

Timing and Synchrony of Ovulation in Red Deer Constrained by Short Northern Summers

Rolf Langvatn,^{1,2,*} Atle Mysterud,^{3,†} Nils C. Stenseth,^{3,‡} and Nigel G. Yoccoz^{3,4,§}

1. Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway;

2. University Center on Svalbard, N-9170 Longyearbyen, Spitsbergen, Norway;

3. Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway;

4. Department of Arctic Ecology, Norwegian Institute for Nature Research, Polar Environmental Centre, N-9296 Tromsø, Norway

Submitted May 19, 2003; Accepted October 23, 2003;

Electronically published May 4, 2004

Online enhancements: tables, figures.

ABSTRACT: Iteroparous mothers often face a trade-off between further investments in current offspring at the expense of the start of the next reproductive cycle. In the strongly seasonal environments at northern latitudes, large herbivores are typically calving in early summer each year to get a long growth season and to hit peak protein levels of vegetation. Late-born offspring are more likely to die since they are smaller in autumn. Low female condition in autumn due to prolonged investment in current-year offspring may lower her ability to ovulate sufficiently early to get a good start for the calves the following spring. On the basis of autopsies of uteri from 10,073 red deer (*Cervus elaphus*), we show that ovulation was delayed as well as more synchronous with increasing population density. This suggests that ovulation beyond a certain date incurs some fitness costs. Ovulation occurs progressively earlier with increasing age up to around 13 yr of age, after which ovulation again occurs later. Low ovulation rates in young compared with prime-aged deer were correlated with late ovulation in the fall. Also, yearling groups with a low rate of ovulation (e.g., because of low weight) also ovulated later, and old senescent deer not calving the previous year ovulated less frequently and markedly later than those raising a calf. Our findings

suggest, therefore, that mothers unable to ovulate before a certain date fail to do so altogether that year.

Keywords: density dependence, life-history evolution, phenology, reproductive strategies, senescence.

The short growing season in the strongly seasonal environments at northern latitudes incurs a severe constraint on the life histories of large mammalian species (Stearns 1992). Mothers allocating extra resources to offspring (so they become larger) typically increase their offsprings' chances of surviving through harsh winters (Gaillard et al. 2000b). However, prolonging offspring investments too much into the autumn may lower the mother's own vital performance and hence her ability to ovulate sufficiently early during the next reproductive cycle (Hogg et al. 1992). Late ovulation provides the next year's offspring with a poor start in life because late-born offspring are more likely to die since they have less time for growth, are born after peak protein levels, and are subsequently small in autumn (Hogg et al. 1992).

Ungulate populations are strongly age structured (Tuljapurkar and Caswell 1997), and density-dependent and density-independent variation in vital rates interact strongly with the age structure in determining the dynamics of ungulate populations (Coulson et al. 2001). For ungulates such as red deer, survival of prime-aged females is typically stable and high but lower and more variable among both young and old individuals (Gaillard et al. 1998, 2000b). Similarly, the proportion of females calving, litter size, and weight and survival of offspring peaks for prime-aged mothers (Gaillard et al. 2000b), and age at first reproduction is typically highly variable and dependent on body weight, which in turn depends on density (Festa-Bianchet et al. 1995) and climate (Langvatn et al. 1996). Evidence of reproductive senescence has recently been reported for a number of ungulate species (Gaillard et al. 2000b). At a proximate level, there is little information regarding whether these key life-history features are due to changes in rates or dates of ovulation, conception, fetal loss, or gestation length. Here we provide evidence dem-

* E-mail: rolf.langvatn@unis.no.

† E-mail: atle.mysterud@bio.uio.no.

‡ Corresponding author; e-mail: n.c.stenseth@bio.uio.no.

§ E-mail: nigel.yoccoz@nina.no.

onstrating that ovulation rate is a key to calving rates and dates and that this is linked to timing of ovulation in autumn acting as a constraint to investment patterns in a strongly seasonal environment.

Ovulation is for most mammalian females a hidden process often assessed indirectly by estrus (Iason and Guinness 1985; Hogg et al. 1992), rutting activity (Komers et al. 1994), or back-calculated from birth dates (Mitchell and Lincoln 1973). Extensive data regarding patterns of ovulation are indeed extremely difficult to obtain from wild populations. Hence, little is known about the role of rate and timing of ovulation for life-history variation in females—in particular, how short summers may act as a constraint on optimal time of ovulation. On the basis of autopsy of luteal structures (Langvatn et al. 1994) from 10,073 Norwegian red deer (*Cervus elaphus*) females from five populations along the west coast of Norway (1966–2000), including all age classes from 1 to 26 yr of age (table 1 in the online edition of the *American Naturalist*), we tested for how the rate and timing of ovulation was affected by age, weight, reproductive history, density, and climate (as measured by the North Atlantic Oscillation; Hurrell 1995; Stenseth et al. 2003). Luteal structures and their regressing stages exhibit characteristics that reflect reproductive events (Harrison and Weir 1977). An individual's reproductive history may therefore be assessed on the basis of the histology of ovaries (Langvatn 1992; Langvatn et al. 1994).

