# Climate, plant phenology and variation in age of first reproduction in a temperate herbivore

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## Summary

1. Density-independent weather effects can have important consequences for the demography of terrestrial herbivores because precipitation, temperature and insolation influence plant phenology, forage quality and biomass production, which in turn affects the habitat carrying capacity. Since forage digestibility influences intake and weight gain, life-history traits of young, growing animals are likely to reflect variation in the prevailing weather.

2. This paper specifically investigates spatial and temporal variation in age at maturation in female red deer (*Cervus elaphus*) in Norway in relation to climate variables known to influence primary production. Our findings are corroborated by analysing differences in age at maturation in 21 cohorts of red deer on the Isle of Rum, Scotland.

3. In Norway the majority of females ovulated as yearlings and calved for the first time as 2-year-olds. The proportion calving for the first time at two years varied from 0·23 to 0·67 between regions and fluctuated from 0·46 to 0·76 between cohorts. On Rum, where age of maturation was delayed at least a year, the proportion calving for the first time as 3-year-olds varied between cohorts from 0·0 to 0·89.

4. In a subset of yearlings culled in Norway at the time of conception, the spatial and temporal differences in ovulation rates were related to the geographical and annual variation in body weight.

5. Both the spatial and temporal variation in the proportion of 2-year-olds calving in Norway, and cohort differences in the proportion calving as 3-year-olds on Rum, were negatively related to variation in May–June degree days 12 months earlier.

6. Although primary production on the preferred herb-rich *Agrostis–Festuca* grasslands was positively correlated with temperature in May and June on Rum, the proportion of females calving as three years old, was negatively correlated with annual differences in May–June primary production.

7. We argue that retarded phenological development, during periods of cooler weather, enhances diet quality because leaf:stem ratios and digestibility of plant parts decline more slowly. Thus, weight gain during the early summer growth spurt should be rapid during cool May–June weather, increasing the probability of conception in the autumn.

8. Since density-independent variation in food availability also influences fitness components which commonly have a more pronounced influence on population demography, for example offspring survival, we argue that our results highlight the potential importance of variation in weather on herbivore abundance.

*Key-words*: climate, plant phenology, diet quality, reproduction, red deer.

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## Introduction

Although population density may commonly influence demographic parameters because intraspecific competition reduces per capita food availability (Begon, Harper & Townsend 1990), in many animal populations density-independent weather effects may also be important because they too influence the resource base (Lack 1954). For example, in species of terrestrial herbivores annual variation in reproduction and survival may be related to variation in the preceeding summer weather (see Albon & Clutton-Brock 1988; Owen-Smith 1990), because both the biomass and nutritive value of forage is influenced by the climate prevailing in the plant growing season (van Soest 1983). If the intrinsic rate of increase of the population is low, as in the larger cervids and bovids, then between-year differences in weather during the period of peak primary production may be at least as important, in generating temporal variation in the plane of nutrition, as the impact of annual changes in population size. Furthermore, since stochastic variation in the resource base will influence the carrying capacity of the habitat, it may not be possible to detect density-dependent effects until confounding density-independent variation has been taken into account (Owen-Smith 1990). Also, density-independent effects may be particularly important in less favourable habitats at the edge of the species' range (Haldane 1956).

In both tropical and temperate grasslands, primary production early in the plant growing season is prolific and biomass rarely limits the intake of grazing herbivores except on the most preferred vegetation communities (McNaughton 1979; Hanley 1984; Robertson 1987; Gordon 1989). However, at this time of the year, comparatively small differences in digestibility of forage plants have profound effects on body weight gain (see Blaxter, Wainman & Wilson 1961; White 1983), because high forage digestibility not only increases relatively metabolisable energy intake but also increases absolute herbage intake (Armstrong, Common & Smith 1986). The close relationship between plant digestibility, and weight gain has important implications for the number of seasons young animals take to reach breeding age. In both domesticated and wild ungulates age at reproductive maturation is associated with the attainment of a critical body weight above which females have an increasing probability of ovulating and conceiving (cattle, Joubert 1963; bison, Green & Rothstein 1991; sheep, Gunn, Doney & Russel 1969; red deer, Hamilton & Blaxter 1980; Albon *et al.* 1986; moose, Sæther & Haagenrud 1985; caribou/reindeer, Parker 1982; Reimers 1983; white-tailed deer, Verme 1969; roe deer, Gaillard *et al.* 1992).

Since body weight is commonly available for harvested species of cervids, and is a proximate factor influencing fertility, several studies have investigated correlations between climatic variables in the plant growing season and temporal variation in subsequent autumn body weights (red deer, Albon 1983; moose, Sæther 1985; reindeer, Skogland 1983). However, there is little consistency, either between or within species, in the climatic factors that appear to be important. Unfortunately, because cervids are often harvested before ovulation in the autumn, and reproduction has to be estimated retrospectively from analysis of ovarian structures (Zuckerman & Weir 1977; Langvatn 1992a), there have been few attempts to relate annual differences in age-specific reproduction directly to climatic variables (see Clutton-Brock & Albon 1989). Although there is evidence that the onset of sexual maturity among females appears to be the demographic variable that is first to respond to resource limitation (Mitchell, Staines & Welch 1977; Fowler 1987; Owen-Smith 1990), we generally have a poor understanding of the indirect impact of climatic variation on reproduction and its consequences for population demography in large herbivores (Picton 1984).

In this paper we investigate spatial and temporal differences in age of first breeding in populations of red deer (*Cervus elaphus*) in Norway and Scotland in terms of a common set of climatic factors known to influence plant phenology and, in particular, plant digestibility at high latitudes (Riley & Skjelvåg 1984). The general observation is that the nutritional quality and digestibility of plants tends to increase with latitude (Deinum 1984), and at a given latitude with decreasing temperature and water supply (Deinum *et al.* 1981; Evans & Wilson 1984; Hay & Heide 1984; Wedin *et al.* 1984). Since in Norway there is a trend for temperature and rainfall in the growing season to decline with increasing latitude and increasing distance from the sea, plant development should be retarded and plant digestibility enhanced along clines from south to north and coast to inland (Albon & Langvatn 1992). Previous research has shown that yearling body weight, which is closely associated with puberty (see above), increases along the same clines (Langvatn & Albon 1986). As a result, we predict that yearling pregnancy rates will follow the same trends, increasing from south-west to north-east. However, the apparent causal relationship could arise because of some other correlation with latitude. Therefore, the association would be more convincing if the climate variables that were correlated with spatial differences in yearling body weights, and by inference pregnancy rates, also explained the observed year-to-year cohort variation in puberty (i) within different regions of Norway, and (ii) in a geographically distinct population on the Isle of Rum, Scotland. Here we show that variation in May–June degree days, the period when most of plant growth occurs at these latitudes (Wedin *et al.* 1984; Albon & Langvatn 1992), explains both the spatial and cohort variation in the proportion calving for the first time at 2 years of age in Norway,

and the cohort variation in the proportion calving for the first time at 3 years of age on Rum.

## Materials and methods

### STUDY AREAS

#### Norway

Red deer in Norway occur in all counties and the majority of municipalities south of the arctic circle (Langvatn 1988). However, they are concentrated within a 100–150 km wide band along the west coast from Boknfjord (59° 20′N, 5° 35′E) to Otteröy (64° 35′N, 11° 15′E) and more than 95% of the ≈ 12 000 animals harvested each year are shot within the six coastal counties from Rogaland to North-Trøndelag (Central Bureau of Statistics, Oslo 1992).

The municipalities within these six counties have been allocated to three latitudinal zones (South, Intermediate and North), and two zones representing proximity to the coast (Coast and Inland, Fig. 1), using climatic, floristic and topographic information (see Langvatn & Albon 1986). In addition, the island Hitra (63° 32′N, 8°45′E) is defined as a separate region because of its extreme oceanic environment and more sedentary population of red deer (Wegge 1975).

The seven regions differ in climate (Table 1), with temperature and precipitation tending to decline from south to north and from coast to inland, while snow depth increases. In summer both the length of the growing season and total degree days (>6 °C, see Gloyne 1968) decline from south-west to north-east (Langvatn & Albon 1986).

