

# Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France

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## Summary

1. Timing and synchrony of reproduction are regarded as crucially important factors for fitness in seasonal environments. Natural selection has probably favoured temperate and arctic female herbivores that match reproduction with onset of plant growth in spring. However, breeding synchrony may also be affected by variation in phenotypic quality of females in a population, because females in poor body condition have been found to delay ovulation and subsequent calving.
2. We compared breeding phenology, i.e. the timing and synchrony of rutting (roaring, sexual aggregation) and calving of red deer (*Cervus elaphus* L.) in France (latitude: 49°N) and Norway (latitude: 63°N). We hypothesized ( $H_1$ ) that calving and rutting were later at the site with latest onset of plant growth.
3. We further quantified overall environmental predictability as the sum of annual constancy and seasonality and tested three different (not mutually exclusive) hypotheses about breeding synchrony: ( $H_{2a}$ ) the population experiencing most seasonal plant phenology should show the highest breeding synchrony; ( $H_{2b}$ ) overall predictability of plant phenology should determine breeding synchrony; and ( $H_{2c}$ ) breeding should be more synchronized in the population with lowest female body weight variation within age classes because they ovulate more synchronously.
4. Calving and rutting, as well as onset of plant phenology, were later in Norway than in France, complying with the first hypothesis. Plant growth in spring was overall more predictable and also more seasonal in Norway than France. Hence we expected higher breeding synchrony in Norway than in France according to  $H_{2a}$  and  $H_{2b}$ . Variance in female body weight was slightly higher in France than in Norway, which should also cause more synchronized breeding in Norway than in France ( $H_{2c}$ ). Contrary to all predictions, variance in rutting and calving dates was around two times higher in Norway than in France.
5. We suggest two alternative explanations of breeding synchrony. A more variable topography in Norway can make optimal birth date more variable on a local scale than in France, thereby maintaining a higher genetic variance for calving date in Norwegian red deer. Further, population age structure may play a role, as ovulation varies according to female age. Clearly, processes of breeding synchrony are far more complex than previously realized.

*Key-words:* birth, *Cervus elaphus*, NDVI, reproduction, seasonality.

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## Introduction

Environmental variability influences vital rates of plants and animals (Murphy 1968; Gillespie 1977). The role that global climate change plays on timing of breeding in plants, amphibians and birds in specific populations has recently received much attention (Stenseth *et al.* 2002; Walther *et al.* 2002), but we still know little about how predictability of climate in different areas affects life history evolution. Seasonality – the within-year amplitude in climate (contingency *sensu* Colwell 1974) – is only one of the components of climatic predictability that can influence the life history of a wide range of taxa over a broad distribution range (Boyce 1979; Zammuto & Millar 1985). In addition, annual constancy (the inverse of between-year variability) in climate and plant phenology composes a separate variance component in climate which has rarely been taken into account and which may be independent of latitude. Even though methods for summarizing and separating seasonality and between-year variance components have been available for a long time (Colwell 1974), no study has used such information to shed light on life history evolution in mammals.

Breeding phenology is regarded as a crucially important component of fitness in temporally variable environments. Timing of breeding is well known to be a heritable trait (Price, Kirkpatrick & Arnold 1988), and a very rapid response to selection for earlier birth date was found in red deer (*Cervus elaphus* L.) on the Isle of Rum, Scotland, during recent global warming (10 days in 30 years; Coulson *et al.* 2003). Ungulates are particularly well-suited for studies of how life history parameters are affected by climate and plant growth predictability as they occupy a wide range of habitats and climatic zones, ranging from the tropics to arctic regions (Whitehead 1972). In tropic and subtropic regions, ungulates may have a close to continuous breeding (Bronson 1989) while they synchronize their mating and calving periods in seasonal environments (Bunnell 1982; Bronson 1989; Berger 1992). Timing and synchronization of calving are important for offspring survival in ungulates (Festa-Bianchet 1988; Coulson *et al.* 2003). Synchronization may lead to lower predation risk through prey saturation (Rutberg 1987; Berger 1992). Moreover, as the digestibility of forage plants peak in early summer, females who match their period of increased energy costs (especially early lactation) to the peak in plant growth season would have a higher fitness (e.g. Festa-Bianchet 1988).

Because the growing season in plants is delayed in the north (due to snow and temperatures below freezing), one often assumes that animal reproduction commences later at high latitudes. Further, reproductive synchrony should be higher in areas of high predictability in timing of plant growth, as this allows selection for a stable, optimal birth date. However, earlier studies relating timing and synchrony of reproduction to latitude report deviating results. Breeding of

white-tailed deer (*Odocoileus virginianus* Zimmermann) was more synchronized north than south of 30°N (Bronson 1989). Lambing season commenced later and was more synchronized at high latitude in mountain sheep (*Ovis* spp.) (Bunnell 1982), while no latitude effect was found (from 43 to 68°N) in mating and calving periods in moose (*Alces alces* L.) (Sigouin, Ouellet & Courtois 1997). Timing of rutting and calving of red deer was earlier reported to vary substantially over a short latitudinal range in Scandinavia (one month earlier in Sweden, compared to Norway and Denmark; Ahlén 1965). However, natural selection for an optimal calving time is not the only factor affecting breeding synchrony. Autumn body condition of primiparous females was found to influence the date of ovulation in Norwegian red deer hinds (Langvatn *et al.* 2004), which will consequently determine date of calving given a fixed gestation time.

