large spatial variations in ovulation peak (fig. 3B; for a given body mass). In Vestfold, the ovulation peak was earlier, by far, than in any other region. In Nordland, females ovulated, on average, 5 days (95% CI: 2.6–7.2 days) later than those in Oppland and Troms, whereas females in Nord-Trøndelag and Hedmark reached their ovulation peak ~ 2 days earlier and later, respectively, than those in Oppland and Troms (e.g., $P = .06$ and $.08$ compared with Troms, respectively).

Over a period of 15 years, we also observed large year-to-year variations in ovulation peak, ovulation rate, and temporal synchrony of ovulation (fig. 3C–3E), but without any specific temporal trend. For instance, the among-year variations in temporal synchrony of ovulation σ can reach

70%, which for yearlings in Oppland corresponds to a difference of 4.9 days (95% CI: -7.3 to -2.7 days) between 1991 (reference year, $\sigma = 7.5$ [95% CI: 5.4–9.7 days]) and 1994 ($\sigma = 2.6$ [95% CI: 1.5–3.9 days]).

In Hedmark, temporal synchrony in ovulation was very strong compared with that in other regions (fig. 3F). This was probably partly because few data were available from the early part of the hunting season and thus from the rutting season (see fig. 2). For the same reason, we obtained a very large CI in Vestfold, lowering the difference with the five other regions (e.g., with Oppland, $P = .06$, corresponding to a difference of 10.9 days [95% CI: -0.3 to 35.0 days] for yearlings in 1991). Oppland, Nordland, Nord-Trøndelag, and Troms had an intermediate position, although a small difference was found between Oppland and Nordland ($P = .01$).

Body mass had a strong effect on both the ovulation peak and ovulation rate (table 2). As female body mass increased, the ovulation peak occurred earlier in the rutting season (MLE: -0.030 ; bootstrap: -0.024 [95% CI: -0.006 to -0.043]), corresponding to an almost 7-day difference between the ovulation peaks of the lightest and the heaviest females.

Effects of year, region, and body mass on ovulation rate q led to large spatiotemporal variation (from 126 to 198 kg, median = 169 kg; see also fig. 4) in the body mass threshold, above which 50% of yearling females ovulated (see Sand 1996). Increasing body mass resulted in higher ovulation rate, but the effects varied with region and age (table 2). Moreover, the variations in body mass had a