#### Rum, Scotland

The Isle of Rum (57° 0′N, 6° 20′W) is 19 km off the Scottish mainland. Approximately 90% of the 100 km², is available to a population of deer that between 1971 and 1992 fluctuated from 1175 to 1730 individuals. Most of the area is managed as a traditional deer 'forest' (Lowe 1971) and approximately

one-sixth of both sexes counted in the spring, before the calving season, are harvested each autumn. In one sector of the island, the North Block, the cull ceased in 1972 and in this study population the number of females increased from 57 in 1971 to 176 in 1992. Nearly all females in this population are individually indentifiable either from natural idiosyncracies or from artificial marks (collars and ear tags) and most have complete life-history data (see Clutton-Brock, Guinness & Albon 1982). Age at first calving varies from 3 to 7 years of age, and is density-dependent (Clutton-Brock, Major & Guinness 1985). In this paper we analysed the proportion of 3-year-olds calving in 21 cohorts born between 1968 and 1989 (excluding 1970). All females were monitored daily during the calving season from late May through early July. For those who calved exact dates of parturition were known and in most cases their calves were caught within a few days of birth (Clutton-Brock, Guinness & Albon 1982).

### SELECTION OF CLIMATIC VARIABLES

The selection of climatic variables was based on the literature on (i) energetic requirements of early development and growth in juvenile red deer, and (ii) plant phenology (see Fig. 2). Metabolism, appetite and growth in deer all vary throughout the year (Kay & Staines 1981). Energy requirements in pregnant females start to increase in March and rise through the last tremestre of gestation (Thorne, Dean & Hepworth 1976; Bartmann 1986). At this time of the year temperature influences the onset of grass growth and, in part, the length of the growing season (Hay & Heide 1984). On Rum primary production in April is closely related to temperature (Albon, Clutton-Brock & Langvatn 1992) and the birth weight of calves is related to April–May mean daily temperature (Albon, Guinness & Clutton-Brock 1983). Energetic demands continue to increase through early lactation in June–July (Arman *et al.* 1974; Krzywinski *et al.* 1980; Loudon, McNeilly & Milne 1983; Loudon & Kay 1984) and forage digestibility is critical for the hinds'

Table 1. Age-specific calving rates by latitudinal region (South, Intermediate and North), the island Hitra and averaged across the whole country

| Age (years) | Region (latitude) | | | | |
|---|---|---|---|---|---|
| | South | Intermediate | North | Hitra | Mean |
| 1 | 0 (219) | 0 (82) | 0 (157) | 0 (50) | 0 (508) |
| 2 | 0·57 (198) | 0·64 (75) | 0·71 (203) | 0·30 (50) | 0·61 (526) |
| 3 | 0·93 (143) | 0·98 (54) | 0·96 (169) | 0·93 (54) | 0·95 (420) |
| 4 | 0·97 (66) | 1·00 (36) | 1·00 (96) | 1·00 (21) | 0·99 (219) |
| 5–12 | 0·99 (196) | 0·99 (85) | 0·99 (251) | 1·00 (77) | 0·99 (609) |
| 13–18 | 0·91 (21) | 1·00 (16) | 0·95 (42) | 0·94 (17) | 0·95 (96) |
| ≥19 | 0·40 (5) | 0·67 (3) | 0·83 (6) | 0·50 (2) | 0·63 (16) |

North

Intermediate

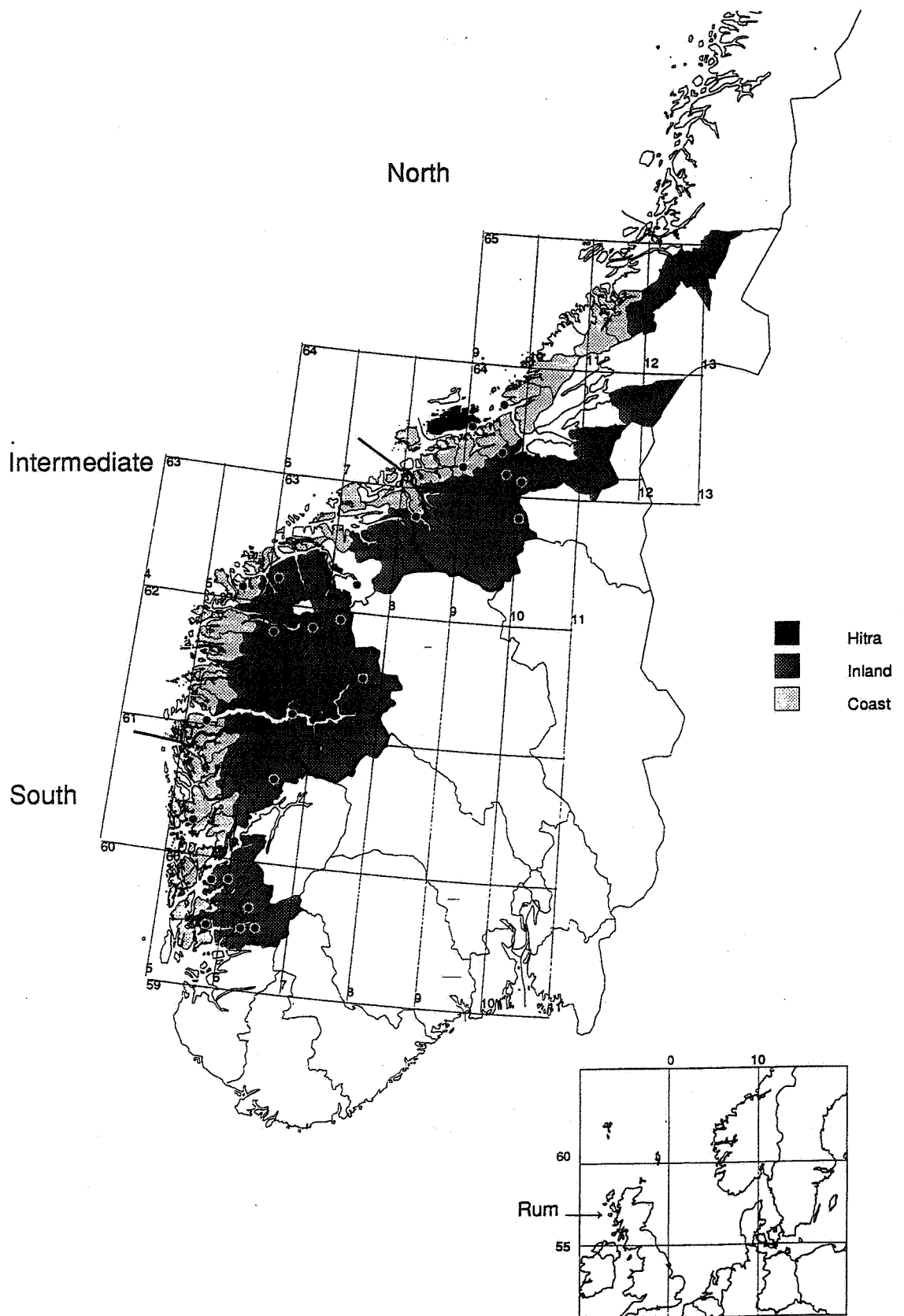South

Hitra

Inland

Coast

Rum

**Fig. 1.** Sampling areas (municipalities), allocated to coast and inland zones within latitudinal regions of Norway. Black points show locations of meteorological stations. The inset shows the location of Rum, Scotland in relation to Norway.