Only recently has an index of plant phenology become available: the Normalized Difference Vegetation Index (NDVI; derived from satellite images), which has been found to satisfactorily reflect variation in plant phenology (e.g. Justice *et al.* 1985; Kerr & Ostrovsky 2003; Slayback *et al.* 2003). Therefore, annual variability of plant phenology can now be analysed directly and not only through its proxies' temperature and precipitation.

In this study, we investigated the effect of timing and overall predictability of plant phenology on breeding phenology (i.e. the timing and synchrony of rutting and calving) in red deer living at widely different latitudes (Norway: latitude 63°N; France: latitude 49°N). Specifically, we explored the relative influence of the two components of climate predictability – seasonality and annual constancy following Colwell (1974). We predict that breeding (rut and calving) will be ( $H_1$ ) later in north (Norway) than in south (France). If seasonality in plant phenology is the most important determinant for breeding synchrony (Rutberg 1984), we predict ( $H_{2a}$ ) a more synchronous breeding in the north (Norway) than in the south (France). However, if overall predictability (i.e. adding the effect of annual constancy) in timing of plant growth is the most important determinant of synchrony, we hypothesize that breeding should be ( $H_{2b}$ ) more synchronized in the country having the highest predictability of plant phenology (NDVI) irrespective of latitude. Primiparous red deer females in poor condition ovulate later than fat, heavy females (Langvatn *et al.* 2004). We therefore suggest the alternative hypothesis that ( $H_{2c}$ ) breeding is more synchronized in the population with lowest variability in female body weight (as a measure of condition).

## Materials and methods

### STUDY AREAS

We used data from one area in Norway and three areas in France (Table 1). Climate in the study areas in France deviates largely from the one in Norway, where seasonal

Table 1. An overview of the study sites (Norway and France), sample sizes and time period from which the data originate

Study area	Latitude	Size (km <sup>2</sup> )	Topography	Calving dates		Group composition		Roaring dates		Body weight	
				n	time	n	time	n	time	n	time
Møre og Romsdal and Sør-Trøndelag, Norway	63°N	10 069	hilly, 0 to > 700 m	59 (captive) + 13 (wild)	1973–2001	3098	1956–84 (Apr–10 Dec)	305 + 474 (two data sets)	1956–84 (10 Sept–15 Nov; 6 Sept–6 Nov)	795	1965–2002
Petite Pierre National Reserve (PPNR), France	48°5'N	28	flat, ~300 m			1917	1980–99 (10 Apr–31 Dec)			804	1978–2001
Vallée de la Truyère (VDT), France	44°52'N	3450	hilly, 650–1100					3716	1990–91 (6 Sept–30 Oct)		
Wassy, France	48°02'N	100	flat, ~250 m	116	1990–99						

fluctuations are lower and temperatures are overall higher. Snowfall also occurs occasionally in France, but snow never covers the ground for an extended period of time as it does in Norway (4–5 months).

#### Norway

The study area (five municipalities in Møre og Romsdal and seven municipalities in Sør-Trøndelag) is forested and very hilly (detailed description in Mysterud *et al.* 2001, 2002). Many observations are conducted at and close to Songli research station, situated in Orkdal municipality, Sør-Trøndelag.

#### France

(1) The Petite Pierre National Reserve (PPNR) is a forested habitat in the Vosges Mountains. (2) The Vallée de la Truyère (VDT) in the Massif Central Mountains comprises open moorland intersected with sparse forested patches. (3) Wassy consists of a mosaic of agricultural fields and woodland, essentially composed of thickets on calciferous soils.

#### CLIMATIC DATA AND NDVI-TESTING ASSUMPTIONS OF H<sub>1</sub> AND H<sub>2</sub>

##### Temperature and precipitation: Norway

Temperature and precipitation were measured on a daily basis on Songli research station from 1988 to 1999.

##### Temperature and precipitation: France

Météo France recorded daily temperature and precipitation from 1976 to 1999 in La Petite Pierre.

