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Antler length of yearling red deer is determined by population density, weather and early life-history

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Abstract In red deer, yearling antler length is a largely nutrition-mediated phenotypic character, and is therefore sometimes used as an indirect estimate of range quality and population condition. However, the parameters affecting yearling antler length have been little studied. We analyse the contributions of density, weather and maternal effects on yearling antler length of 581 individual stags born 1970–1996 on the Isle of Rum (Scotland). We show that antler length is a good measure of yearling condition: the probability of overwinter survival in yearlings that developed antlers was 3 times higher than for yearlings that did not develop antlers, and yearling antler length was correlated with the number of antler points the following year. Between years, variation in yearling antler length was best explained by variation in red deer density and June temperature at 12 months of age. Both of these variables were negatively correlated with antler length, and most likely this effect is due to changes in nutrient availability. Population density affects biomass availability for the individual, while low temperatures in early summer prolong the availability of high forage quality. At the individual level, antler length increased with birth weight and decreased with birth date, reflecting the persistent and pervasive influence of conditions in early life.

Keywords *Cervus elaphus* · Density dependence · Birth date · Birth weight · Viability indicator

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Introduction

Antler quality, especially yearling antler length, is frequently used as a quality index for male cervids, and to evaluate range quality and population condition in continental Europe and the United States (Ullrey 1982; Rasmussen 1985; Raesfeld and Reulecke 1988). In yearlings, antler growth is closely related to the individual's physiological capability and is thus especially sensitive to changes in nutrient availability (Suttie and Kay 1982). Nutrient availability in turn is determined by population density, affecting per capita biomass availability, as well as density-independent stochastic weather parameters, which affect nutritional quality of the available forage.

In red deer (*Cervus elaphus*) yearling antler length is known to be related to changes in population density (Clutton-Brock and Albon 1989), but to our knowledge no study has yet analysed density-independent parameters which might affect yearling antler length and their interactive effects with density. We examined between- and within-cohort variation in yearling antler length, analysing data from 581 individual yearling stags on the Isle of Rum (Scotland) over 24 years. We investigated whether yearling antler length does reflect individual body condition, as measured by winter survival and antler points in 2-year-olds. We determined the relative contributions of density, weather, yearling birth weight and birth date, and maternal effects on yearling antler length.

In the study area, median cohort yearling antler length declined sharply when density increased rapidly after culling had ceased (Clutton-Brock and Albon 1989). At continuously high densities, however, we expect that variation between cohorts will best be explained by density-independent weather effects. As antlers are a sexually selected trait, variation in antler length should best be explained by those parameters that most strongly affect adult male breeding success: spring weather in the year of birth and, at the individual level, birth weight. Spring rain in the cohort's year of birth is positively correlated with mean cohort breeding success (Rose et al. 1998), while April/May temperatures affect birth weight

(Albon et al. 1983; Coulson et al. 1998), which is the main determinant of male lifetime reproductive success (Rose 1995; Kruuk et al. 1999a).

We, therefore, predict that (1) between cohorts, variation in yearling antler length will be positively related to both spring temperature and rainfall in the cohort's year of birth, and (2) within cohorts, antler length will be most strongly related to birth weight. Individual differences in phenotypic traits are also attributable to differences in maternal investment via pre- and postnatal food supply (Bernardo 1996). Maternal investment is affected by maternal phenotype parameters such as mother's cohort (Albon et al. 1987, 1992), age (Guinness et al. 1978; Clutton-Brock et al. 1985a), reproductive status at conception (Clutton-Brock et al. 1989) and sex of the previous year's calf (Clutton-Brock et al. 1981). We hypothesise that, because of the high costs of lactation (Clutton-Brock et al. 1989), mothers that had reared a calf until winter in the year of conception will produce young with shorter yearling antler length.

Materials and methods

We examined antler length in 581 individual yearling stags born between 1970 and 1996. All data were collected in the 12-km² North Block, Isle of Rum, Scotland (57°01'N, 06°17' W, NM-402996); for a detailed description of the study area see Clutton-Brock et al. (1982). Total hind population density tripled during the study years, increasing from 56 in 1971 to a maximum of 191 in 1992.

Definitions of parameters used

The parameters used in this study are defined as follows:

1. *Yearling antler length* is the mean length (cm) of the left and right antler (excluding pedicle) at the age of 16 months. Antler length was estimated on the animal. When checked against cast antlers estimated measures proved to be reasonably accurate. Nearly all data on yearling antler length were collected by one person (F. Guinness), thereby increasing reliability of the data. Yearling antler length data were available for approximately 80% of all yearlings in 24 cohorts born between 1970 and 1993 ($n=581$). The annual yearling population size is shown in Fig. 1.
2. *Antler points* is the combined number of tines on the right and left antler.
3. *Birth date* is given as the number of days after 1 May in the year of birth (Clutton-Brock et al. 1982).
4. *Birth weight* was calculated for calves up to 12 days after birth by subtracting an assumed weight gain of 0.36 kg from the capture weight for each day between birth and capture (Guinness et al. 1978).
5. *Survival* was defined as survival through the second winter until 24 month of age.
6. *Temperature* was calculated as mean monthly temperature, calculated from the mean daily temperature. Data were collected at Kinloch, Rum, 5 m above sea level. Due to equipment failure, there are no temperature data for March, June and July 1995.
7. *Rainfall* is defined as total precipitation (mm) per month.
8. *NAO* (Northern Atlantic Oscillation) is an index for winter (December-March) conditions, combining precipitation and temperature, with high, positive values reflecting warm, moist winters, and low, negative values associated with relatively