Fig. 2. Climatic variables used in the analysis of yearling pregnancy rates. Summary of selection criteria in terms of impact on plane of nutrition and energy balance is shown (see text for details).

| Month | J | F | M | A | M | J | J | A | S | O | N | D | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age (months) | | | −3 | −2 | −1 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |

**Stage of development:** Last tremestre of gestation | Birth | Peak lactation | Winter growth check | Growth spurt | Puberty

**Degree days:** Early plant phenology: influence lactation | Senescence in plants: influence length of growing season | Early plant phenology: influence rate of growth | Senescence in plants: maintenance of growth to puberty

**Temperature:** Start of plant growth: influence birth weight | Maintenance of growth: influence thermal energy balance | Start of plant growth: recovery from wintergrowth check | Maintenance of thermal energy balance

**Precipitation:** Biomass and nutrient content in plants: influence lactation | Magnitude of second plant growth peak: influence autumn/early winter nutrition | Biomass and nutrient content in plants: influence rate of growth | Magnitude of second plant growth peak: maintenance of growth to puberty

**Snow depth:** Mother's food access: influence foetal growth | Rate of thawing and emergence of new vegetation | Calf's food access, energy cost: influence rate of weight loss

energy supply. Cool, dry weather will tend to slow plant development, retard the 'dilution' of leaf with stem, reduce lignification and thus slow the rate of decline in plant digestibility (Terry & Tilley 1964; Wilson 1982; Deinum 1984; Evans & Wilson 1984; Hay & Heide 1984). A year later, in the second summer of life, the growth spurt of yearlings (Fennessy, Moore & Corson 1981; Adam & Moir 1985; Milne *et al.* 1987) will depend on herbage quality in May and June, the 2 months of greatest primary production. The timing of the winter check in calf body growth will depend, in part, on the occurrence and magnitude of the secondary peak in plant growth in September. On Rum, rainfall in September depresses net aerial primary production (Albon & Clutton-Brock 1988). As temperature falls and frost becomes increasingly common, plant senescence will be accelerated and the biomass of live material declines rapidly. With the onset of winter, snow fall may be important, particularly in Norway, because it affects both access to food and, when very deep, mobility and energy expenditure (Parker, Robbins & Hanley 1984; Fancy & White 1985, 1986).

We have attempted to describe the phases of peak energy demands for early development and highlighted the magnitude and direction of relationships between climate and plant growth in the same periods. Although they have been described separately, temperature, rainfall and snow fall may have additive or confounding effects (see below).

METEOROLOGICAL DATA

Meteorological data across our regions in Norway were obtained from the Norwegian Meteorological Institute, Oslo. Values for climatic variables in Appendix 1 are means calculated from two to six stations within each region (see Fig. 1), and for all inland regions they are adjusted to the level of 250 m above sea level. Weather data for Rum were collected at the meterological station in Kinloch, Rum (5 m a.s.l.).

Not surprisingly, compared to Norway, Rum experiences mild winters with little snow (Appendix 1). However, in May, June and July, the months of maximum plant growth, temperatures of Rum were no higher than those across much of Norway. Even compared to the coastal regions of Norway, Rum had higher rainfall in most months.

SAMPLING AND MEASUREMENTS OF DEER

In Norway, deer were sampled during the annual autumn harvest. Hunting is controlled through licenses issued by local wildlife boards in each municipality. Red deer may only be shot between 10 September and 15 November. However, between these dates the actual hunting periods vary between counties.

In cooperation with local wildlife boards, hunters were asked to provide mandibles from all animals shot, together with records of sex, date, locality and body weight. If a female, they were asked to also provide the reproductive tract (uterus with ovaries) and to record the state of lactation and whether a calf was associated.

Body weight in this study is dressed weight (live weight minus head, skin, viscera, bleedable blood and metapodials (Langvatn 1977)). Dressed weight in hinds is ≈58% of live weight (Langvatn 1986). In some cases hunters were not able to weigh the animals

and hence recorded an estimated weight. Estimated weights were excluded from the analysis.

Age determination in calves and yearlings was based on tooth eruption patterns (Mitchell & Youngson 1969). Older animals were aged using annuli in the cementum of the first incisor (Table 2), following a procedure described by Reimers & Nordby (1968).

As reported earlier (p. 655), individuals on Rum were monitored from birth and during the calving season observed daily, thus exact information on age and age of first parturition were available.

### ANALYSIS OF REPRODUCTION (NORWAY)

#### Yearling pregnancy rate

Yearlings ovulate and conceive later than 2- or 3-year-olds (see Fig. 3) and only in recent years were they sampled around the time of conception. Although there were significant annual differences in ovulation rates (see below) there were too few years to investigate associations with climatic variables because of the complication of sampling date. In order to increase

the sample of cohorts, yearling pregnancy rates were assesed retrospectively in 2- and 3-year-olds using histological techniques described below. Estimates for yearling pregnancy rates based on cohorts sampled as 2-year-olds were significanty correlated with estimates based on cohorts sampled a year later as 3-year-olds ($r^2 = 0.55$, $P < 0.01$). Sampling cohorts in this way provided us with a total of 21 cohorts; 14 cohorts using 2- and 3- year-olds combined, 6 cohorts using 2-year-olds alone and one using 3-year-olds alone (Table 4).

#### Histology of ovaries

The analysis of reproduction used in this study is described in detail by Langvatn (1992a,b). Ovulation in yearling hinds was recorded from the occurrence of primary *corpus luteum* (PCL) in the ovaries or from the presence of a *corpus luteum verum* (CLV). In 2-year-old hinds, conception as a yearling was established on the basis of lactation and presence of a *corpus rubrum* (CR). Data on weight and appearence

**Table 2.** Number of hinds 2 and 3 years old sampled in different regions of Norway across the years 1969–91

| | Region | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | South Coast (11) | Inland (12) | Intermediate Coast (21) | Inland (22) | Hitra (30) | North Coast (31) | Inland (32) | Total |
| Age (years) | | | | | | | | |
| 2 | 124 | 167 | 58 | 90 | 98 | 240 | 103 | 880 |
| 3 | 57 | 90 | 33 | 22 | 54 | 109 | 59 | 424 |
| Number with reproduction scored as 'yearlings' | 181 | 257 | 91 | 112 | 152 | 349 | 162 | 1304 |
| Calving rates as 2-year-olds standardized to the 1989 cohort | 0·58 | 0·61 | 0·60 | 0·67 | 0·23 | 0·69 | 0·70 | |
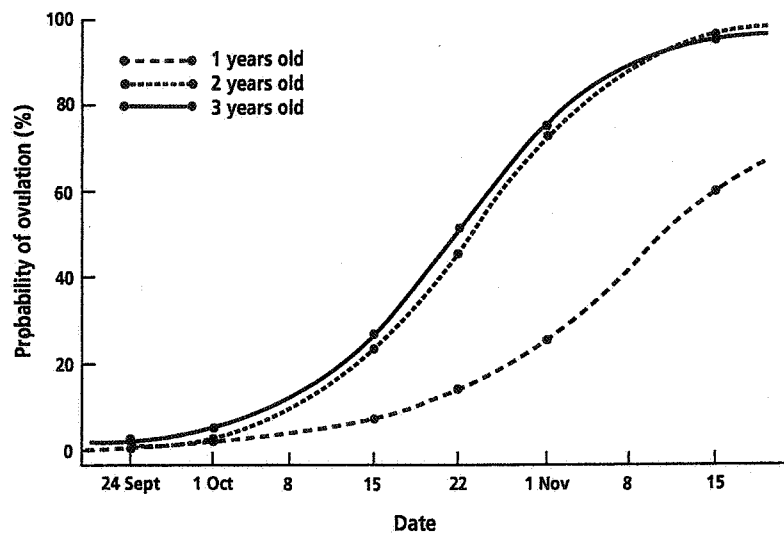


**Fig. 3.** Logistic regression curves showing the probability of ovulation in females of 1, 2 and 3 years old in relation to date of sampling. Yearlings ovulate significantly later than older animals (Data for Norway).