##### Normalized Difference Vegetation Index (NDVI)

Data collected by the National Oceanic and Atmospheric Administration satellites are freely accessible on the web (<http://eosdata.gsfc.nasa.gov/>). From these, NDVI, ranging from –1 to 1 values have been produced from visible and near-infrared reflectance measurements ( $NDVI = (NIR - VIS)/(NIR + VIS)$ , where NIR is the near infrared light, and VIS the visible light reflected by the vegetation). Negative NDVI values correspond to an absence of vegetation (Justice *et al.* 1985; Kerr & Ostrovsky 2003; Slayback *et al.* 2003), i.e. it may show time of snowmelt and onset of vegetation season. Variation in the NDVI reflects variation in plant phenology well (Justice *et al.* 1985). The spatial scale of resolution (pixel size) is 64 km<sup>2</sup> and NDVI values are available for all the study areas on a 10-day basis, from 13 July in 1981 to 21 September in 2001. The Norwegian municipality of Orkdal covers 10 pixels. Study areas in France were much smaller than the Norwegian municipality. In order to prevent possible confounding effects of scale,

we decided to use NDVI pixels from extended areas around the French study sites. We used 12 pixels for Wassy and PPNR and 9 pixels for VDT.

#### BREEDING PHENOLOGY OF RED DEER

Sample sizes and times of data collection are given in Table 1.

#### CALVING PHENOLOGY – BIRTH DATES

(TESTING  $H_1$ ,  $H_{2A}$  AND  $H_{2B}$ )

##### Norway

Exact dates of birth were sampled in an enclosure (20 ha) at Songli Research Station. The enclosed red deer originated from wild deer in the area. During summertime deer in the enclosure grazed exclusively on natural forages (Langvatn & Hanley 1993). In winter-time they received *ad libitum* supplementary forage. Adult males (3–11 years of age) were present throughout autumn in all years and there was therefore no restriction to timing of conception. All calves born within the enclosure were found. Data from wild red deer were observed in the same main area.

##### France (Wassy)

We recorded the capture date of all calves lighter than 11 kg (an upper weight threshold for newborn calves in France) through a 2-month period. If the French red deer follow the same growth curve as the Norwegian deer, calves are on average  $5.6 \pm \text{SE } 0.58$  days when they are 11 kg. Mean date for calves weighing 10–11 kg was only 1 day more than calves weighing between 6 and 8 kg (presumably very recently born); means (as well as medians) were 19 and 20 May, respectively, and variances were also the same (heavy calves = 39.7; light calves = 43.7;  $F = 0.907$ ,  $P = 0.549$ ). Therefore variance due to imprecise estimates of birth time is negligible compared to observed variation in birth date.

#### RUTTING PHENOLOGY SEXUAL AGGREGATION (TESTING $H_1$ , $H_{2A}$ AND $H_{2B}$ )

##### Norway

In spring and summer, the majority of observations of deer groups were conducted from a car in agricultural landscapes and by farmers who recorded observations of deer on their properties (Bonenfant *et al.* 2004). From early autumn research personnel observed deer groups on foot in woodland terrain. From onset of the hunting season (10 September), red deer hunters recorded observations of groups and roaring. Each individual of a sighted group was sexed (male, female, unidentified) and aged [unsexed calf, adult (more than 1 year), yearling and unidentified].

##### France (PPNR)

Research personnel sighted groups that were sexed (male, female and unidentified) and aged [calf, adult (1 year or more) and unidentified].

#### RUTTING PHENOLOGY – ROARING DATES (TESTING $H_1$ , $H_{2A}$ AND $H_{2B}$ )

##### Norway

We had available two different data sets on roaring in autumn: (1) hunters registered a total number of 305 roaring males during 4161 observation hours (observation time  $\times$  number of observers). Hunter observations are less frequent during the break in the hunting season (2–9 October); (2) research personnel recorded roaring males at Songli research station (8000 ha) in Orkdal municipality. Roaring males were much more abundant at Songli than in other hunting terrains, because this valley composes a corridor for migrating deer passing through on their way from summer to winter ground. In the Songli data set, observations are abundant in the time interval not covered by hunters. To combine the two data sets we calculated the average number of roaring males between 16 and 21 October, i.e. the short time interval where data from both areas are abundant (Songli: 150 roaring males in 215 observation hours; hunting data set: 161 roaring males in 786 observation hours). The average number of roaring males per observation time was 3.4 times higher in Songli than in other hunting grounds. We consequently divided Songli observations by 3.4 and pooled the data.

##### France (VDT)

Roaring census started at 06 : 00 h in the morning and terminated at 08 : 00 h, as early morning is the most active period for roaring in this area.

#### FEMALE BODY WEIGHT-TESTING $H_{2C}$

For Norway (Orkdal municipality), body weights are dressed weight (58% of live weight), i.e. live weight minus head, skin, viscera, bleedable blood and metapodials (Langvatn 1977), while in France this was dressed weight with head also included.

#### STATISTICAL ANALYSES

##### Smoothing of NDVI values

Because we aimed at characterizing spring season, we restricted our NDVI analyses from the first available NDVI measure in January to the start of August. At this date, every time-series has reached a 'summer plateau' and the covered period allowed us to capture both seasonality and annual constancy in the NDVI pattern. The measurement error of the NDVI is largely

influenced by weather conditions, pollution and snow cover at the specific time of remote sensing (Justice *et al.* 1985). We therefore minimized measurement error influence with a smoother. For the four study sites, yearly time-series were smoothed using locally weighted regressions (Swets *et al.* 1999), which put low weight (0.005) to local valley points (NDVI values lower than the previous measure) because they most probably occur due to cloud cover at the time of sensing rather than reversed plant phenology. We also tried two other smoothing procedures: (1) non-weighted least squares smoothing and (2) cumulative maximum of the NDVI from midwinter to mid-summer. Methods gave qualitatively the same results (regarding differences in predictability between the Norwegian site and the French sites) as the chosen smoothing procedure.