Material and Methods

The data used in this article derive from municipalities in six Norwegian counties: Rogaland (number of municipalities, $n = 6$) and Hordaland ($n = 21$; termed population P1), Sogn og Fjordane ($n = 23$; termed population P2), Møre og Romsdal ($n = 25$), Sør-Trøndelag ($n = 13$; termed population P3), and Nord-Trøndelag ($n = 2$; termed population P4). The island Hitra is termed population P5 (Myserud et al. 2001c). Data on dressed weight and uteri of 10,073 female red deer were collected during the annual autumn harvest from 1966 to 2000. Only data from 2,394 hinds from years 1968 to 1989 have been used in a previous analysis and mainly to evaluate ovulation rate in primiparous hinds (Langvatn et al. 1996). Ovulation was recorded from the occurrence of a *primary corpus luteum* (PCL), while a *corpus rubrum* (CR) in the ovaries showed that the hind had bred last year (Langvatn 1992; Langvatn et al. 1994). The autopsy of ovaries is highly reliable when it comes to determining PCL and CR, as has been assessed from captured individuals with a known reproductive history (Langvatn 1992). A more detailed description of the methodology on analysis of ovaries is provided elsewhere (Langvatn 1992; Langvatn et al. 1994).

As data derive from females harvested at different stages of ovulation, patterns of date of ovulation (i.e., time when a PCL was recorded) may be detected and modeled as date of culling. Body weight is a good proxy of condition, and it is strongly density dependent over the period considered (Myserud et al. 2001a).

Data on covariates such as age (estimated using annuli in the cementum of the first incisor; Reimers and Nordby 1968; Hamlin et al. 2000), date of culling (Yoccoz et al. 2002), distance from the coast, degree of latitude, and proportion of high altitude habitat (Myserud et al. 2001c) are provided elsewhere.

As an index for local density, we used total harvest in a municipality divided by the area of red deer habitat as approved by the management authorities (Myserud et al. 2001a, 2002a). During the study period, the red deer population has been increasing steadily, and the harvest has increased 10-fold (and the number of deer killed in traffic also, even after controlling for increase in traffic; Statistics Norway 2002; Myserud 2004). There has therefore been underharvesting in the sense that the harvest is smaller than the annual production. The gap between the actual harvest and the quota is smaller now than previously (Statistics Norway 2002), and body weights are still decreasing (R. Langvatn, unpublished data), indicating that the population size is still increasing; that is, we have not yet reached a situation of overharvesting. The range of densities observed at the municipality scale was fairly similar among populations (P1: min = 0.04, max = 1.51; P2: min = 0.07, max = 1.49; P3: min = 0.01, max = 2.30; P4: min = 0.23, max = 0.85; P5: min = 0.25, max = 1.40). We also ran population-specific models to ascertain that differences in density dependence between populations (e.g., Milner-Gulland et al. 2000) did not affect our results (for P1–P3; not enough data for P4 and P5).

As an index of global winter climate, we used the North Atlantic Oscillation (NAO; Hurrell 1995; Stenseth et al. 2003), which is a large-scale fluctuation in atmospheric mass between the subtropical North Atlantic region (centered on the Azores) and the subpolar North Atlantic region (centered on Iceland) measured between December and March. The NAO is known to have a strong effect on the life history of the Norwegian red deer (Post et al. 1997; Myserud et al. 2001b; review in Myserud et al. 2003).

Statistical Analyses

We used logistic regression within both a generalized additive models framework (GAM; Venables and Ripley 1994) and a generalized linear models framework (GLM; Venables and Ripley 1994) to analyze variation in ovulation. We used GAM with smoothing splines to explore possible nonlinear relationships. Nonlinear relationships

were then modeled using polynomials and threshold models in GLM, which provided simpler ways of comparing parameter estimates than did splines.

We are interested in estimating the proportion of females having ovulated at the end of the breeding season (i.e., proportion ovulating), the time at which a given proportion has ovulated (i.e., time of ovulation), and the rate at which the proportion of females ovulating changes with date (i.e., synchrony). Because there is considerable variation in ovulation between year classes, and since we expected age-dependent interactions with density, climate, and previous reproduction (Gaillard et al. 1998, 2000b; Coulson et al. 2001), it was not practical to use a single global model including all age classes. We expected a variable ovulation rate in young and old hinds (Gaillard et al. 2000b), which was confirmed by initial analyses with GAM. The 1- and 2-yr-old hinds and females older than around 13–15 yr of age had variable ovulation rates, while the ovulation rate was close to 100% for females aged between 3 and 13 yr. We therefore assessed ovulation in four GLMs, for 1 yr olds, 2 yr olds, prime aged (3–13), and older hinds (equal to or older than 13 yr of age). For some of these age classes, we do not expect that 100% ovulates, and we therefore used both polynomials and threshold models to find the level (a certain date) after which no further ovulation occurred. Threshold models provide a simple way (only one extra parameter for the threshold) to model relationships reaching a plateau, whereas polynomials will often require two or three extra parameters. However, threshold models may be biased if there is a real plateau but a very slow increase. Figures are all based on predicted values from the models, and output from all models are presented in tables.

We included several covariates known to affect body weight (e.g., Mysterud et al. 2002a) and that may or may not affect ovulation. Fitting a too complex model would result in estimates with lower bias but lower precision, and bias is a more important issue in observational studies (Cochran and Rubin 1973). We therefore used AIC_C and BIC (a criterion similar to AIC_C but more conservative; Miller 2002) as a guide for model selection but sometimes chose to use models more complex than the best model according to AIC_C so as to minimize bias for parameter estimates as well as provide estimates for variables that were biologically interesting, even if not retained in the best AIC_C model (e.g., previous reproduction). All of the main patterns reported were included in the best AIC_C model, and predicted values for ovulation rates were calculated using the most parsimonious models because these were not affected by the inclusion of these supplementary variables.