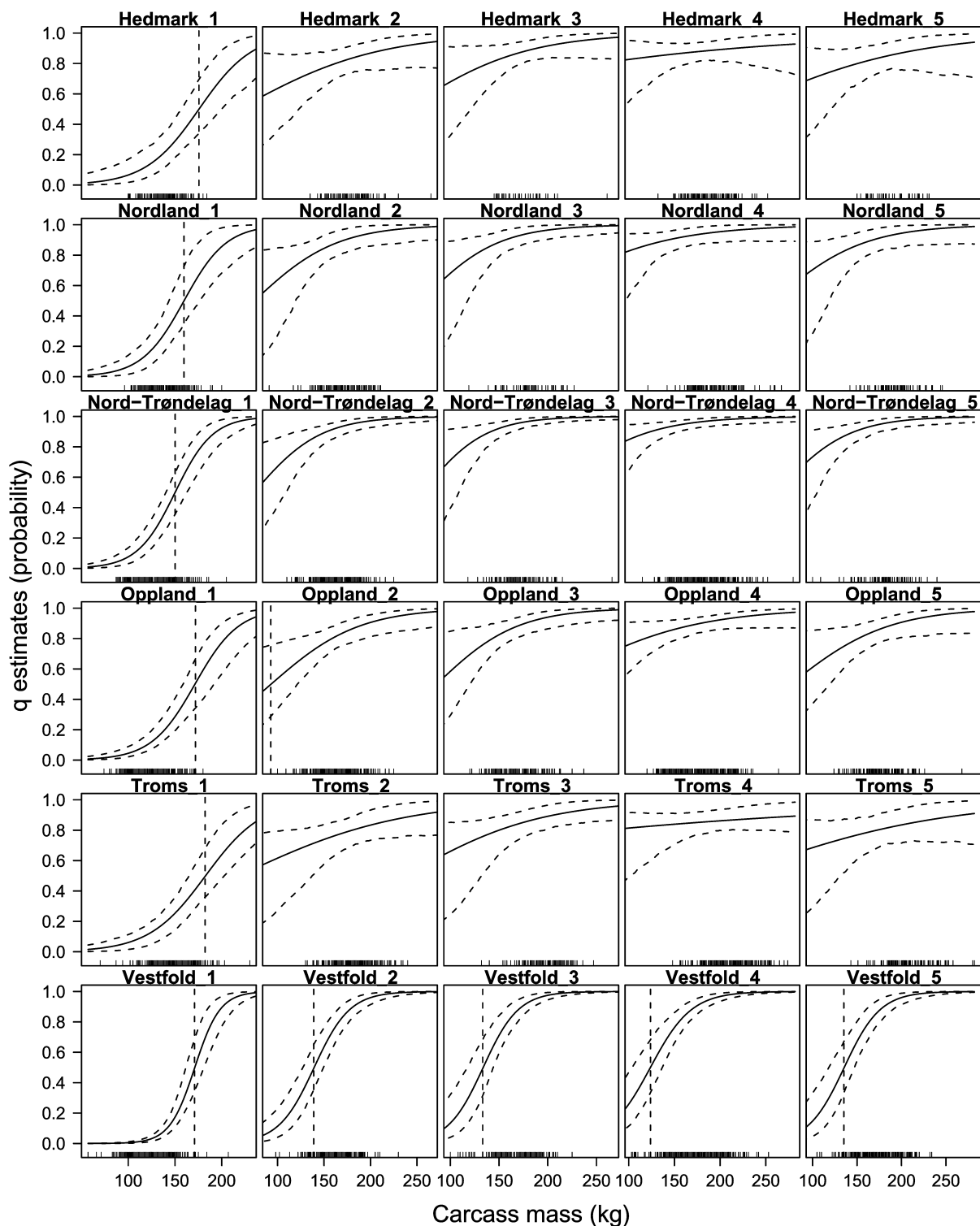


Figure 4: Ovulation rate q according to region (see fig. 1) and age group (1 = yearling, 2 = 2.5 years, 3 = 3.5 years, 4 = 4.5–10.5 years, and 5 = ≥ 11.5 years). Values were predicted (maximum likelihood estimates from the best model and bootstrap 95% confidence intervals) for the year 2005 (representative of other years, according to fig. 3D) and for the range of body masses encountered in the data set within each age group. Vertical dashed lines correspond to the body mass within each age group and region for which median ovulation rate is equal to 50% (e.g., see Sand 1996). It ranges from 150 kg (Nord-Trøndelag) to 182 kg (Troms). Tick marks show the distribution of carcass mass values available over the study period.

stronger influence on the ovulation rate in yearlings than in older age classes. Vestfold was the exception, as the slope of the effect of the body mass effect was positive and steep regardless of age class (fig. 4; table 4). In this region, a female weighing more than 200 kg had an ovulation probability of almost 1, whereas for individuals that weighed less than 100 kg it was close to 0 and was much lower compared with other regions. In the other regions, the effects of body mass on the ovulation rate decreased as females got older (e.g., in Hedmark, but see Nord-Trøndelag; table 4). Yearling females also required higher body mass to attain a given fecundity (fig. 4).