#### Predictability of the NDVI

Analyses of the NDVI predictability were performed using non-parametric indices on the smoothed NDVI-data following Colwell (1974). Predictability (P) is separated into two components termed constancy (C) and contingency (M). Constancy assesses the importance of year-to-year stochastic variations, i.e. it is the inverse of between-year variability. The lower the value of C, the more unpredictable the climate/plant growth is among years and *vice versa*. Contingency measures how much of the overall predictability P is due to a seasonal pattern repeated within each year (contingency thus reflects how strong the seasonality is).

#### TIMING OF RUT

We used two different indices for timing of rut – sexual aggregation and roaring. The first method identifies rut by estimating thresholds for onset and peak of sexual aggregation, the second using first and mean date of roaring. Red deer are sexually segregated except during the mating season (Clutton-Brock, Guinness & Albon 1982; for our areas, see Bonenfant *et al.* 2004). We defined mixed groups as a single male observed with 1–3 reproductive females in both France and Norway (including the most common ‘harem sizes’ in Norway and France; and excluding the large foraging groups on agricultural land commonly observed in Norway).

#### GAM-models

We modelled the temporal variation in the proportion of mixed groups (binary response variable taking values 0 or 1) by fitting generalized additive models (GAMs) with a logit link (Hastie & Tibshirani 1990). GAMs use non-parametric smoothing functions (splines) that describe the relationship between the proportion of mixed groups and time. The flexibility of the fitted models, i.e. the number of degrees of freedom (d.f.<sub>spline</sub>) associated with a smoothing spline, was selected by repeated fitting of the GAM (with different degrees of freedom for

‘time’). We fitted the model with varying d.f.<sub>spline</sub> for one variable and held d.f.<sub>spline</sub> for the other variables constant. Thereafter we compared the fits of the different models in an ANOVA setting (Venables & Ripley 1999). Separate GAMs were used for France and Norway. All statistical analyses were performed in the statistical package S-Plus (Venables & Ripley 1999).

#### Threshold models

We expected a constant but non-zero proportion of mixed groups until the onset of rut (cf. Bonenfant *et al.* 2004), characterized by a rapid increase and subsequent decrease at the peak of rut in the proportion of mixed groups. Logistic threshold models were thus useful tools for assessing the onset and the peak of the mating season.

Models considered were given as:

$$\text{Logit (Expected proportion of mixed groups)} \\ \left\{ \begin{array}{l} = a; \text{ if Julian date} \leq t_1 \\ = a + b \times \text{Day}; \text{ if Julian date} > \tau_1 \end{array} \right\} \\ \text{for the onset of rut}$$

$$\text{Logit (Expected proportion of mixed groups)} \\ \left\{ \begin{array}{l} = a; \text{ if Julian date} \geq t_2 \\ = a + b \times \text{Day}; \text{ if Julian date} < \tau_2 \end{array} \right\} \\ \text{for peak of rut}$$

where  $\tau_1$  and  $\tau_2$  are the threshold values defining the dates for which the proportion of mixed groups starts and peaks, respectively. We used profile likelihood to estimate the onset and the peak of rut dates (Ulm 1989). Peak of rut ( $\tau_2$ ) was estimated first by using the complete dataset. We estimated the onset of rut ( $\tau_1$ ) by using a subset of the data ranging from Julian date 150 (May 30; from when group composition was constant) to the estimated Julian date ( $\tau_2$ ) when rut peaked. The profile likelihood method allows for computation of confidence intervals for the threshold value estimates (Ulm 1989), enabling a between-population comparison of the dates at which the onset and the peak of rut took place.

#### TESTING DIFFERENCE IN TIMING AND SYNCHRONY OF ROARING AND CALVING

In Norway calving was registered over a period of 28 years and roaring was observed over a period of 16 years. In France calving was recorded during 10 years, while roaring was observed during only 2 years (Table 1). Synchrony should be quantified as variability of these traits within years, not for the pooled data set. In order to separate between-year variability and within-year variability in calving and roaring, we fitted linear mixed-effects models (LME in S-plus for Windows 2000 with nlme-library 3.1) with observation date as response, no fixed effects and year as the random effect. These models give the mean date with confidence

limits (used to test difference in timing of each trait between countries), in addition to estimates of the within-year variance and the between-year variance for each country. We used residual maximum likelihood (REML) estimation because it provides more reliable estimates of the variance components (Venables & Ripley 1999). We compared within-year variance (i.e. synchrony) and between-year variance in calving time and roaring time by the use of a *F*-ratio test (Zar 1984: 125). In Norway, most of the calving data come from an enclosure where the same females gave birth over several years (12 captive females; one to 13 records per female). We tested for dependency of the mother on calving date by comparing two models: one with only 'year' as a random effect and one also including the effect of 'mother' nested within 'year'. We selected the one with lowest Aikake information criterion (AIC) (which was without 'mother' as a random effect).