To assess interactions between two continuous predictors (such as density), we restricted the analysis to a mul-

tiplicative term of the standardized variables. The predictor variables were standardized (mean 0, variance 1) to facilitate the interpretation of the interaction and polynomial terms (Mysterud et al. 2001a). The NAO index is already standardized (it is defined as a normalized pressure difference; Hurrell 1995). When variables are standardized, the coefficient for a variable included in an interaction term is the strength of this variable when the other variables in the interaction are average (because the interaction term is then 0). Similarly for a second-order polynomial, the linear term represents the slope at the average, and the quadratic term represents the curvature at the average.

Goodness of fit of the logistic regression models could not be properly assessed on the basis of the residual deviance or Pearson residuals because most observations were unique (i.e., 0/1) and asymptotic results do not hold (McCullagh and Nelder 1989). Residual deviances were, however, always less than their associated number of degrees of freedom, so we had no indication of overdispersion (see online tables and figures). The differences in deviance as well as in AIC_C/BIC are not affected by having 0/1 observations. To assess goodness of fit, we chose an approach considering the fit of a simple model based on only culling date and weight as predictor variables and considering these variables as categorical (we used six categories chosen to give approximate similar sample sizes) and not continuous variables (Cox and Snell 1989). Such simple models fitted all age classes (age = 1: $\chi^2 = 35.46$, $df = 33$, $P = .353$; age = 2: $\chi^2 = 39.58$, $df = 33$, $P = .200$; age = 3–13: $\chi^2 = 27.73$, $df = 31$, $P = .635$; age > 13: $\chi^2 = 39.3$, $df = 28$, $P = .076$), and therefore we were confident that the more complicated models used in this article fitted the data appropriately.

Results

The estimated proportion of 1-yr-old females ovulating averaged 50%–70% (fig. 3 in the online edition of the *American Naturalist*). Increasing density lowered the proportion of yearlings that ovulated, and ovulation was also delayed at high density (fig. 3A; tables 2, 3 in the online edition of the *American Naturalist*). There was no residual effect of density after the positive and slightly nonlinear relationship between likelihood of ovulation and weight was controlled for (fig. 3B, 3C; tables 2, 3), indicating that the density effect in yearlings is mediated through body weight. Because one may argue that density dependence may differ between populations, we also ran separate models for populations P1–P3 (sufficient data not available to do so for P4 and P5). The effect of density (model without body weight) was similar whether running a full model (-0.744 [-1.177 , -0.311]) or population-specific models

(P1: -0.720 [$-1.482, 0.041$]; P2: -1.077 [$-1.927, -0.228$]; P3: -0.932 [$-1.797, -0.067$]).

For 2-yr-olds, the proportion ovulating averaged above 95% (fig. 4 in the online edition of the *American Naturalist*). Both low body weight and high density delayed ovulation (fig. 4; tables 4, 5 in the online edition of the *American Naturalist*), and in contrast to yearlings, the effect of density was stronger than the effect of body weight. The effect of body weight was marked for deer with a weight under mean weight, but it was less important for deer above mean weight (as indicated by the significant second-order term for $st[\text{body weight}]$; table 5).

The effect of density was similar whether running a full model (-0.822 [$-1.299, -0.345$]) or population-specific models (P1: -0.258 [$-0.857, 0.340$]; P2: -1.234 [$-3.075, 0.607$]; P3: -1.360 [$-2.500, -0.219$]). The proportion ovulating was not affected by density or body weight in the most parsimonious model. However, running a model including only significant factors (rather than the model chosen by AIC_c) gave the slightly different result that proportion of females ovulating as 2-yr-olds decreased to 88% for those with low body weight at high density and 92% for those with high body weight at high density. There were no changes at low density (results not shown).

Between 3 and 13 yr of age, close to 100% of females ovulated (fig. 1; tables 6, 7 in the online edition of the *American Naturalist*). Ovulation occurred earlier in the autumn with increasing age up to about 13 yr of age (fig. 1A). On October 10, 33% of 11-yr-old females had ovulated, but only 14% of the 3-yr-olds had done so (fig. 1A). However, high population density delayed ovulation among prime-aged females. The date at which the first 10% of females having ovulated was 9 d earlier at low density than at high density (fig. 1B). Ovulation also becomes more synchronous at high density (fig. 1B). While the proportion of females having ovulated raised from 10% to 80% in 21 d at low density, this happened in only 13 d at high density (fig. 1B). Body weight was not a significant predictor of ovulation in prime-aged females, although it entered the model with the lowest AIC_c (see online tables and figures). Parameter estimates for population specific models for the effect of age (full model: 0.133 [$0.073, 0.195$]; P1: 0.114 [$0.013, 0.216$]; P2: 0.151 [$-0.003, 0.304$]; P3: 0.224 [$0.088, 0.360$]), $st[\text{density}]$ full model: -0.427 [$-0.633, -0.222$]; P1: -0.321 [$-0.591, -0.0517$]; P2: -0.588 [$-1.148, -0.027$]; P3: -0.707 [$-1.275, -0.138$]), and $st[\text{date of culling} \times \text{density}]$ full model: 0.728 [$0.415, 1.048$]; P1: 0.460 [$-0.011, 0.931$]; P2: 0.332 [$-1.323, 1.986$]; P3: 0.647 [$-0.129, 1.424$]) were consistent with the full model.