Discussion

Ovulation Patterns in Female Moose

The peak and distribution of ovulation dates in our study support previous findings from Scandinavian and North American populations of moose (Edwards and Ritcey 1958; Peek 1962; Markgren 1969; Lent 1974; Crichton 1992; Schwartz and Hundertmark 1993; Sigouin et al. 1997) that the ovulation peak falls in late September and early October and that most of the ovulation activity occurs over less than 10 days (table 3). As in other ungulates (e.g., Dauphiné and McClure 1974; see Sadleir 1987 for a review), ovulation in Norwegian female moose is highly synchronous, a pattern expected for northern ungulates as an adaptation to plant seasonality (see below; Bunnell 1982) and/or predation (Rutberg 1987). The ovulation rates in our study (table 3) are also in accordance with those in previous studies: ovulation rates among yearling females were more variable and lower compared with the high ovulation rate reported for adults (e.g., see Pimlott 1959; Peek 1962; Simkin 1965; Schladweiler and Stevens 1973; Sæther and Haagenrud 1985; Crichton 1992; Schwartz and Hundertmark 1993), a general pattern observed in most ungulate species (Sadleir 1987; Festa-Bianchet 1988a; Gaillard et al. 1992; Bon et al. 1993; Hewison 1996; Bertouille and de Crombrughe 2002; Langvatn et al. 2004; for a review, see Gaillard et al. 2000). In some

populations (i.e., Vestfold, see table 3; see also Edwards and Ritcey 1958; Testa 2004), the yearling ovulation rates were close to 0, meaning that most females did not mate before 2.5 years of age. As was reported for Swedish moose by Markgren (1969), we also observed that ovulation rates increase with age, peak at prime age (see also, e.g., Crichton 1992), and remain high even in senescent females.

Age and Body Mass Variations in Ovulation Patterns

In cervids, both age and phenotypic quality of females have been widely found to influence the timing of ovulation and birth (Sadleir 1987; but see Dauphiné and McClure 1974; Schwartz and Hundertmark 1993). In particular, young (primiparous) females and females in poor body condition are expected to delay ovulation and subsequent calving (in moose, see Crichton 1992; Sæther and Heim 1993; Testa and Adams 1998; Keech et al. 2000; in other ungulates, see McGinnes and Downing 1977; Berger 1982; Verme 1985; Clutton-Brock et al. 1987; Festa-Bianchet 1988a; Bon et al. 1993; Langvatn et al. 1996, 2004; Adams and Dale 1998). Accordingly, we observed delayed ovulation in yearlings and the lightest females, which supports the prediction that the physical condition of females during mating plays an important role in determining the timing of parturition (Adams and Dale 1998). In addition, our results support previous findings that senescent females show delayed ovulation (in moose, Crichton 1992; in red deer, Langvatn et al. 2004). Such age dependency may partly result from poorer physical condition in young and old females (Clutton-Brock et al. 1982; Festa-Bianchet 1988a), which cannot be accounted for by variation in body mass, suggesting that future studies should rely on better proxies of nutritional status, such as body fat (Pond 1978). However, age effects on the timing of ovulation can also be a physiological phenomenon, because it is suggested that young ungulate females need more stimulation from males to ovulate than older females do (Geist 1971; Verme et al. 1987; Bowyer 1991; Langvatn et al. 1996, 2004; Adams and Dale 1998).

Table 4: Regression coefficients (maximum likelihood estimates and bootstrap 95% confidence intervals [CIs], logit scale) for the relationships between ovulation rate (q) and body mass according to region (see fig. 1) and age (see table 2)

Region	Age group				
	Yearling	2.5 years	3.5 years	4.5–10.5 years	≥11.5 years
Hedmark	.0350 (.0201–.0580)	.0133 (–.0021 to .0316)	.0163 (–.0015 to .0405)	.0055 (–.0101 to .0240)	.0104 (–.0060 to .0308)
Nordland	.0443 (.0286–.0766)	.0226 (.0045–.0558)	.0256 (.0063–.0614)	.0147 (–.0019 to .0448)	.0197 (–.0001 to .0517)
Nord-Trøndelag	.0498 (.0372–.0701)	.0281 (.0127–.0484)	.0311 (.0100–.0565)	.0203 (.0037–.0417)	.0252 (.0073–.0475)
Oppland	.0429 (.0299–.0565)	.0212 (.0054–.0345)	.0242 (.0048–.0450)	.0133 (–.0002 to .0250)	.0182 (.0004–.0338)
Troms	.0331 (.0227–.0534)	.0114 (.0008–.0310)	.0144 (.0021–.0430)	.0035 (–.004 to .0217)	.0084 (–.0030 to .0313)
Vestfold	.0740 (.0604–.0961)	.0523 (.0381–.0702)	.0553 (.0404–.0772)	.0444 (.0323–.0611)	.0493 (.0345–.0713)