#### BODY WEIGHT VARIABILITY

We ln-transformed body weights to stabilize variance. We tested for differences in relative variability between Norway and France (PPNR) in body weight using an *F*-test on variance of ln-transformed body weight (Lewontin 1966).

## Results

#### PREDICTABILITY OF CLIMATE AND PLANT PHENOLOGY

Onset of plant growth was later in Norway (NDVI values close to 0 in beginning of April) than in France (NDVI values well above 0 from beginning of March). Predictability of NDVI was higher in Norway because the seasonal component is more pronounced (Table 2; but note that predictability of the French calving site Wassy is nearly as high as in Norway due to strong annual constancy). The higher seasonality ( $H_{2a}$ ) and the higher overall predictability ( $H_{2b}$ ) of plant growth in Norway predicted shorter breeding interval for this population.

#### BREEDING PHENOLOGY

##### *H*<sub>1</sub> timing of breeding

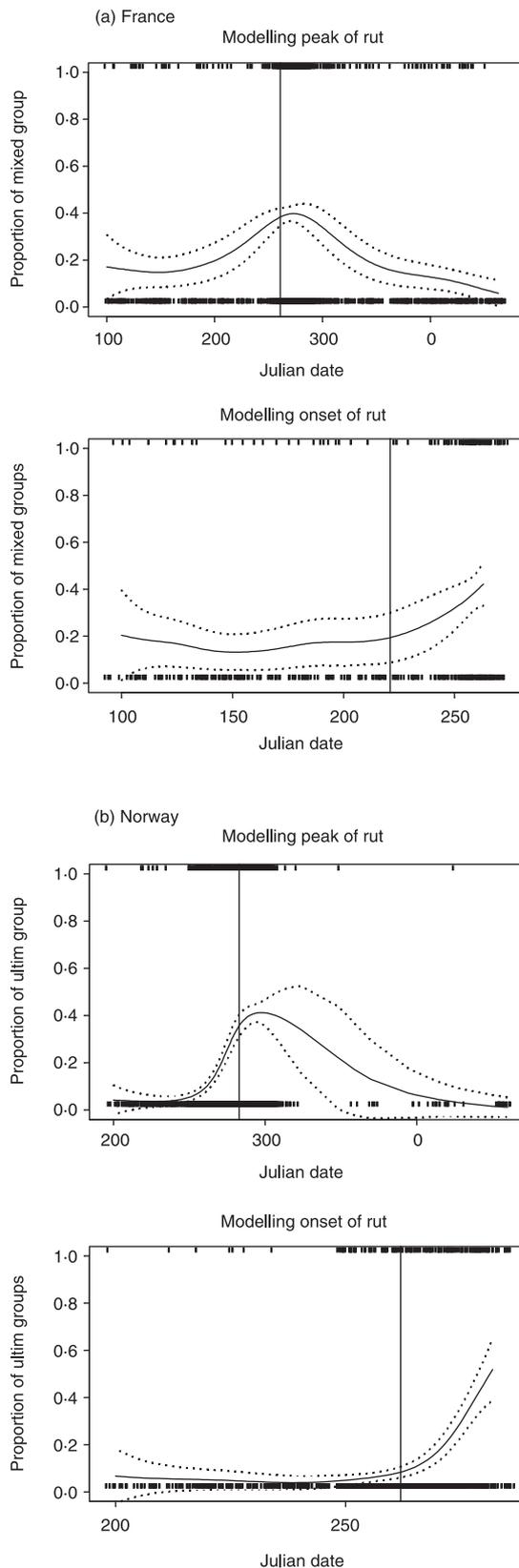
Rutting and calving occurred later at high latitude (Norway) than low latitude (France) as expected, due to the colder climate and delayed plant phenology at high latitudes. In France, males and females already tended to start aggregating during the first half of August [9 August, 95% CI = (14 May, 12 September); Figs 1a and 2a] and the first roar was heard 6 September. Rut peaked in late September [peak aggregation: 19 September, 95% CI = (20 August, 27 September), Figs 1a and 2a; mean roaring date: 27 September, 95% CI = (24 September, 30 September); Fig. 3]. In Norway (high latitude), sexes did not start to aggregate before mid-September [September 19, 95% CI = (14 September, 23 September 23); Figs 1b and 2b], and the first roaring male was registered 17 September. In Norway, rut peaked in early to mid-October [peak aggregation: 10 October, 95% CI = (7 October, 13 October 13); mean roaring date: 15 October, 95% CI = (13 October, 17 October); Fig. 3]. In France, calving took place between 4 May and 10 June, mean date of calving being May 20 [95% CI = (18 May, 22 May 22); *n* = 116]. In Norway, calving of captive deer ranged from 31 May to 22 July, the mean date being 17 June [95% CI = (14 June, 20 June 20); *n* = 59]. The smaller sample of births of wild deer ranged in time from 6 June to 4 July (mean date: 17 June; *n* = 13), corresponding well with observed birth time in captivity.