From about 13 to 15 yr of age, the proportion of females ovulating declined markedly with age and went below 50% for the oldest age classes (fig. 2; tables 8, 9 in the online

edition of the *American Naturalist*). Previous reproductions strongly affected ovulation (fig. 2). For a 21-yr-old female, the chances of ovulation by November 1 were close to 80% for females that ovulated the previous year, while the chances were below 30% for those not calving the previous year.

Note that a low rate of ovulation was associated with a late date of ovulation. Prime-aged females with a very high rate of ovulation (fig. 1) ovulated before 1-yr-olds (fig. 3). This was evident also within the age groups. For example, for 45-kg primiparous females that had a low (end) rate of 0.6 ovulating (fig. 3B), one-half of them had ovulated by November 12. For those weighing 60 kg and hence with a high (end) rate of 0.94 ovulating, one-half of them had ovulated by October 31 (fig. 3B). Also, senescent individuals not calving last year had both a low proportion and a late date of ovulation (fig. 2B) compared with those that raised a calf last year (fig. 2A).

Discussion

We here report the most extensive analysis of ovulation in a wild mammal. While patterns of reproductive rates are fairly well known on the basis of calving rates or individual performance assessed from body weight (reviews in Sæther 1997; Gaillard et al. 2000b), the role of ovulation as a mechanism for such patterns is scarce and is usually assessed on small data sets using indirect indices (see "Introduction"). Further, while phenological events in plants (Post and Stenseth 1999), amphibians (e.g., Forchhammer et al. 1998), and birds (Hüppop and Hüppop 2003) are very well studied, data on animal phenological events such as calving dates are usually quite limited and usually not extensively analyzed (but see, e.g., Sinclair et al. 2000). Indeed, some novel phenological patterns of timing and synchrony of ovulation not reported for calving dates were found: timing of ovulation was gradually earlier up to about 13 yr of age, and after that, it was delayed; higher density led to a more delayed but also more synchronous ovulation; most important, we underline the close correlation between late and low rate of ovulation.

A consistent pattern of variation in reproductive rates related to maternal age is that calving rates increase from young to prime-aged females. In accordance with this, ovulation rates increased from yearling (fig. 3) to the prime-age stage (fig. 1). The evidence for senescence for the oldest age classes has been more scarce and frequently debated (e.g., Gaillard et al. 1994), but data on calving rates, weight of calves, and maternal weight are now beginning to become substantial also for very old individuals (Bérubé et al. 1999; Coulson et al. 2001; Mysterud et al. 2001a; Weladji et al. 2002). From about 13 to 15 yr of age, the proportion of females ovulating declined markedly