Note: When 0 is included in the 95% CI, the effect of body mass is not significant.

The reproductive output of any ungulate species is largely the result of its body size and the environmental factors acting on it (e.g., see Schladweiler and Stevens 1973; Skogland 1985; Sadleir 1987; Langvatn et al. 1996; Sæther 1997; Festa-Bianchet et al. 1998; Garel et al. 2005). Indeed, in female ungulates, body mass is well known to affect ovulation, pregnancy, and birth rates in primiparous females (e.g., in moose, Pimlott 1959; Markgren 1969; Sæther and Haagenrud 1983, 1985; Sæther and Heim 1993; Sæther et al. 1996; Solberg et al. 2002; in others, Langvatn et al. 1996; Cook et al. 2004) and mature females (e.g., in moose, Testa and Adams 1998; Keech et al. 2000; in others, Verme 1965; Reimers 1983; Cameron and Ver Hoef 1994; Bertouille and de Crombrughe 2002). Several authors have thus reported a body mass threshold above which most females reproduce (Albon et al. 1983; Bauer 1987; Sadleir 1987; Verme and Ozoga 1987; Gaillard et al. 1992; Sæther and Heim 1993; Cameron and Ver Hoef 1994; Hewison 1996). The body mass threshold reported here (169 kg) is close to the threshold reported in a study of Swedish moose (~155 kg, according to fig. 3 in Sand 1996). We also found a strong body mass effect on ovulation rate (fig. 4), in that heavier females of all age classes are more likely to ovulate than lighter ones. However, this effect was strongly age dependent (table 2, model 1, interaction age \times body mass; see also, for moose, Sæther and Haagenrud 1983; Schwartz and Hundertmark 1993; Sand 1996; Solberg et al. 2002; for roe deer [*Capreolus capreolus*], Gaillard et al. 1992; for red deer, Langvatn et al. 2004), with a decreasing effect as females aged (table 4) except in Vestfold (but see below). For instance, prime-aged females with body masses of <140 kg ovulated with a probability largely above 50%, whereas yearlings would have ovulation probabilities <50% for such body masses (fig. 4).

In moose, several characteristics may affect the allocation of energy to reproduction: (1) body growth continues after the attainment of sexual maturity (Garel et al. 2006) and can be impaired by early maturity (Sæther and Haagenrud 1985; Sand 1998), and (2) maternal characteristics are of prime importance for phenotypic quality of young (Keech et al. 2000; Solberg et al. 2007), fecundity (production of twins; Franzmann and Schwartz 1985; Sand 1996), and thus lifetime reproductive success. Accordingly, the strong relationship between ovulation rate and body mass in yearling females and the lower reproductive cost, relative to body mass, in adult females (see table 4; fig. 4), suggest a trade-off between early maturation and further growth (see Sand 1996). It also indicates a higher cost of reproduction in young animals, as expected from theoretical models (e.g., Engen and Sæther 1994). In addition, yearlings ovulated later than adult females (fig. 3A). Given that low body mass also leads to delayed ovulation, a yearling female in poor condition would produce a late-born

calf that may experience low body growth and subsequent low reproduction and survival rates (e.g., Albon et al. 1987; Festa-Bianchet 1988b; Loison et al. 1999). Moreover, females in poor condition are expected not to shorten their gestation period (in bison [*Bison bison*], Berger 1992) but to extend it (Schwartz and Hundertmark 1993; Sæther et al. 1996). Yearlings without high body condition should therefore be selected to delay ovulation by one more year. Such results give a mechanistic explanation for the low ovulation rate among yearling females (see Sand 1996; Langvatn et al. 2004) and emphasize the importance of studying breeding phenology to understand life-history evolution in female ungulates.