**Table 3.** Sample sizes and population of 2-year-olds calving in Norway and 3-year-olds calving on Rum by cohort (year of birth) 1968–89. In Norway the composition of cohort in terms of number of 2- and 3-year-old females with reproduction scored as 'yearlings' is also shown (see text for details)

| | Cohort (year of birth) | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | Total |
| **Norway** | | | | | | | | | | | | | | | | | | | | | | | |
| Age 2 | 21 | 44 | 42 | 54 | 41 | 35 | 2 | — | 94 | 3 | — | 15 | 5 | 121 | 74 | 50 | 38 | 1 | 1 | 88 | 27 | 124 | 880 |
| Age 3 | 12 | 12 | 16 | 14 | 17 | — | — | 27 | — | 2 | — | — | 79 | 43 | 31 | 35 | 1 | — | 46 | 2 | 87 | — | 424 |
| Number with reproduction scored as 'yearlings' | 33 | 56 | 58 | 68 | 58 | 35 | 2 | 27 | 94 | 5 | — | 15 | 84 | 164 | 105 | 85 | 39 | 1 | 47 | 90 | 114 | 124 | 1304 |
| Calving rates as 2-year-olds standardized to North coast region (31) | 0·52 | 0·48 | 0·59 | 0·62 | 0·62 | 0·65 | 0·73 | 0·68 | 0·70 | 0·58 | — | 0·46 | 0·59 | 0·64 | 0·69 | 0·59 | 0·60 | (0·99) | 0·68 | 0·66 | 0·63 | 0·69 | — |
| **Rum** | | | | | | | | | | | | | | | | | | | | | | | |
| Number of 3-year-olds | 8 | 9 | 6 | 8 | 12 | 16 | 19 | 16 | 15 | 13 | 15 | 16 | 17 | 10 | 17 | 20 | 23 | 17 | 17 | 22 | 9 | 27 | — |
| Proportion calving | 0·38 | 0·89 | — | 0·75 | 0·42 | 0·25 | 0·37 | 0·19 | 0·00 | 0·08 | 0·13 | 0·06 | 0·35 | 0·30 | 0·12 | 0·10 | 0·04 | 0·24 | 0·12 | 0·05 | 0·00 | 0·19 | — |

of the uterus served to substantiate the analysis of ovaries, particularly in hinds 1 and 2 years old. Uteri from yearling hinds that had ovulated were heavier and more vascularized than uteri from those who had not ovulated. The same criteria also served to substantiate parity in 2-year-old hinds. Uteri from parous, 2-year-old hinds were heavier, more vascularized and with larger cornua than uteri from nulliparous hinds of the same age (Langvatn 1992b). In hinds 3 years and older the reproductive history was traced on the basis of presence/absence of *corpora albicantia* (CA) and CR. The presence of a CA in 3-year-old hinds indicates pregnancy as a yearling (Langvatn 1992a).

## STATISTICAL ANALYSIS

In the data set for Norway we had 91 region-years with values for the number in a cohort sampled and the number of that sample that calved at 2 years of age. For Rum the data comprised 21 cohorts, from a single population, for which we knew the number in each cohort sampled and the number of that sample that calved at 3 years of age. The data from Norway and Rum were analysed in separate models but using the same generalized linear models (McCullagh & Nelder 1983). In both populations variation in the proportion calving was investigated in a logistic regression model where the number calving, the dependent variable, was assumed to be a binomially distributed variable with the number of binomial trials equivalent to the number of deer sampled in the cohort. The independent variables were values for precipitation and temperature (see above) in months and years prior to conception in the autumn. In the Norwegian data set we had additional categorical parameters that described the region or latitude and longitude (coast-inland). In the Rum data set additional information included estimates of the number of resident hinds to remove potentially confounding density dependent effects. The logistic regression models were of the form:

$$P(Y_i = 1) = \frac{\exp(A + B_1 x_{i1} + B_2 x_{i2} \cdots + B_N x_{iN})}{1 + \exp(A + B_1 x_{i1} + B_2 x_{i2} \cdots + B_N x_{iN})}$$

where $A, B_1, B_2, \ldots B_N$ are coefficients of independent variables $x_i1$ (e.g. *May–June degree days*), $x_i2$, etc., and $i = 1, 2, 3 \ldots N$ are the the cohorts sampled.

The parameters of this logistic regression model were estimated by maximum likelihood using the generalized linear model facility in the Genstat 5 statistical package (Genstat 5 Committee, 1993). This provides a convenient index of goodness-of-fit of a model including a particular set of parameters, and can be used to determine whether the inclusion of extra parameters in the model significantly improves the fit. In Genstat, this is simply done by comparing the difference between 'deviance' values of any two models

**Table 4.** Deviance explained by climate variables fitted after regions in the model of age of first breeding in Norwegian red deer. The values were all standardized about the mean in each region and thus represent the between-year variation

| Explanatory variables | | | | |
|---|---|---|---|---|
| Area | Region (including Hitra) | 100·95 | d.f. = 6 | |
| | Residual deviance | 58·99 | d.f. = 84 | |

| Reduction in residual deviance | | | | |
|---|---|---|---|---|
| | First year | | Second year | |
| Climate variables | $\chi^2$ | Significance | $\chi^2$ | Significance |
| Degree days | | | | |
| May–June | 2·90 | $P < 0·1$ | 10·51 | $P < 0·01$ |
| Sep–Oct | 0·86 | NS | 2·14 | NS |
| Temperature | | | | |
| April–May | 0·10 | NS | 0·00 | NS |
| Oct–Nov | 3·03 | $P < 0·1$ | 2·55 | NS |
| Precipitation | | | | |
| May–June | 1·62 | NS | 1·24 | NS |
| Aug–Sep | 0·65 | NS | 0·01 | NS |
| Snow depth | | | | |
| Jan–Mar | 0·12 | NS | 0·96 | NS |

which are distributed approximately as chi-square ($\chi^2$) with degrees of freedom equivalent to the difference in the number of parameters fitted in each model.

## Results

### AGE-SPECIFIC CALVING RATES IN NORWAY

In our total sample the proportion of females that conceived as yearlings and gave birth for the first time as 2-year-olds was 0·61 (Table 1). Calves never conceived. Among 3-year-olds the proportion calving increased to 0·95, and in all age classes from 4 to 12 years exceeded 0·99. Between 13 and 18 years of age the proportion calving declined slightly to 0·95, and in the small number of females 19 years and older it fell to 0·63. Across the country there was only significant variation in the proportion calving as 2-year-old females. For example, on the island of Hitra puberty was generally delayed and the proportion calving as 2-year-olds was only 0·30 compared to 0·71 on the mainland at similar latitudes (Table 1). However, in 3-year-olds from Hitra the proportion calving increased to 0·93 and among 4–12-year-olds all females were apparently pregnant.

### AGE AND THE TIMING OF OVULATION IN NORWAY

Very few animals in any age class ovulated before 1 October (Fig. 3). Among 2- and 3-year-olds, the proportion that had ovulated by 15 October was 0·23 and 0·27, respectively. By 22 October the proportion of 2- and 3-year-olds that had ovulated had increased to 0·50 and 1 week later this had increased to 0·72.

Virtually all individuals who were going to ovulate had done so by mid-November. In contrast, female yearlings ovulated later ($\chi^2 = 106·8$, d.f. = 1, $P < 0·001$). By 29 October the proportion that had ovulated was only 0·25 and this proportion did not reach 0·50 until 10 November, nearly three weeks later than in 2- and 3-year-olds.

### OVULATION AND BODY WEIGHT IN INDIVIDUAL YEARLINGS IN NORWAY

The probability of a yearling female ovulating increased significantly with increasing body weight ($\chi^2 = 59·3$, d.f. = 1, $P < 0·001$). For example, on 10 November a 45 kg yearling had only a 0·25 probability of having ovulated compared to 0·78 for a 55 kg yearling (Fig. 4).