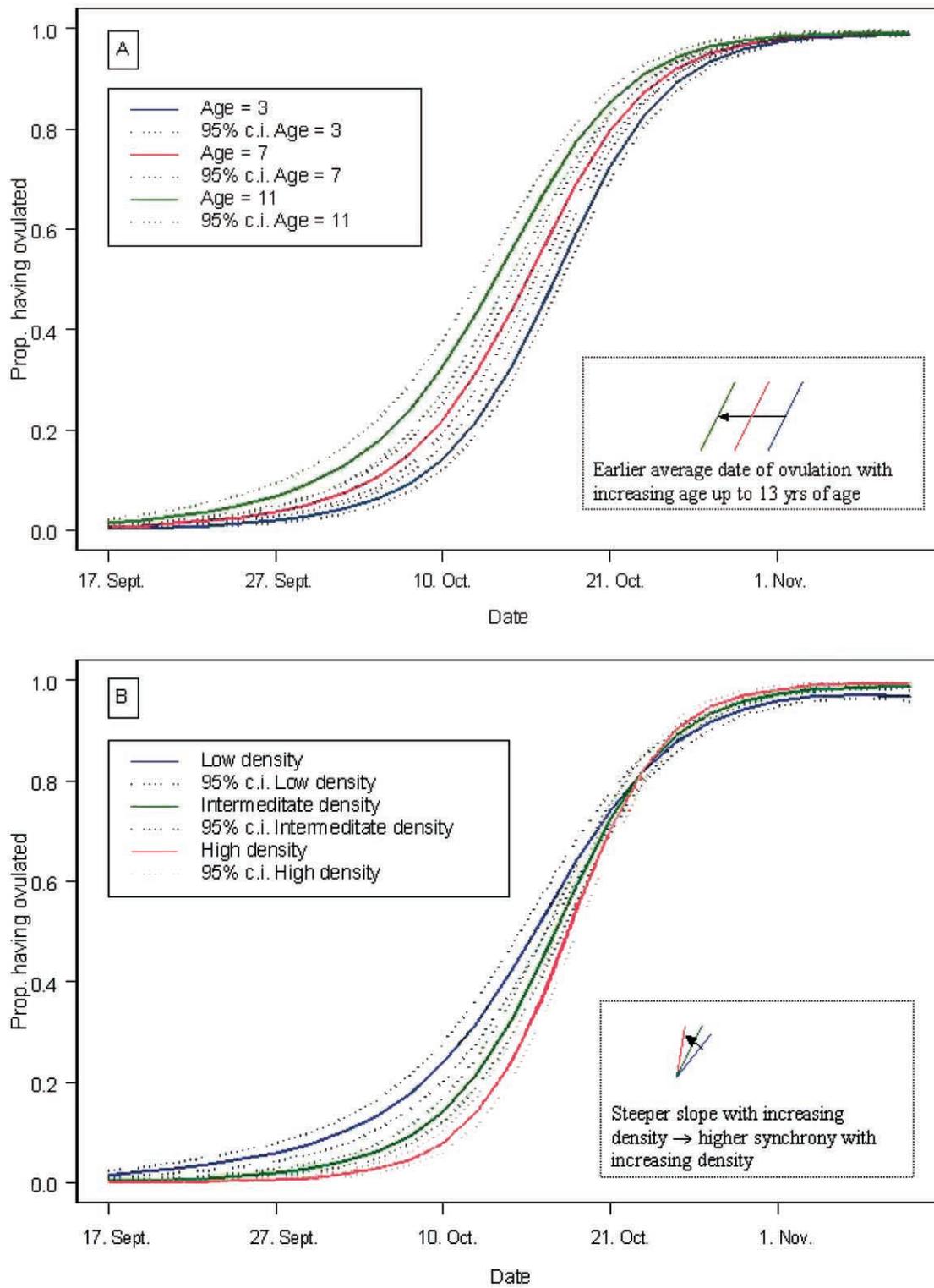


Figure 1: Relationship between proportion of prime-aged (3–13 yr of age) females ovulating and time of culling depending on (A) female age and (B) population density.

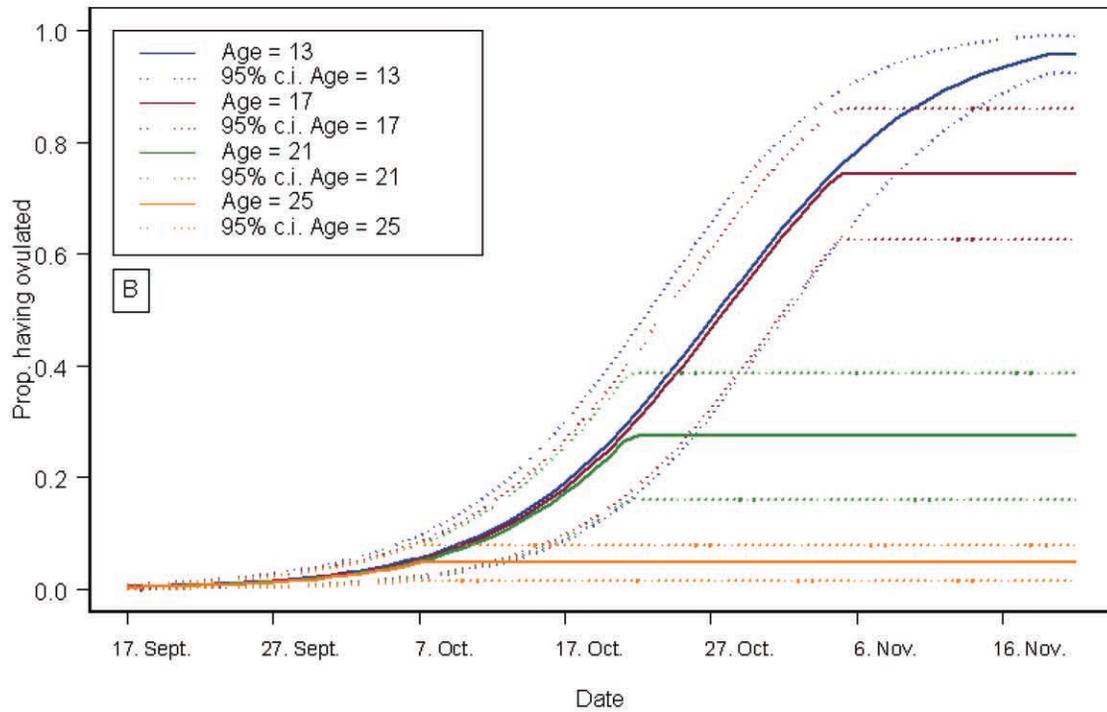
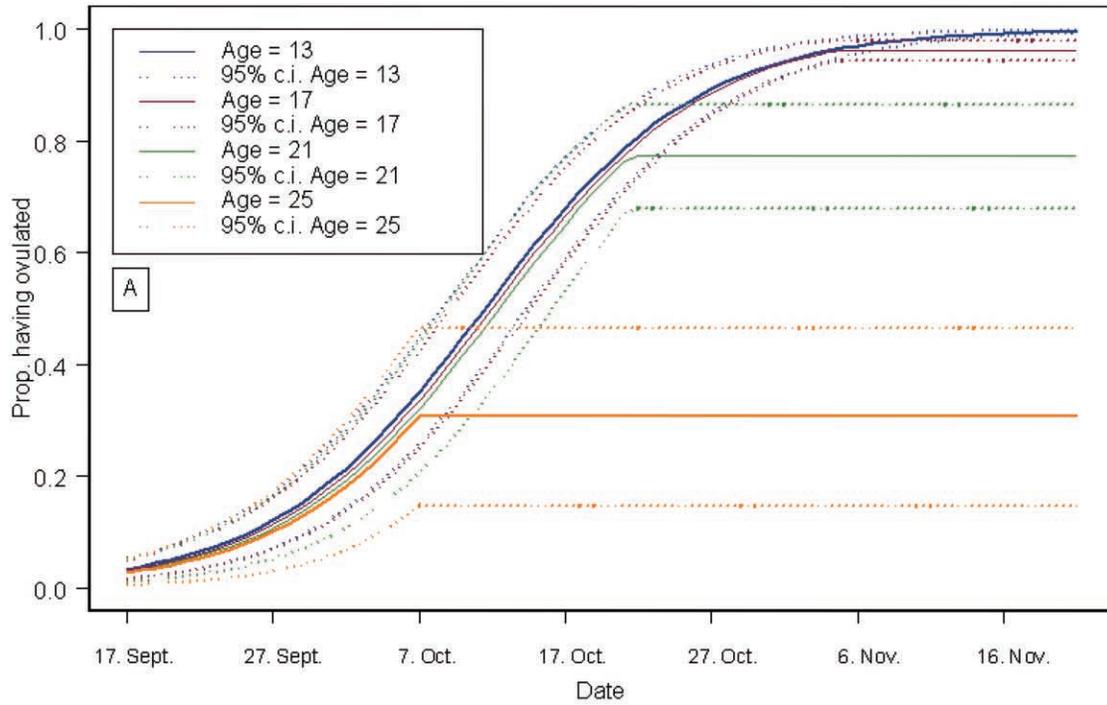