##### *H*<sub>2</sub> SYNCHRONY OF BREEDING

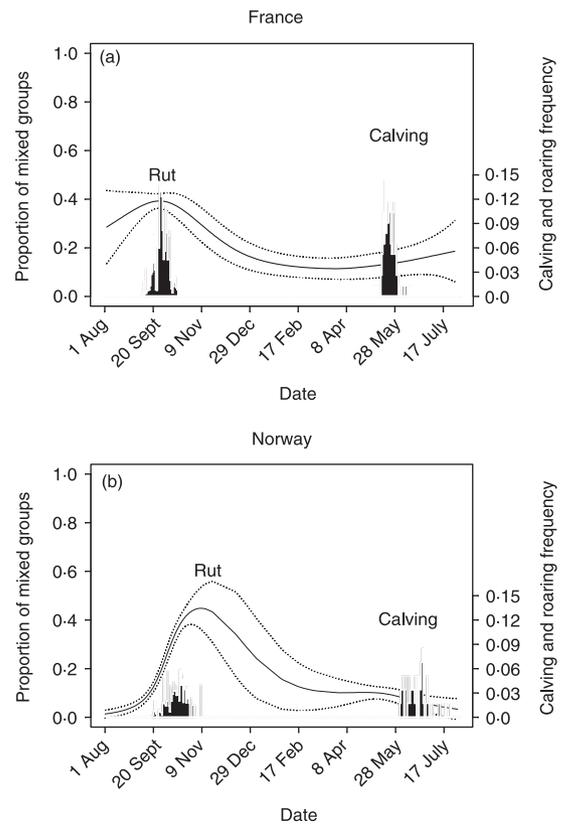
The variance in rutting date within years (measured by roaring activity) was 2.2 [95% CI = (2.0, 2.6);  $F_{419,3822} = 2.24$ ,  $P < 0.001$ ; Fig. 3a] times higher in Norway than in France, and calving date was 2.4 [95% CI = (1.5, 4.1);  $F_{44,106} = 2.42$ ;  $P < 0.001$ ; Fig. 3b] times more variable within years in Norway than in France. This shows that breeding is consistently less synchronous in Norway than in France. We therefore rejected both  $H_{2a}$  and  $H_{2b}$ . Body weight variance was slightly higher in France than in Norway for all age groups

**Table 2.** Predictability of temperature (April–July), precipitation (April–July) and the NDVI from January to August in France and Norway (full names of study areas in Table 1). Overall predictability (column 1) is divided into constancy (inverse of between-year variability) and contingency (within year variability–seasonal amplitude)

Study site	Parameter	Predictability	Constancy	Contingency
Wassy, France	NDVI	0.626	0.257 (41%)	0.369 (59%)
VDT, France	NDVI	0.548	0.296 (54%)	0.252 (46%)
PPNR, France	NDVI	0.459	0.265 (58%)	0.193 (42%)
	Temperature	0.716	0.225 (32%)	0.491 (68%)
	Precipitation	0.402	0.371 (92%)	0.031 (8%)
Orkdal, Norway	NDVI	0.630	0.145 (23%)	0.485 (77%)
	Temperature	0.759	0.323 (43%)	0.436 (57%)
	Precipitation	0.367	0.295 (80%)	0.072 (20%)



**Fig. 1.** Onset and peak of rut based on aggregation of adult males with females in (a) France and (b) Norway was found using a threshold model. Tick marks represent the observation of a mixed group (1) or a unisex group (0).

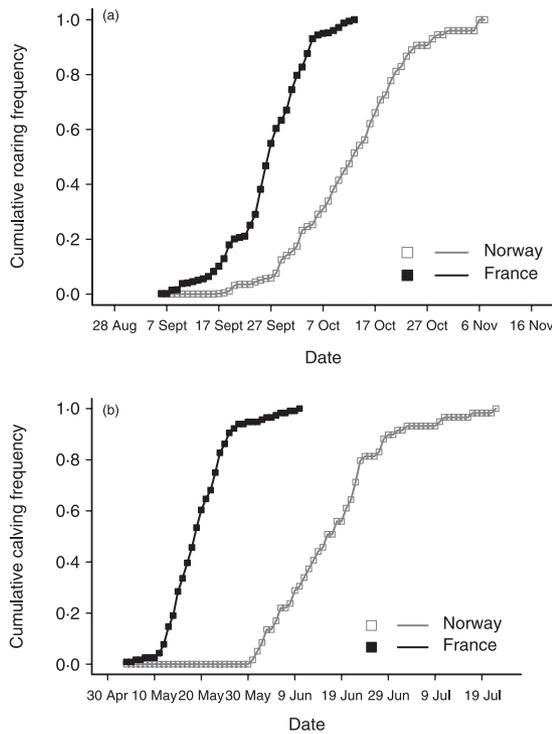


**Fig. 2.** Timing of rut and calving in (a) France and (b) Norway. Lines represent proportion of mixed groups, and histograms represent roaring rates and calving rates.

older than calves (Table 3). The hypothesis that female body weight was more variable in the population with lowest breeding synchrony ( $H_{2c}$ ) was therefore not supported.