Spatiotemporal Variations in Ovulation Patterns

Contrary to Solberg et al. (2002), we found temporal and regional variations in ovulation peak μ and rate q , even after accounting for spatiotemporal variations in body mass (see table 2). Moreover, we observed much more variation, especially temporal variation, than previously observed in moose populations, both in the timing of ovulation/calving (Markgren 1969; Lent 1974; Schwartz and Hundertmark 1993; Sigouin et al. 1995, 1997; Bowyer et al. 1998) and in reproductive rates (Simkin 1965; Schladweiler and Stevens 1973; Boer 1992). Our results, nevertheless, may not contradict a constant timing of births as long as female moose would be able to adjust gestation length to compensate for differences in ovulation dates (in bison [*B. bison*], Berger 1992). Differences in some previous findings probably also occurred because (1) we took advantage of a large data set and a long time series (cf. only 5 years in Bowyer et al. 1998) and (2) our study encompasses larger variations in environmental conditions (cf. Sigouin et al. 1997). Moreover, (3) instead of rough indexes of breeding phenology (e.g., Sigouin et al. 1995), the histological analyses of ovaries, combined with our model, offer us a standardized way to conduct spatiotemporal comparison of ovulation patterns, allowing for detection of variations of just a few days (table 3; fig. 3A–3C).

Beyond specific age and body mass effects, spatiotemporal variations among μ , q , and ovulation synchrony σ are of particular importance for understanding the evolution of female ovulation patterns. Several studies of moose (Edwards and Ritcey 1958; Markgren 1969) and other female ungulates (Bunnell 1980; Bauer 1987; Sadleir 1987; Verme and Ozoga 1987) suggest that photoperiod is the ultimate factor regulating breeding phenology. Because we worked along a latitudinal gradient (fig. 1), this may partly explain the spatial variations in μ and σ (fig. 3B, 3C, 3E, 3F). However, as photoperiod may explain neither similar values of μ and σ among regions experiencing different photoperiods (e.g., Oppland and Troms;

figs. 1, 3B, 3F; see also, for deer, Sadleir 1987; Bowyer 1991) nor year-to-year variations, other factors must act in synergy with the light regime (Bauer 1987; Sadleir 1987; see below).

Whereas timing of mating may have evolved as a response to predation during calving (Bunnell 1982; Rutberg 1987), other studies (e.g., in Dall sheep [*Ovis dalli*], Rachlow and Bowyer 1991; in moose, Bowyer et al. 1998; in roe deer, Linnell and Andersen 1998; in reindeer [*Rangifer tarandus*], Post et al. 2003) suggest that it can be an adaptation to synchronize the offspring/mother requirements with food availability after calving (Dauphiné and McClure 1974; Bunnell 1980, 1982; Thompson and Turner 1982; Rutberg 1987; Risenhoover and Bailey 1988; Bowyer 1991; Keech et al. 2000; Côté and Festa-Bianchet 2001). Timing of breeding would thus be constrained because females who match their period of increased energy costs (especially early lactation) to the peak in plant growth in early summer (Albon and Langvatn 1992) would experience higher fitness by optimizing their investment in offspring growth and by increasing offspring survival and lifetime reproductive success. Assuming a constant gestation period (Schwartz and Hundertmark 1993; but see Sæther et al. 1996), the body mass effect on timing of ovulation (table 2) suggests that the timing of parturition reported here is the result of environmental factors acting on females before mating rather than of predation avoidance at calving (see also Keech et al. 2000). Moreover, the temporal variations in ovulation synchrony (table 2) provide less support for the predator avoidance hypothesis. Therefore, latitudinal, altitudinal, and temporal variations in plant phenology (Herfindal et al. 2006a, 2006b), and thus in environmental conditions, probably largely contributed to the spatiotemporal variations in ovulation pattern reported here (e.g., in mountain sheep [*Ovis* spp.]; Bunnell 1982).