### BODY WEIGHT AND SPATIAL AND TEMPORAL VARIATION IN PUBERTY IN NORWAY

Yearling ovulation rates varied in space (Table 2) and time (Table 3). Ovulation rates increased significantly from south to north (excluding Hitra: $\chi^2 = 16·4$, d.f. = 2, $P < 0·001$) and from west to east ($\chi^2 = 6·3$, d.f. = 1, $P < 0·01$), as well as varying between the 7 years when animals were shot late enough in the season to overlap the ovulation period ($\chi^2 = 16·8$, d.f. = 6, $P < 0·01$). When body weight was included in the space–time model of ovulation rates in mainland regions, the spatial and temporal variation was no longer significant (Latitude: $\chi^2 = 2·9$, d.f. = 2, $P > 0·1$, Longitude: $\chi^2 = 0·6$, d.f. = 1, $P > 0·5$, years: $\chi^2 = 11·9$, d.f. = 6, $P > 0·05$). Similarly, there was no significant difference in the probability of ovulating at
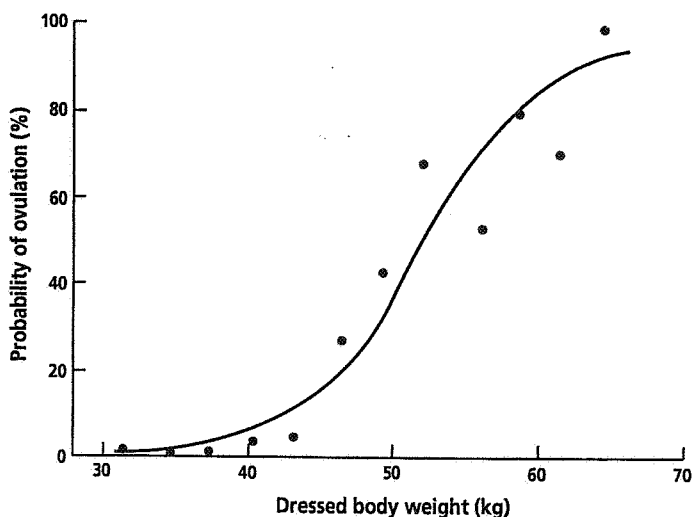
**Fig. 4.** Logistic regression curve showing the relationship between the probability of ovulation and bodyweight in yearling females in Norway. Weights are standardized to 15 November, end of the hunting season. Points are the proportion ovulating in 3-kg weight groups centered about 32, 35, 38, 41, 44, 47, 50, 53, 56, 59, 62 and 65 kg.

a given weight for yearlings sampled on Hitra compared to the mainland ($\chi^2 = 0.6$, d.f. $= 1$, $P > 0.5$). Thus, the substantial spatial and temporal variation in ovulation rates was explained by the geographical and annual variation in body weight.

### CLIMATIC CORRELATES OF SPATIAL AND COHORT VARIATION IN PUBERTY IN NORWAY

In the larger sample of individuals for which we had calculated the proportion calving for the first time at 2 years old, retrospectively, we found, that after accounting for geographical variation (our seven regions), cohort differences were significantly negatively correlated to the accumulated degree days in May and June (standardized about the mean in each region: $\chi^2 = 10.51$, d.f. $= 1$, $P < 0.01$), when the animals were $\approx 12$ months of age. Although none of the other climatic variables were significant when fitted alone (Table 4), there was a significant reduction in the residual deviance associated with May–June degree days in the year of birth (standardized about the mean in each region: $\chi^2 = 4.14$, d.f. $= 1$, $P < 0.05$). Again, the relationship was negative, thus a higher proportion calved for the first time at 2 years of age when accumulated degree days above 6 °C in May and June of the first two summers of life were low. The effect of May–June degree days at 12 months was twice as great as at birth a year earlier (0.0044 and 0.0023, respectively), though the difference was not significant.

Since degree days decline with increasing latitude, the temporal results above would predict that the correlation between the proportion calving for the first time as 2 years old on the mainland and with increasing latitude, arises because of the influence of degree days on the probability of ovulating as a yearling. This was indeed the case, for when we fitted region

specific mean May–June degree days (at 12 months) and relative (between-year) May–June degree days consecutively in a model, excluding Hitra, both were significant (mean May–June degree days: $\chi^2 = 9.87$, d.f. $= 1$, $P < 0.01$; relative May–June degree days: $\chi^2 = 11.14$, d.f. $= 1$, $P < 0.001$). Thus, for mainland populations mean May–June degree days was as good a predictor of regional differences in the proportion calving for the first time at 2 years old as latitude (see Table 5: difference in models $\chi^2 = 0.18$, d.f. $= 1$, $P > 0.9$). In practice, since variation in May–June degree days was a statistically useful predictor of age at maturation, in both space and time, it was equally appropriate to fit the raw, unadjusted values. Figure 5 shows the logistic regression line, predicting the proportion calving for the first time at 2 years old, given May–June degree days ($\chi^2 = 21.00$, d.f. $= 1$, $P < 0.001$), fitted through the observed data for all region-year (cohort) samples. This relationship accounted for 37.5% of the total deviance.

### CLIMATIC CORRELATES OF COHORT VARIATION IN PUBERTY ON RUM

Compared to Norway, maturation was delayed at least a year on Rum, probably because body growth was retarded. Two-year-olds on Rum weighed less than yearlings in Norway (c. 60 vs. 80 kg live wt). Nonetheless, cohort variation in the proportion of females calving for the first time at 3 years of age was significantly related to some of the climatic variables considered in the Norwegian study. High rainfall in the August and September immediately prior to conception in October depressed the number calving for the first time in the following summer ($\chi^2 = 7.42$, d.f. $= 1$, $P < 0.01$). The proportion calving also showed a tendency to decline with increasing number of days snowlie in the winter (January–March) prior

**Table 5.** Deviance explained ($\chi^2$) by region, latitude, coast–inland and climatic variables in the model of proportion of 2-year-olds calving in Norway. The influence of climatic variables is investigated in both the first and second years of life

| | Total deviance 46·95, 76 d.f. | | Total deviance 55·95, 82 d.f. | |
| | First year | | Second year | |
| Explanatory variables | $\chi^2$ | Significance | $\chi^2$ | Significance |
| --- | --- | --- | --- | --- |
| Region (5 d.f.) | 9·81 | $P < 0\cdot1$ | 11·84 | $P < 0\cdot05$ |
| Latitude | 8·30 | $P < 0\cdot01$ | 10·05 | $P < 0\cdot01$ |
| Coast–Inland* | 0·90 | NS | 1·01 | NS |
| Cohort (19 d.f. first year, 20 d.f. second year)* | 13·93 | NS | 16·08 | NS |
| **Degree days** | | | | |
| **May–Jun** | | | | |
| Regional mean | 7·98 | $P < 0\cdot01$ | 9·87 | $P < 0\cdot01$ |
| + Annual variation | 2·08 | NS | 11·14 | $P < 0\cdot001$ |
| Unadjusted values | 8·53 | $P < 0\cdot01$ | 21·00 | $P < 0\cdot001$ |
| **Sep–Oct** | | | | |
| Regional mean | 8·15 | $P < 0\cdot01$ | 9·85 | $P < 0\cdot01$ |
| + Annual variation | 2·25 | NS | 0·58 | NS |
| Unadjusted values | 10·08 | $P < 0\cdot01$ | 3·03 | $P < 0\cdot1$ |
| **Temperature** | | | | |
| **April–May** | | | | |
| Regional mean | 3·79 | $P < 0\cdot1$ | 4·51 | $P < 0\cdot05$ |
| + Annual variation | 0·34 | NS | 0·03 | NS |
| Unadjusted values | 3·70 | $P < 0\cdot1$ | 2·69 | NS |
| **Oct–Nov** | | | | |
| Regional mean | 3·80 | $P < 0\cdot1$ | 4·32 | $P < 0\cdot05$ |
| + Annual variation | 2·37 | NS | 2·20 | NS |
| Unadjusted values | 0·59 | NS | 1·08 | NS |
| **Precipitation** | | | | |
| **May–June** | | | | |
| Regional mean | 7·87 | $P < 0\cdot01$ | 9·10 | $P < 0\cdot01$ |
| + Annual variation | 0·87 | NS | 0·05 | NS |
| Unadjusted values | 1·17 | NS | 4·61 | $P < 0\cdot05$ |
| **Aug–Sept** | | | | |
| Regional mean | 7·38 | $P < 0\cdot01$ | 8·79 | $P < 0\cdot01$ |
| + Annual variation | 0·69 | NS | 0·03 | NS |
| Unadjusted values | 5·51 | $P < 0\cdot05$ | 4·98 | $P < 0\cdot05$ |
| **Snow depth** | | | | |
| **Jan–Mar** | | | | |
| — Regional mean | 6·19 | $P < 0\cdot05$ | 7·47 | $P < 0\cdot01$ |
| + Annual variation | 0·03 | NS | 1·33 | NS |
| Unadjusted values | 3·80 | $P < 0\cdot1$ | 2·05 | NS |

—— * Reduction in residual deviance after fitting latitude.

to conception ($\chi^2 = 3\cdot54$, d.f. $= 1, P < 0\cdot1$). However, snow is comparatively rare (mean number of days snow lie (Jan–Mar) $= 12$ days, max $= 28$) and mean winter daily temperature is probably a more appropriate index of winter severity. Low temperatures in January to March, prior to conception, were associated with lower calving rates in 3-year-olds ($\chi^2 = 8\cdot28$, d.f. $= 1, P < 0\cdot01$).