There was a main effect of year (categorical) on calving time (ANOVA: Norway:  $F_{27,44} = 2.15$ ,  $P = 0.012$ ; France:  $F_{9,291} = 2.63$ ,  $P = 0.006$ ) and roaring time (ANOVA: Norway:  $F_{13,419} = 2.66$ ,  $P = 0.001$ ; France:  $F_{1,3822} = 226$ ,  $P < 0.001$ ). Between-year variance in calving time was considerably higher in Norway than France [8.2 times higher; 95% CI = (2.3, 21.6);  $F_{27,9} = 8.21$ ;  $P = 0.001$ ] while differences in between-year variation in roaring between countries was not statistically significant [1.5 times higher in Norway; 95% CI = (0, 9.9);  $F_{13,1} = 1.55$ ,  $P = 0.564$ ], probably because we have only 2 years of roaring observations in France leading to large confidence limits.

In France, 80% of all roars were heard within a period of 16 days (between 18 September and 6 October; both years pooled), while 80% of roaring males in Norway were heard within a period of 25 days (between 29 September and 24 October; all years pooled). In France, 80% of calves were born within a 13-day period (13 May–26 May;  $n = 116$ ) while in Norway 80% of calves were born within a 22–23-day period (captive deer: 31 May–23 June; 23 days,  $n = 59$ ; wild deer: 4 June–26 June; 22 days,  $n = 13$ ).



**Fig. 3.** Cumulative plot of relative (a) roaring and (b) calving frequencies in France and Norway (all years pooled). Note that high roaring activity in a given period result in a steep cumulative curve, and that in periods with constant roaring rate the cumulative plot will be linear.

**Discussion**

Because we are comparing two areas with virtually no predators, and because the birth date responds quickly to selection (Coulson *et al.* 2003), climate-related variation in resource availability is likely to be a critical factor for timing and synchrony of births (Linnell & Andersen 1998). We separated components of predictability and found that plant phenology was overall more predictable at the northern site (Norway) than the southern sampling site (France) caused by higher seasonality at the northern site. Subsequently, there was support for the well-known hypothesis ( $H_1$ ) that breeding phenology is earlier south (France) than at the northern site (Norway), but no support for the hypotheses that strong seasonality ( $H_{2a}$ ; Rutberg 1984) or overall predictability ( $H_{2b}$ ) in plant phenology would

lead to a more synchronous breeding. Our data are diverse, deriving from three different areas of France and also including birth data from captive deer in Norway (Table 1). Despite this, calving and roaring were consistently earlier and more synchronous in France than in Norway. The conclusions thus seem not to depend on the use of diverse data sources. Further, we found no support for more synchronized breeding in the population with the highest variation in female body condition ( $H_{2c}$ ).

Temperature and precipitation are key factors for plant growth. Temperature is probably the limiting factor at northern latitudes (Deinum 1984), while precipitation may be limiting in southern regions. NDVI values in spring were lower in Norway than in France (i.e. later plant phenology). The fact that Norwegian red deer breed later than their French conspecifics is therefore not surprising. Gaillard *et al.* (1993) found neither among-year differences in average date of calving nor among-year differences in the dispersion of births in a 5-year study of roe deer (*Capreolus capreolus* L.). In our study we found that breeding time differed largely among years. Between-year variation was found in ovulation, probably caused by a continuous effect of density increase in the Norwegian red deer (Langvatn *et al.* 2004), supporting the existence of yearly variation in calving and rutting observed in our study. Changes in density are particularly important in forming the life history of red deer (Clutton-Brock, Rose & Guinness 1997) and led to a more synchronous ovulation period in Norway (Langvatn *et al.* 2004).

In addition to this effect of timing of spring phenology, vegetation predictability may shape several aspects of reproductive strategies in ungulates such as litter size and breeding frequency and phenology (e.g. Gaillard, in press). Climate-related variation in vital rates is also well documented in cervids (review in Gaillard *et al.* 2000). For example, on Rum, large variations in April and May temperatures result in large annual variation in grass growth during the last 2 months of gestation (Clutton-Brock & Albon 1989). However, earlier studies relating breeding synchrony to latitude, and hence seasonality, have reported deviating results (e.g. Bunnell 1982; Bronson 1989; Sigouin *et al.* 1997). Here, we emphasize that annual constancy, and not only seasonality, should be taken into account as it contributes to overall environmental predictability (Colwell 1974).