Spatiotemporal variations could also partly be the result of the large variations in age and sex structure across Norway (e.g., see Garel et al. 2006), as the age and proportion of males may affect both the synchrony and the timing of breeding (Komers et al. 1999; Noyes et al. 2002; Holand et al. 2003, 2006b; Sæther et al. 2003), as well as the reproductive rates (Milner-Gulland et al. 2003). Moreover, as discussed above, carcass mass is probably not a perfect proxy of female condition, indicating that region and year effects included spatiotemporal variations in environmental conditions (Berger 1982; Sadleir 1987; Rachlow and Bowyer 1991; Cameron and Ver Hoef 1994; Keech et al. 2000) that were not accounted for by body mass.

Finally, the body mass threshold for start of ovulation (50%) in yearling females shows large spatiotemporal variation (>70 kg; see "Results"), whereas the effects of body mass on q vary according to region. This was particularly

apparent in Vestfold, where all females were strongly dependent on a high body mass to ovulate (see table 4; fig. 4), with the consequence that yearlings were almost entirely outside the reproducing part of the population (e.g., see also Edwards and Ritcey 1958). Such spatial differences have also been reported in roe deer (Hewison 1996) and moose (Markgren 1969; Sæther et al. 1996; Sand 1996). This pattern could be related to the environmental conditions faced by the population (high density in Vestfold; see Garel et al. 2006; Herfindal et al. 2006a), supporting the hypothesis that the body-mass-to-ovulation relationship is an adaptation to maximize the lifetime reproductive success by optimizing body growth, survival, and reproduction (Sæther et al. 1996; Sand 1996). For instance, in bighorn sheep (*Ovis canadensis*), the cost of early maturation on mass gain and subsequent reproductive success strongly increases with density; therefore, in such conditions, very few yearlings reproduced (Festa-Bianchet et al. 1995). Our results also indicate that geographical variation in age of maturity cannot be explained only by regional differences in body size but is also strongly influenced by different size-dependent selection pressures on age of maturity (Stearns and Koella 1986; Stearns 1992) in different parts of the distributional range (Sæther et al. 1996).

Representativeness of Harvested Females

The most common statistical assumption in analyses of data collected by hunters is that sampled individuals represent a random sample of the individuals in the population (e.g., in red deer, Martinez et al. 2005). We know that hunters tend to prefer shooting females from the less productive age classes, probably because they avoid shooting adult females who are still in the company of their calves (Solberg et al. 2000; Nilsen and Solberg 2006). Because fecundity also tends to increase with body mass (e.g., Solberg et al. 2002), age-specific variation in ovulation rates and body mass among adults (fig. 4) could therefore be underestimated (see also Markgren 1969). However, as variations in ovulation rates are affected only to a small extent by variations in body mass within adult age groups (except in Vestfold; fig. 4), hunter selectivity probably has a small effect on the observed pattern. Similarly, as body mass has no strong effect on σ (table 2), we do not expect that hunter selectivity is likely to skew the pattern of ovulation synchrony. Finally, it appears that females have relatively similar body masses, independent of reproductive costs (i.e., with or without a calf/calves at heel; e.g., females that did not breed in the previous year vs. females that did breed: 168.9 vs. 171.0 kg, 172.6 vs. 176.2 kg, 185.3 vs. 183.6 kg, and 180.7 vs. 182.5 kg, for 2.5-, 3.5-, 4.5–10.5-, and ≥ 11.5 -year-olds, respectively). This rough

analysis provides some confidence that hunter selectivity for less fecund females is not biasing our estimate of μ .