Figure 2: Relationship between proportion of females having ovulated and time of culling for old age-classes using logistic regression models with thresholds. Females with a calf the previous year (A) were more likely to ovulate the next year than those that did not have a calf the previous year (B).

with age and went below 50% for the oldest age classes (fig. 2). This provides further evidence of the prevalence of reproductive senescence in ungulates and, more specifically, that previously reported lower offspring production of older females (e.g., Bérubé et al. 1999) is at least partly due to lower ovulation rates. It is worth noticing that senescence in reproduction and body weight do not coincide (Bérubé et al. 1999) since senescence with respect to body weight is about 20 yr in female red deer (Mysterud et al. 2001a).

The relative importance of body weight as a factor determining pattern of ovulation decreased with age. Among 1-yr-old hinds, spatial and temporal variation in ovulation rate was a function of body weight, with smaller females ovulating later and at a lower rate (fig. 3). This was also the result in a previous analysis of ovulation in Norwegian red deer but with much less data and performed on a much coarser spatial scale (Langvatn et al. 1996). In contrast, for prime-aged (3–13 yr) and old females (>13 yr), weight was not a significant predictor of ovulation, though it was included in the most parsimonious model (see online tables and figures). The 2-yr-old hinds fell in between, with a low effect of body weight on timing but no (or weak) effect on the rate of ovulation (fig. 4). However, the effect of body weight was not linear—the effect of weight was marked for deer with a weight under mean weight but less important for deer above mean weight.

Density dependence in vital rates is one of the key and well-known patterns found for large mammals (Fowler 1987; Sæther 1997; Gaillard et al. 2000b), and it is known to affect young and very old individuals more than prime-aged females (Gaillard et al. 2000b; Coulson et al. 2001). Very little is known regarding how population density affects timing and synchrony of animal phenological events such as ovulation. Density delayed ovulation for yearlings (fig. 3A), 2-yr-olds (fig. 4), and prime-aged females (fig. 1). Delayed ovulation at high density may be related either to female condition (Loudon et al. 1983) or possibly to availability of males, which may change with density (Clutton-Brock et al. 1997), because male presence may induce and advance estrus in females (McComb 1987; Komers et al. 1999; review in Mysterud et al. 2002b). The more synchronous ovulation at high density for prime-aged females (indicated by a steeper slope of the regression model; fig. 1B) is strong evidence of a time constraint on ovulation in seasonal environments. In bighorn sheep (*Ovis canadensis*), ewe and lamb mortality was associated with late estrus in the previous rut (Hogg et al. 1992). That density also affected rate of ovulation in hinds breeding for the first time (primiparous; fig. 3A) confirms that ovulation rate (and not differential embryonic or foetal loss) probably accounts for the most substantial part of the lower calving rates among younger females at higher

density observed in several ungulate species (Clutton-Brock et al. 1987; Festa-Bianchet et al. 1995). The density effect on ovulation in primiparous hinds was explained alone by the parallel decrease in body weight with increasing density (table 2).

Despite the fact that reproductive rates are stable and high for prime-aged individuals, the timing of ovulation was, surprisingly, quite variable even within this group (fig. 1). Ovulation occurred earlier in the autumn with increasing age up to about 13 yr of age (fig. 1A). However, this variation is within the range of dates at which this does not affect ovulation rates, suggesting a benefit to early ovulation. Late-born calves are smaller than earlier-born calves in autumn, and low autumn body weight is known to decrease the winter survival of calves (review in Gaillard et al. 2000b). There is a positive correlation between individual quality and life span (Gaillard et al. 2000a). Differential mortality may hence lead to increasing individual quality with increasing age (Laaksonen et al. 2002) and warrants some caution when interpreting transversal data. However, this was not likely the mechanism behind this pattern of increasingly earlier ovulation with age. First, natural survival of prime-aged females is usually high and constant (reviews in Gaillard et al. 1998, 2000b; for Norwegian red deer, Langvatn and Loison 1999), giving little room for differential mortality to affect the pattern. Second, from the age of 13 to 15 yr when differential mortality can be expected to be strong, ovulation date was delayed with increasing age, which is the opposite of what is expected if differential mortality occurred and the best individuals survived and ovulated earlier. Third, in bighorn sheep, although the sample size was limited, estrus seemed to peak in 3-yr-old ewes (Hogg et al. 1992), fitting the same overall pattern as our data on ovulation. For the older females, the dates after which no ovulation occurred were reached for some, resulting also in lower rates of ovulation. Cervids may recycle about 3 wk after the first seasonal ovulation (Guinness et al. 1971). However, very late-born offspring are fairly infrequent (Guinness et al. 1978; Holand et al. 2003), and ovulation rates match observed calving rates (Gaillard et al. 2000b), a clear indication that conception usually takes place after the first ovulation (Langvatn 1992) and that reovulation is unlikely to be important.