**Table 3.** Mean, variance and a *F*-test of variance of ln-transformed body weight in five age categories of French and Norwegian female red deer. Variance was slightly higher in France in all age groups 1 year or older (significantly in 3-year-old individuals and approaching significance in the remaining age groups). Note that  $SD(\ln(\text{body weight})) \sim CV(\text{body weight})$

Age (years)	Mean France	Mean Norway	SD(ln[bodyweight]) France	SD(ln[bodyweight]) Norway	<i>F</i>	No. d.f.	Denom d.f.	<i>P</i>
0	30.3	25.8	0.209	0.217	0.925	237	124	0.608
1	46.1	48.4	0.156	0.131	1.43	123	106	0.0588
2	55.1	55.1	0.143	0.116	1.51	40	89	0.111
3	57.4	61.6	0.128	0.0989	1.69	59	62	0.0426
> 3	59.1	67.4	0.127	0.109	1.37	128	167	0.0570

Females cannot foresee how conditions will be the following spring at timing of conception 8 months earlier (and given that gestation time is relatively fixed). Therefore, evolution of birth synchrony through natural selection is more likely in predictable environments. Because of harsher climate and more restricted plant growth season, the reward in terms of juvenile growth rate and survival (and therefore the selection pressure) for matching the optimal date of birth is probably higher in Norway than in France. Nevertheless, we observed a much narrower 80% birth interval in France (13 days) than in Norway (22–23 days). A 25-day 80% birth interval for red deer was reported for Rum, Scotland (Clutton-Brock *et al.* 1982). French red deer therefore have an extremely narrow birth interval compared to Norway and Scotland but similar, or even higher, synchrony has been reported for other ungulate species (Rutberg 1987).

A higher variability in red deer female autumn body weights in the population with the lowest breeding synchrony ( $H_{2c}$ ) could be an alternative explanation for the contrasting observations in the two species. However, we failed to find support for  $H_{2c}$ . Surprisingly, body weights of Norwegian female red deer varied less than in their French conspecifics, although they experience harsher winter climate. A condition-dependent winter mortality on calves in Norway (Loison, Langvatn & Solberg 1999), removing the individuals which would turn into light weight adults, may explain parts of this effect. In roe deer, where plant growth and quality are even more important than for the red deer, timing and synchrony of births were equal in Norway (the island of Storfosna; Linnell & Andersen 1998) and France (Trois Fontaines; Gaillard *et al.* 1993). The close proximity with our red deer study sites makes it unlikely that the predictability of climate and plant phenology differ. Being an income breeder (i.e. not relying on stored reserves such as capital breeders), roe deer condition does not change greatly over the year (Andersen *et al.* 2000) and the variation in female body condition is expected to vary less than in red deer. Moreover, as roe deer are mono-oestrus and have delayed implantation (Sempere, Mauget & Mauget 1998), delay in mating dates cannot generate late births as in red deer.

Other factors than climate and body condition may also influence breeding synchrony. The landscape in Norway has a very variable topography (Mysterud *et al.* 2001) with a strong effect on snow accumulation (Mysterud *et al.* 2000). Deer giving birth in Norway may migrate to the altitude where snow has recently melted and therefore feed on high-energy forage for a longer period than most French deer (Albon & Langvatn 1992), decreasing the penalty of mismatch between birth time and plant phenology on the calving site. Moreover, large variation in topography and snow distribution may lead to variation in optimal birth date on a spatial scale smaller than the scale where individuals mix (through dispersal and migration), and only part of the population migrates. Hence, gene flow between different subpopulations may constrain evolution on

optimal timing of breeding in our study, as was shown for the relationship between hatching time and changing local climate in birds (Thomas *et al.* 2001). The Norwegian study site for roe deer is as flat as the French study site, which may explain the similar synchrony observed. However, roe deer in the hilly VDT study area in France was also less synchronous than in Norway, and synchrony on Rum, Scotland matches that of Norway, despite being less hilly than Norway. This does not fit with topography as a single factor explaining synchrony.

Differences in female age structure may also affect the synchrony pattern (Langvatn *et al.* 2004). Yearlings ovulate much later than adult females (median date 6 November compared to mid-October for adults Langvatn *et al.* 2004). Breeding synchrony is therefore sensitive to the age composition of females in the population, in particular to the proportion of yearlings. The proportion of yearlings on the west coast of Norway is as high as 10% due to heavy harvesting (Langvatn & Loison 1999). The red deer population on Rum is naturally regulated (Clutton-Brock *et al.* 1982) and hence has a more flat age structure (a higher proportion of older females). Whenever hunting leads to higher proportion of younger females, it may give a less synchronous breeding. Similarly, a low proportion of prime-aged males can also give a less synchronous rutting season (review in Mysterud, Coulson & Stenseth 2002).

We conclude that breeding in red deer occurred 3 weeks later at high (Norway) than low (France) latitudes. Despite higher seasonality and predictability of plant phenology, and lower variance in female body condition, breeding was two times more variable in Norway compared to France. Clearly, processes of breeding synchrony are far more complex than argued previously, and factors such as topography and population sex- and age-structure may affect the geographical pattern.

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