Whereas ovulation and birth patterns are probably highly similar, ovulation rate does not perfectly match the reproductive output of females, as it does not distinguish between females producing a single calf or twins and does not account for loss of ova (Markgren 1969; Crichton 1992; Schwartz and Hundertmark 1993; Testa and Adams 1998). In females ≥ 11.5 years of age, significant ovum loss has been recorded (Schwartz and Hundertmark 1993), which may explain why such females often show evidence of senescence in their reproductive output (Ericsson et al. 2001) despite high ovulation rates (table 3; fig. 4). Ovum loss could also be negatively related to body mass (Testa and Adams 1998), which means that the patterns reported here could underestimate the relationship between body mass and reproductive performance. However, as most of the females were hunted too early in the gestation period to determine pregnancy by gross examination of the uteri for embryos, ovary data are still, in our opinion, a very good alternative to studies of reproductive patterns. Moreover, it is during this period that large numbers of reproductive tracts can be collected.

Another sampling specificity in our study is the lack of ovary data in the early part of the rutting season for the Hedmark and Vestfold regions (fig. 2), which resulted in large CIs in parameter estimates (e.g., in Vestfold; fig. 3F). These regions could have been removed from the analysis. However, by working with a global model that included all regions we gained statistical power, and by testing for interactions between regions and the main effects of body mass and age we also accounted for the regional differences in ovulation synchrony and peak due to lack of data in the early part of the mating season. Moreover, by using harvested females from all regions, we got a more representative overview of the ovulation pattern in Norwegian moose.

Management Implications

As in studies of calving phenology (e.g. Thompson and Turner 1982; Ballard et al. 1991; Bowyer 1991; Rachlow and Bowyer 1991; Adams and Dale 1998; Linnell and Andersen 1998; Côté and Festa-Bianchet 2001), understanding ovulation patterns may have both evolutionary and management implications. In our study, the strong relationship between ovulation rate and body mass among yearling females suggests that yearling body mass is a reliable index for monitoring the population-specific variation in reproductive performance (*sensu* Morellet et al. 2007; see also Boer 1992; Cameron and Ver Hoef 1994). As yearlings have yet not produced calves and thus are not in the company of a calf during the hunting season

(a selection criterion for hunters), yearling body mass should also be free of sampling bias. Moreover, from a management perspective, it is crucial to get information on ovulation patterns to determine when the hunting season should be opened. Such information can then be used to limit the potential evolutionary consequences of hunting (e.g., see Coltman et al. 2003; Garel et al. 2007) for instance, by avoiding shooting dominant males before they contribute to the genetic pool of future generations.

Conclusion

Information about the variations in breeding phenology is of prime interest in determining the timing of births, given that a fixed gestation period can be assured. Timing of birth is an important component of fitness in seasonal environments, and in a context of increasing evolutionary changes in animal species (Palumbi 2001) and of global warming inducing rapid vegetation changes (Post 2003), we offer biologists a new way of modeling the breeding phenology to track responses to new selection pressures (for birth timing, e.g., see Visser et al. 1998; Coulson et al. 2003). Our study was focused on variation in age/body-mass-to-ovulation relationships among and within populations while controlling for temporal variation. Further analyses will have to be devoted to explaining the spatio-temporal variation in ovulation patterns observed here (see fig. 3), for example, by including environmental covariates in the model (e.g., density; Langvatn et al. 2004; M. Garel, E. J. Solberg, B.-E. Sæther, V. Grøtan, J. Tufto, and M. Heim, unpublished data). In addition, our model may also be used to study other biological patterns such as birth phenology.

Acknowledgments

We are indebted to the thousands of participants who made this study possible. We thank the Research Council of Norway (programs "NORKLIMA" and "Landskap i endring") and the Directorate for Nature Management for financial support. We are grateful to the European Commission for granting a Marie Curie Training Site Fellowship to M. Garel through the project ENDOCLIMA. We also gratefully acknowledge IN2P3 for providing computer resources.

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