However, since the population on Rum increased threefold after the cessation of culling in 1972, the proportion of 3-year-olds calving for the first time declined significantly with increasing numbers of resident females ($\chi^2 = 34\cdot08$, d.f. $= 1, P < 0\cdot001$). With-

out accounting for additional factors, density dependence explained nearly 50% of the total deviance.

After controlling for the density-dependent effects, August–September rainfall did not significantly reduce the residual deviance ($\chi^2 = 1\cdot52$, d.f. $= 1$, $P > 0\cdot2$), and the apparent association before statistically accounting for density dependence (described above) probably reflected the fact that rainfall at this time of the year was significantly correlated with the number of resident females ($r = -0\cdot490$, $t_{19} = 2\cdot45$, $P < 0\cdot05$). In contrast, the residual deviance in the proportion of 3-year-olds calving was significantly reduced by the number of days of snowlie

Fig. 5. Logistic regression curve fitted through region–cohort values for proportion of females calving as 2-year-olds in Norway plotted against degree days in each location in May–June each year. Symbols: squares = South, triangles = Intermediate, circles = North; solid symbols = coast, open symbols = inland.

in the winter ($\chi^2 = 6\cdot30$, d.f. = 1, $P < 0\cdot05$) and, also, by April mean daily temperature ($\chi^2 = 6\cdot63$, d.f. = 1, $P < 0\cdot01$) immediately prior to conception. Neither of these climatic variables was significantly correlated to changes in population size.

Earlier research on Rum indicated that, after accounting for density-dependent variation, warm weather in April–May, shortly before birth, was associated with an increased proportion of a cohort calving for the first time 3 years later (Albon, Clutton-Brock & Guinness 1987). Here, in a larger sample of cohorts, the influence of April–May temperature at birth showed a similar relationship after accounting for the density-dependent variation ($\chi^2 = 4\cdot84$, d.f. = 1, $P < 0\cdot05$). When we incorporated both April–May temperature prior to birth and the size of the resident female population, April temperature prior to conception still significantly reduced the residual deviance ($\chi^2 = 5\cdot61$, d.f. = 1, $P < 0\cdot05$).

Finally, as in Norway, age of first breeding was significantly negatively related to May–June degree days in the previous summer ($\chi^2 = 5\cdot77$, d.f. = 1, $P < 0\cdot05$). As accumulated degree days increased the probability of calving at 3 years declined. Thus our best model, accounting for 73% of the cohort variation in the proportion calving for the first time at 3 years old, incorporated four variables that significantly and independently reduced the deviance: population size (Fig. 6a), May–June degree days (Fig. 6b) and April temperature in the year prior to conception, and April–May temperature before birth.

MAY–JUNE DEGREE DAYS, PRIMARY
PRODUCTION AND PUBERTY ON RUM

Measurements of monthly primary production on the preferred herb-rich *Agrostis–Festuca* swards on Rum since 1982 indicated that both May production and June production tended to be higher when the respec-

tive months were warm (May: $r = 0\cdot625$, $P < 0\cdot1$; June: $r = 0\cdot639$, $P < 0\cdot1$). As a result, cumulative production across May and June tended to increase in years when accumulated degree days in these same 2 months was high ($r = 0\cdot601$, $P < 0\cdot1$). June production, which tends to be the month of peak primary production was significantly correlated to accumulated degree days in May and June ($r = 0\cdot709$, $P < 0\cdot05$).

In this more recent sample of cohorts we found evidence that variation in age of first reproduction was directly related to measures of primary production. The proportion calving for the first time at 3 years of age was significantly related to estimates of primary production in May, 12 months earlier (Fig. 7: $\chi^2 = 4\cdot48$, $P < 0\cdot05$). High primary production was associated with few individuals breeding for the first time.

## Discussion

Our results demonstrate that temporal (cohort) and spatial variation in age of first reproduction in female red deer is negatively correlated with May–June degree days immediately prior to the autumn in which conception may occur. In Norway the proportion conceiving as yearlings and calving for the first time at 2 years was associated, proximately, with variation in autumn body weight and, ultimately, with variation in May–June degree days in the second summer of life. Similarly, on the Isle of Rum, Scotland, where the onset of reproduction was delayed at least a year, cohort variation in the proportion calving at 3 years of age, was significantly negatively correlated with May–June degree days, in the third summer of life, after adjusting for density-dependent effects.

On Rum, the monitoring of individuals from birth, together with a more complete understanding of the factors influencing life-history traits (Clutton-Brock
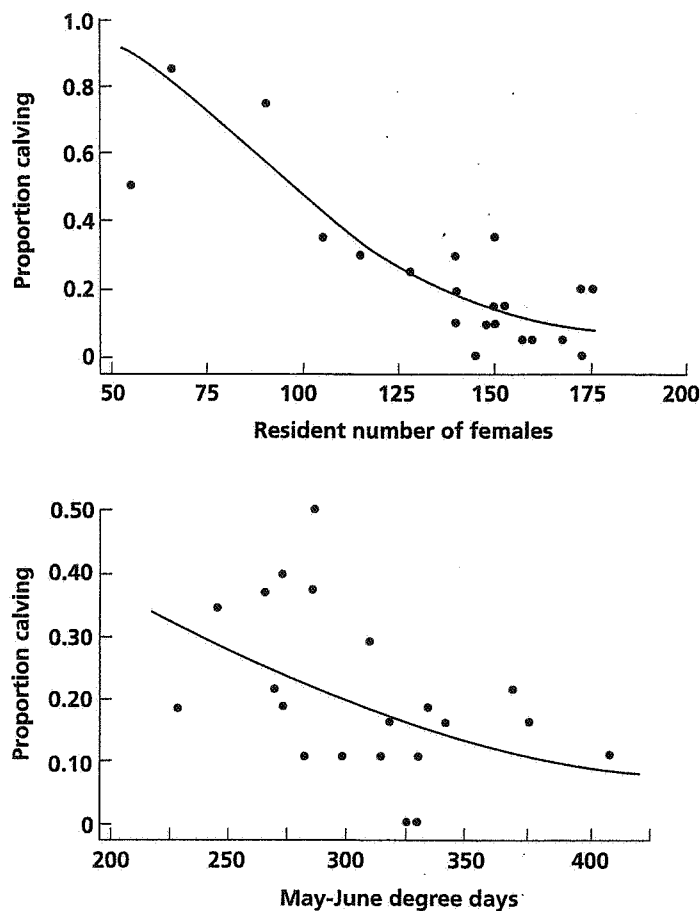
**Fig. 6.** Logistic regression curve illustrating the relationship between proportion of 3-year-old hinds calving in cohorts on Rum and (a) number of females resident in the study area, after controlling for May–June degree days and April temperature in the year of conception, and April–May temperature in the cohorts' year of birth, and (b) May–June day degrees 12 months earlier, after controlling for female population size, April temperature in the year of conception and April–May temperature in the cohorts' year of birth (see text for details).
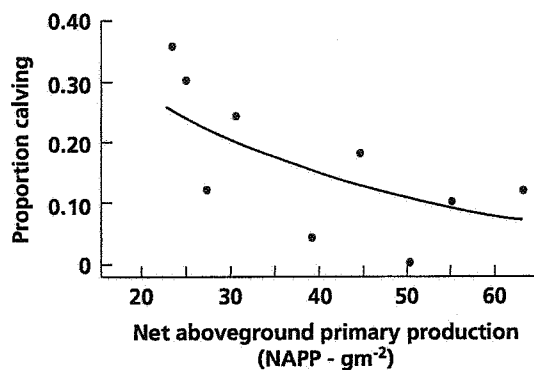


**Fig. 7.** Logistic regression curve showing the relationship between proportion of 3-year-old hinds calving on Rum and nett aboveground primary production (NAPP) on herb-rich *Agrostis–Festuca* swards in May prior to conception in October (see text for details).

reflect that in Norway we had explained a comparatively small proportion of the variance (37·5% compared to 75%). Had we been able to control for more of the confounding variables the estimate for Norway may have been larger.