Cost of reproduction in large herbivorous mammals is mainly due to lactation costs (Clutton-Brock et al. 1989), and lactating hinds typically have less fat than do nonlactating hinds (Bateson and Bradshaw 2000). Nine lactating red deer hinds kept on poor-quality hill pasture in Scotland resumed estrus at a later date than did nonlactating hinds and frequently failed to resume estrus in the year following the birth of a calf (Loudon et al. 1983). For red deer on Rum, Scotland, lactating hinds gave birth to calves at a

later date than did yield hinds (Clutton-Brock et al. 1983, 1989). The Norwegian red deer populations used in this study are much more productive than the Scottish conspecifics (Langvatn et al. 1996), and previous calving increased markedly the likelihood of ovulation in senescent females (fig. 2). Hence, there are high- and low-quality individuals that are more or less likely to ovulate. Similarly, there was a slight positive correlation between first and later reproduction in bighorn sheep (Bérubé et al. 1999), and fertility was higher for ewes that had previously produced a lamb than for ewes that had been barren the previous year (Festa-Bianchet 1989; Festa-Bianchet et al. 1998). Although body weight in Norwegian red deer older than 2 yr did not affect ovulation, calving date was related to body condition in Scottish red deer (Mitchell and Lincoln 1973; Guinness et al. 1978). Hence, gestation length may be more variable than previously acknowledged, just as was reported for bison (*Bison bison*; Berger 1992).

Acknowledging the constraints set by a short growing season represents a central key to the understanding of life-history evolution and the resulting population ecology of northern species. Our analysis emphasizes the central role of timing of ovulation in this respect. Prime-aged females do avoid ovulating too late under adverse environmental conditions at high population density. Most strikingly, a strong link between late ovulation and low rate of ovulation was found. This suggests that females in too poor condition to ovulate before a given date in the autumn do not ovulate at all. This may indeed provide a mechanistic explanation for the observed pattern of lower calving rates in younger and older females and with increasing density and decreasing body weight in young females.

Acknowledgments

We gratefully acknowledge several useful comments provided by S. Albon, T. Coulson, M. Festa-Bianchet, J.-M. Gaillard, L. Kruuk, and E. J. Milner-Gulland and the financial support of the Research Council of Norway to A.M. (project 129208/720 and EcoClim) and N.C.S. (EcoClim).

Literature Cited

- Bateson, P., and E. L. Bradshaw. 2000. The effect of wound site and blood collection method on biochemical measures obtained from wild, free-ranging red deer (*Cervus elaphus*) shot by rifle. *Journal of Zoology (London)* 252: 285–292.
- Berger, J. 1992. Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. *Ecology* 73:323–329.
- Bérubé, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* 80:2555–2565.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1983. The costs of reproduction to red deer hinds. *Journal of Animal Ecology* 52:367–383.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. *Journal of Animal Ecology* 56:857–871.
- . 1989. Fitness costs of gestation and lactation in wild mammals. *Nature* 337:260–262.
- Clutton-Brock, T. H., K. E. Rose, and F. E. Guinness. 1997. Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society of London B* 264:1509–1516.
- Cochran, W. G., and D. B. Rubin. 1973. Controlling bias in observational studies: a review. *Sankhya* 35:417–446.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292:1528–1531.
- Cox, D. R., and E. J. Snell. 1989. *Analysis of binary data: monographs on statistics and applied probability*. Chapman & Hall, London.
- Festa-Bianchet, M. 1989. Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). *Journal of Animal Ecology* 58:785–795.
- Festa-Bianchet, M., J. T. Jorgenson, M. Lucherini, and W. D. Wishart. 1995. Life-history consequences of variation in age of primiparity in bighorn ewes. *Ecology* 76:871–881.
- Festa-Bianchet, M., J.-M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist* 152:367–379.
- Forchhammer, M. C., E. Post, and N. C. Stenseth. 1998. Breeding phenology and climate. *Nature* 391:29–30.
- Fowler, C. W. 1987. A review of density dependence in populations of large mammals. Pages 401–441 in H. H. Genoways, ed. *Current mammalogy*. Plenum, New York and London.
- Gaillard, J.-M., D. Allainé, D. Pontier, N. G. Yoccoz, and D. E. L. Promislow. 1994. Senescence in natural populations of mammals: a reanalysis. *Evolution* 48:509–516.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13:58–63.
- Gaillard, J.-M., M. Festa-Bianchet, D. Delorme, and J. Jorgenson. 2000a. Body mass and individual fitness in fe-

- male ungulates: bigger is not always better. *Proceedings of the Royal Society of London B* 267:471–477.
- Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000b. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Guinness, F., G. A. Lincoln, and R. V. Short. 1971. The reproductive cycle of the female red deer, *Cervus elaphus* L. *Journal of Reproduction and Fertility* 27:427–438.
- Guinness, F. E., R. M. Gibson, and T. H. Clutton-Brock. 1978. Calving times of red deer (*Cervus elaphus*) on Rhum. *Journal of Zoology (London)* 185:105–114.
- Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *Journal of Wildlife Management* 64:441–449.
- Harrison, R. J., and B. J. Weir. 1977. Structure of the mammalian ovary. Pages 113–217 in L. Zuckerman and B. J. Weirs, eds. *The ovary*. Academic Press, New York.
- Hogg, J. T., C. C. Hass, and D. A. Jenni. 1992. Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behavioral Ecology and Sociobiology* 31:243–251.
- Holand, Ø., K. H. Røed, A. Mysterud, J. M. Kumpula, M. Nieminen, and M. E. Smith. 2003. The effect of sex ratio and male age structure on reindeer calving. *Journal of Wildlife Management* 67:25–33.
- Hüppop, O., and K. Hüppop. 2003. North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London B* 270:233–240.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269:676–679.
- Iason, G. R., and F. E. Guinness. 1985. Synchrony of oestrus and conception in red deer (*Cervus elaphus* L.). *Animal Behaviour* 33:1169–1174.
- Komers, P. E., F. Messier, P. F. Flood, and C. C. Gates. 1994. Reproductive behavior of male wood bison in relation to progesterone levels in females. *Journal of Mammalogy* 75:757–765.
- Komers, P. E., B. Birgersson, and K. Ekvall. 1999. Timing of estrus in fallow deer is adjusted to the age of available mates. *American Naturalist* 153:431–436.
- Laaksonen, T., E. Korpimäki, and H. Hakkarainen. 2002. Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. *Journal of Animal Ecology* 71:23–31.
- Langvatn, R. 1992. Analysis of ovaries in studies of reproduction in red deer (*Cervus elaphus* L.): application and limitations. *Rangifer* 12:67–91.
- Langvatn, R., and A. Loison. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildlife Biology* 5:213–223.
- Langvatn, R., S. Bakke, and S. Engen. 1994. Retrospective studies of red deer reproduction using regressing luteal structures. *Journal of Wildlife Management* 58:654–663.
- Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age at first reproduction in a temperate herbivore. *Journal of Animal Ecology* 65:653–670.
- Loudon, A. S. I., A. S. McNeilly, and J. A. Milne. 1983. Nutrition and lactational control of fertility in red deer. *Nature* 302:145–147.
- McComb, K. 1987. Roaring by red deer stags advances the date of oestrus in hinds. *Nature* 330:648–649.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Chapman & Hall, London.
- Miller, A. J. 2002. *Subset selection in regression*. Chapman & Hall, London.
- Milner-Gulland, E. J., T. N. Coulson, and T. H. Clutton-Brock. 2000. On harvesting a structured ungulate population. *Oikos* 88:592–602.
- Mitchell, B., and G. A. Lincoln. 1973. Conception dates in relation to age and condition in two populations of red deer in Scotland. *Journal of Zoology (London)* 171:141–152.
- Mysterud, A. 2004. Temporal variation in the number of car-killed red deer *Cervus elaphus* in Norway. *Wildlife Biology* (in press).
- Mysterud, A., N. G. Yoccoz, N. C. Stenseth, and R. Langvatn. 2001a. The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proceedings of the Royal Society of London B* 268:911–919.
- Mysterud, A., N. C. Stenseth, N. G. Yoccoz, R. Langvatn, and G. Steinheim. 2001b. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* 410:1096–1099.
- Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001c. Plant phenology, migration and geographic variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* 70:915–923.
- . 2002a. Large-scale habitat variability, delayed density effects and red deer populations in Norway. *Journal of Animal Ecology* 71:569–580.
- Mysterud, A., T. Coulson, and N. C. Stenseth. 2002b. The role of males in the population dynamics of ungulates. *Journal of Animal Ecology* 71:907–915.
- Mysterud, A., N. C. Stenseth, N. G. Yoccoz, G. Ottersen, and R. Langvatn. 2003. The response of the terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. Pages 235–262 in J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck, eds. *The North Atlantic Oscillation*. American Geophysical Union, Washington, D.C.

- Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* 80: 1322–1339.
- Post, E., N. C. Stenseth, R. Langvatn, and J.-M. Fromentin. 1997. Global climate change and phenotypic variation among red deer cohorts. *Proceedings of the Royal Society of London B* 264:1317–1324.
- Reimers, E., and Ø. Nordby. 1968. Relationships between age and tooth cementum layers in Norwegian reindeer. *Journal of Wildlife Management* 32:957–961.
- Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution* 12:143–149.
- Sinclair, A. R. E., S. A. R. Mduma, and P. Arcese. 2000. What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology* 81:2100–2111.
- Statistics Norway. 2002. Official hunting statistics of Norway. Statistics Norway, Oslo and Kongsvinger.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K.-S. Chan, N. G. Yoccoz, and B. Ådlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London B* 270:2087–2096.
- Tuljapurkar, S., and H. Caswell. 1997. *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman & Hall, New York.
- Venables, W. N., and B. D. Ripley. 1994. *Modern applied statistics with S-plus*. Springer, New York.
- Weladji, R. B., A. Mysterud, Ø. Holand, and D. Lenvik. 2002. Age-related reproductive effort in reindeer (*Rangifer tarandus*): evidence of senescence. *Oecologia* (Berlin) 131:79–82.
- Yoccoz, N. G., A. Mysterud, R. Langvatn, and N. C. Stenseth. 2002. Age- and density-dependent reproductive effort in male red deer. *Proceedings of the Royal Society of London B* 269:1523–1529.

Associate Editor: Patricia G. Parker