## TEMPERATURE AND HERBAGE DIGESTIBILITY

The negative relationship between age of reproductive maturation and May–June degree days may seem surprising at first sight because, at least on Rum, cool weather in these months tended to be associated with low grass production. However, in most years, May and June are the main growing seasons at these high latitudes (Wedin *et al.* 1984), and the availability of green biomass is probably rarely limiting. Even in years of comparatively low primary production the biomass is probably close to asymtotic levels of the cervid foraging functional response curve, and thus the effect of biomass on the intake of metabolizable energy is probably of secondary importance compared to forage quality (see Wickström *et al.* 1984). Certainly on Rum, with the relatively heavy grazing pressure at

& Albon 1989), enabled us to control for some of the potentially confounding effects. As a result, the apparent differences in the magnitude of the regression coefficients for May–June degree days between Rum (0·0097) and Norway (0·0044) may

high population density, offtake (defoliation) from the most preferred vegetation communities is lower than production until July or August (Iason, Duck & Clutton-Brock 1986; Gordon 1989). Although, there may be little or no cost of reduced food availability in regions and/or years with low accumulated degree days in May–June, the retarded development of vegetation is beneficial because the digestibility of all plant parts declines more slowly (Deinum *et al.* 1981; Wilson 1982; Deinum 1984; Wedin *et al.* 1984; Albon & Langvatn 1992). In addition, slow maturation of plants increases the leaf:stem ratio and delays the 'dilution' of the sward with relatively indigestible stem and leaf sheath (Terry & Tilley 1964; Deinum 1984). Furthermore, when herbage growth is retarded grazers will crop a greater proportion of production and therefore maintain more of the plants at the highly digestible, immature stage (Illius 1985).

Our results are supported by evidence for elk in Yellowstone Park where the proportion of females with calves at foot, proportion of females with yearlings at foot and the per capita growth rate were all negatively correlated with summer herbaceaous green phytomass (Merrill & Boyce 1991). In this location less green phytomass is available in middle to late summers when spring melt and 'green-up' occurs early. Furthermore, Merrill & Boyce (1991) speculate that in years of high snow accumulation, delayed phenology may provide a higher quality diet for a longer period in late summer and fall than in years of early or average phenological development.

Although we did not have measurements of the chemical composition of the grasses and herbs in our studies, other workers have demonstrated that comparatively small differences in plant digestibility can have a marked influence on growth, particularly in young animals (Blaxter, Wainman & Wilson 1961; see also White 1983). Not only does digestibility reflect metabolizable energy intake but it also influences organic matter intake and, as a result, animals tend to increase herbage intake when plant digestibility is high (Armstrong *et al.* 1986). Since young animals are physiologically programmed, via increasing appetite, to grow rapidly from the end of the first winter (Ryg & Langvatn 1982; Suttie & Hamilton 1983), small differences in digestibility of graminoids in the early summer will have more effect on weight gain to autumn than differences in digestibility later in the season, when plants have reached maturity, senesced, and consequently have relatively low nutritional value.

An alternative explanation for our associations is that low temperature in May–June is associated with high rainfall and this stimulates more grass growth. However, the two climate variables were not negatively correlated and plant biomass at this time of the year was not correlated with rainfall. Furthermore, in Norway regional differences in the proportion calving at 2 years were correlated with rainfall but year-to-year variation was not (Tables 5 & 6).

Although plant digestibility at the start of the growing season is particularly high (see Albon & Langvatn 1992), production in April is typically less than 50% of that in May (T. Clutton-Brock, unpublished data) and therefore the biomass of live grasses at this time may limit the intake of grazing herbivores. Thus, in contrast to May and June, warm weather in April is likely to increase the plane of nutrition by increasing biomass (Albon, Clutton-Brock & Langvatn 1992) with little or no trade-off between quantity and quality of forage. Presumably this relationship explains why the proportion of 3-year-olds calving on Rum was positively related to April temperature immediately prior to conception.

In Norway, unlike on Rum, April is generally a winter month: snow lies deep on all but the lowest, coastal land and even there the number of days when temperature is above the threshold at which grass grows are rare (Appendix 1). However, on the island of Hitra, where the significantly lower pregnancy rate in yearlings was accounted for by substantially lower body weights, spring comes relatively earlier and, like on Rum, cohort variation in age of reproductive maturation was positively related to April temperature immediately prior to conception.

### BIRTH-YEAR EFFECTS

In addition to the effect of May–June degree days immediately prior to conception, we found evidence in Norway of an independent effect of degree days in May–June a full year earlier, around the time of birth, on the proportion of a cohort calving at 2 years old. In contrast, on Rum, we found no significant associations with May–June degree days, either at birth or as yearlings. However, we did confirm earlier observations that the proportion of 3-year-olds calving on Rum for the first time was positively associated with April–May temperatures, shortly before birth (Albon, Clutton-Brock & Guinness 1987). Thus, both in Norway and on Rum, cohort differences in age at maturation were associated with climatic conditions around the time of birth. The apparent difference in the critical months presumably reflects that spring is earlier on Rum (Table 1).

The mechanism underlying the association between spring temperatures, when *in utero*, and the onset of reproductive maturation may reflect a climate-associated energy balance in females at this time of the year (Simpson *et al.* 1978; Parker 1988), when nutritional plane and maternal body condition influence *in utero* growth (Bartmann 1986; Burkey 1989), birth weight, lactation and early calf growth (Thorne, Dean & Hepworth 1976). On Rum grass production in April, which is typically the first month of the growing season, is higher in warmer years and is a good predictor of birth weight (Albon *et al.* 1992).

Although we did not specifically undertake an analysis of the influence of climatic variables on autumn body weight in yearling female red deer in Norway, there is considerable evidence from studies of moose and reindeer that annual variation within a region is associated with the prevailing weather in summer, rather than winter (Reimers, Klein & Soerumgaard 1983; Sæther 1985; see also Skogland 1983). For example, Sæther (1985) found that moose were heavier after cool, dry summers in regions which normally have a humid, maritime, climate (north of 64°N). However, in regions with a drier, more continental climate (inland and south of 60°N), where water supply tends to limit plant development, Sæther (1985) found heavier moose weights after relatively wet summers. Clearly, the contrasting effects of weather on plant phenology and forage digestibility in maritime and continental, temperate climates warrants further study if one is to understand the mechanisms underlying summer weight gain in large herbivores and to predict the demographic consequences.

## SUMMER WEATHER AND PARASITE BURDENS

Although the observed and inferred relationships between climate, plant growth, diet quality, animal growth and body size appear to provide a reasonable explanatory model for variation in age of sexual maturity, other factors may be involved. For example, it has been demonstrated that gastro-intestinal helminths may affect viability and reproductive performance in ruminants (Symons *et al.* 1981; Halvorsen 1986), and that prevalence and intensity of parasite loads tend to increase with population density (Kistner 1982). Moreover, the epidemiology of nematodes is weather sensitive (Taylor & Muller 1974; Armour 1978), and the intermediate free-living, stages appear to proliferate in warm, humid summers (Levine 1963; Gettinby & Paton 1981). Consequently, weather conditions which ultimately may have a negative effect on age of sexual maturation in red deer, through its effect on the resource base, also may enhance the proliferation of parasites to increase prevalence and total parasite load, especially in young individuals (Mason 1977). However, quantifying the effect of confounding factors like reduced plane of nutrition and increased parasite burden on demographic performance may be difficult without well designed experiments (Gulland *et al.* 1993).

## CONCLUSIONS

Although we have had to speculate about the mechanism underlying the association between the age of first reproduction and degree days in May–June the relationship appears to be robust in that we have demonstrated the correlation in two independent populations. Our results suggest a sensitivity to subtle changes in phenology associated with the prevailing temperature in April vs. May–June. We argued that warm weather at the onset of grass growth has positive benefits but high temperatures in May–June lead to low-quality diets as the plants mature quickly and digestability declines (see also Merrill & Boyce 1991). Such a fine-tuned system may have wider implications for the dynamics of herbivore populations. For example, although density-independent, weather-induced, variation in the food resource base was expected to have a pronounced effect on age at maturation, other fitness components including survival of both offspring and adults, are related to body growth and condition (Clutton-Brock & Albon 1989; Owen-Smith 1990) and commonly have more pronounced effects on population dynamics (Fowler 1987). Finally, our findings provide some support for Haldane's (1956) hypothesis that, in more marginal habitats, particularly at the edge of the species' range, density-independent factors are likely to be more important than density-dependent factors (see also Elliott 1987).

## Acknowledgements

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**Appendix 1**

Climatic variables for the Isle of Rum and for each of seven regions in Norway shown in Fig. 1. The values are means (±SD) for the period 1969–91 (Norway) and 1971–91 (Rum). In inland regions in Norway (12, 22, 32) the values are adjusted to an altitude of 250 m a.s.l.

| Region | Month | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Jan | Feb | Mar | Apr | May | June | July | Aug | Sep | Oct | Nov | Dec | Annual |
| **Degree days (>6 °C)** | | | | | | | | | | | | | |
| Isle of Rum | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Norway | | | | | | | | | | | | | |
| 11 (South–coast) | — | — | — | — | — | — | — | — | — | — | — | — | 1109·5(94·0) |
| 12 (South–inland) | — | — | — | — | — | — | — | — | — | — | — | — | 1084·3(116·2) |
| 21 (Interm. coast) | — | — | — | — | — | — | — | — | — | — | — | — | 978·0(78·8) |
| 22 (Interm. inland) | — | — | — | — | — | — | — | — | — | — | — | — | 932·5(116·6) |
| 30 (Hitra) | — | — | — | — | — | — | — | — | — | — | — | — | 885·7(98·0) |
| 31 (North–coast) | — | — | — | — | — | — | — | — | — | — | — | — | 880·1(90·0) |
| 32 (North–inland) | — | — | — | — | — | — | — | — | — | — | — | — | 770·9(147·6) |
| **Temperature** | | | | | | | | | | | | | |
| Isle of Rum | 4·6 | 4·6 | 5·5 | 7·1 | 9·8 | 11·9 | 13·6 | 13·7 | 11·8 | 10·0 | 6·4 | 5·9 | 8·7 |
| Norway | | | | | | | | | | | | | |
| 11 | 0·9(2·9) | 0·3(2·4) | 2·5(1·7) | 5·0(1·1) | 10·0(1·1) | 12·7(1·2) | 14·2(1·2) | 13·9(1·2) | 10·5(1·1) | 8·0(1·1) | 4·0(1·5) | 2·1(2·2) | — |
| 12 | -3·8(3·9) | -3·9(3·2) | -0·3(1·9) | 3·1(1·2) | 8·6(1·1) | 11·9(1·4) | 13·2(1·2) | 12·4(1·3) | 8·3(1·0) | 5·1(1·2) | 0·1(2·0) | -2·4(2·8) | — |
| 21 | 0·2(2·7) | 0·2(2·4) | 2·1(1·6) | 4·4(1·3) | 9·3(1·1) | 12·1(1·2) | 13·6(1·0) | 13·4(1·1) | 9·7(1·2) | 7·1(1·3) | 3·1(1·5) | 1·3(1·5) | — |
| 22 | -2·3(3·0) | -2·4(2·6) | 0·1(1·7) | 3·1(1·3) | 8·3(1·0) | 11·3(1·3) | 12·7(1·0) | 12·0(1·1) | 7·9(1·2) | 5·0(1·3) | 0·8(1·8) | -1·3(2·5) | — |
| 30 | -0·5(2·6) | -0·3(2·3) | 1·6(1·6) | 4·1(1·2) | 8·7(1·3) | 11·4(1·3) | 13·0(1·0) | 13·0(1·2) | 9·7(1·1) | 6·8(1·2) | 2·6(1·5) | 0·7(2·5) | — |
| 31 | -2·3(3·1) | -1·8(2·4) | 0·8(1·6) | 3·6(1·3) | 8·9(1·3) | 12·0(1·5) | 13·6(1·0) | 13·2(1·2) | 9·1(1·2) | 5·8(1·1) | 1·1(1·5) | -0·8(2·8) | — |
| 32 | -6·4(2·6) | -5·8(2·9) | -2·5(2·1) | 1·0(1·6) | 6·9(1·4) | 10·3(1·6) | 11·7(1·3) | 11·1(1·3) | 6·7(1·5) | 3·1(1·2) | -2·3(1·7) | -4·7(3·1) | — |
| **Precipitation** | | | | | | | | | | | | | |
| Isle of Rum | 291 | 172 | 221 | 132 | 107 | 161 | 165 | 162 | 260 | 241 | 342 | 257 | 2511 |
| Norway | | | | | | | | | | | | | |
| 11 | — | — | — | 108·9(53·6) | 95·4(51·1) | 109·7(44·7) | 147·9(75·9) | 181·0(85·7) | 285·1(109·2) | 259·7(117·7) | — | — | 2334·3(1029) |
| 12 | — | — | — | 78·7(44·6) | 79·0(44·5) | 83·4(34·1) | 107·1(59·6) | 138·3(64·4) | 228·4(87·0) | 220·3(111·6) | — | — | 1872·1(546) |
| 21 | — | — | — | 123·2(64·7) | 96·8(49·1) | 92·7(38·2) | 121·0(57·2) | 160·3(54·3) | 294·8(93·1) | 263·5(124·9) | — | — | 2345·0(1199) |
| 22 | — | — | — | 50·7(29·4) | 42·0(18·5) | 50·3(16·2) | 67·3(23·5) | 80·0(25·6) | 141·8(50·7) | 132·7(68·0) | — | — | 1183·4(891) |
| 30 | — | — | — | 77·3(31·8) | 57·2(29·7) | 63·1(30·1) | 92·3(33·8) | 95·6(34·5) | 156·9(60·4) | 148·9(78·3) | — | — | 1210·4(308) |
| 31 | — | — | — | 110·7(56·6) | 65·2(30·3) | 74·2(30·2) | 115·5(43·3) | 110·0(35·6) | 212·5(73·2) | 190·3(117·6) | — | — | 1832·7(1299) |
| 32 | — | — | — | 66·1(31·6) | 49·4(29·0) | 64·9(21·3) | 103·0(34·3) | 83·9(33·1) | 121·5(43·5) | 108·0(61·9) | — | — | 1324·9(1755) |
| **Snow depth** | | | | | | | | | | | | | |
| Isle of Rum* | 4 | 3 | 1 | — | — | — | — | — | — | — | 1 | 2 | 11 |
| Norway | | | | | | | | | | | | | |
| 11 | 8·0(10·1) | 11·2(12·2) | 6·1(9·1) | 0·7(1·2) | 0·0(—) | — | — | — | — | 0·0(—) | 1·3(2·0) | 3·2(4·0) | — |
| 12 | 14·7(12·1) | 19·8(15·1) | 12·2(13·8) | 0·7(1·2) | 0·0(—) | — | — | — | — | 0·0(—) | 2·5(3·1) | 7·0(7·4) | — |
| 21 | 13·8(12·0) | 14·9(14·0) | 12·8(12·1) | 3·5(4·5) | 0·0(—) | — | — | — | — | 0·3(0·6) | 4·0(4·0) | 9·8(8·6) | — |
| 22 | 18·3(17·1) | 25·5(22·0) | 19·0(19·5) | 6·6(9·1) | 0·2(0·2) | — | — | — | — | 0·4(0·2) | 5·0(4·6) | 11·8(11·2) | — |
| 30 | 12·4(13·3) | 17·4(17·3) | 9·3(8·2) | 2·1(1·7) | 0·0(—) | — | — | — | — | 0·2(0·5) | 3·0(3·6) | 7·5(7·3) | — |
| 31 | 34·5(28·1) | 47·2(33·2) | 43·5(28·2) | 22·4(20·1) | 1·7(2·7) | — | — | — | — | 0·7(1·2) | 8·7(8·3) | 20·7(16·1) | — |
| 32 | 59·2(34·7) | 75·4(38·7) | 82·0(35·6) | 59·0(31·8) | 10·3(15·1) | — | — | — | — | 2·4(3·5) | 16·9(15·3) | 38·7(25·5) | — |

* Mornings with snow lie at sea level.