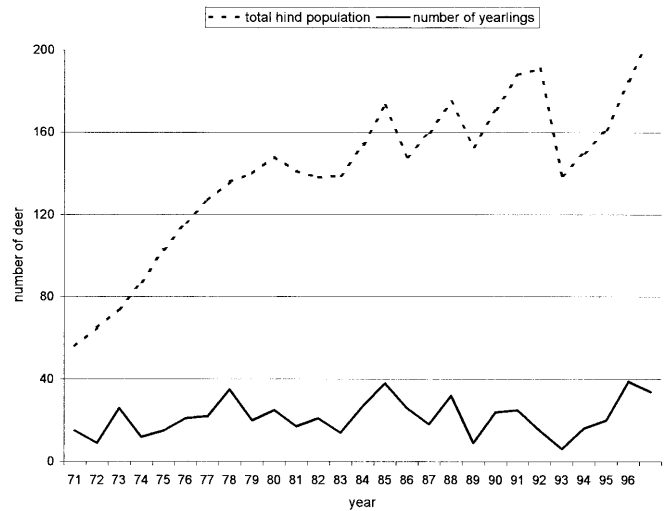


Fig. 1 Changes in total female population size and annual yearling population size for the study years 1970–1997 (yearling cohorts born 1969–1996)

cold and dry winter conditions. The NAO is based on atmospheric pressure between the sub-tropical and the sub-polar North Atlantic region (Hurrell 1995; but see Post et al. 1997 for more detail).

9. *Local female population density* is a measure of the spatial proximity of individuals as calculated by hierarchical cluster analysis (Coulson et al. 1997).
10. *Total female population density* is the number of adult females (≥ 1 year old) resident in the study area in at least 10% of surveys of the study area in at least four months of the year (Clutton-Brock et al. 1982). Because female density has been shown to be more strongly related to several fitness parameters than the combined density of males and females (Clutton-Brock et al. 1985b), we used total female population density as a measure of density. The annual female population size is shown in Fig. 1.
11. *Mother's home range area* was divided into 36 matrilineal groups that ranged within four topographical areas (see Guinness et al. 1978 for detailed description).
12. *Mother's age* is the age of the individual's mother in years.
13. *Mother's reproductive status at yearlings conception*. We differentiated between two categories: non-lactating hinds (summer yields, hinds that had lost their calf before 1 October; in practice most calves died within a week after birth) and lactating hinds, whose calf survived to at least October.
14. *Sex of previous offspring* refers to the sex of the calf born in the year before the respective yearling's birth.

The choice of variables that we used to model yearling antler length was based on their known effects on fitness correlates in red deer and a priori on their expected effect on yearling antler length via their influence on body reserves, nutrient availability or energy expenditure (Table 1).

Statistical analysis

The survival of yearlings was analysed using the Fisher exact test and generalised linear mixed models assuming a binomial error distribution and a logit link function. Stochastic between-year variation and variation between mothers were taken into account by including year and mother as random effects (Littell et al. 1996). The Spearman rank correlation coefficient (abbreviated r_s) was used to evaluate the correlation between antler length of yearlings and the number of antler points they had as 2-year-olds. Where the Pearson correlation coefficient was used it is abbreviated

Table 1 Variables used to model yearling antler length based on their known effects on fitness correlates in red deer and on their expected effect on yearling antler length via their influence on body reserves, nutrient availability or energy expenditure

Variables tested	Known effect of tested variable on:	Expected effect of tested variable on yearling antler length via:
Birth weight	Summer mortality, individual mating success (Guinness et al. 1978; Clutton-Brock et al. 1987a; Rose 1995)	Body size, body reserves, autumn body weight
Birth date	Calf mortality, individual mating success (Guinness et al. 1978; Rose 1995)	Length of milk intake before weaning, weight increase before winter growth check
Total population density	Birth date, calf mortality (Clutton-Brock and Albon 1989)	Per capita biomass availability
Local population density	Calf winter survival (Coulson et al. 1997)	Per capita biomass availability
Mother's home range area		Food quality, availability of shelter
Mother's cohort	First and second generation birth weight and survival (Albon et al. 1992)	Mother's body size and body reserves
Mother's age	Suckling duration (Clutton-Brock and Albon 1989)	Mother's body reserves, maternal investment
Mother's reproductive status in the previous year	Fecundity, date of conception, calf winter survival, birth weight (Albon et al. 1986; Clutton-Brock et al. 1982, 1983, 1989)	Body reserves – lactation
Sex of offspring in previous year	Probability of conception, birth date of subsequent calf (Clutton-Brock et al. 1981; Bérubé et al. 1996)	Mother's body reserves – lactation
Dec-February temp and rain in utero	Body weight, body size (Post et al. 1997)	Mother's energy loss and fetal nutrition
April/May temp in utero	Mean birth weight (Albon et al. 1983)	Plant phenology/ primary production
April/May rain in utero	Mean cohort mating success (Rose et al. 1998)	Mother's energy loss due to thermal requirements, primary production
May-July temp/ rain year of birth	June rain: calf summer mortality (Clutton-Brock and Albon 1989)	Length of growing season – milk quality; thermal requirements for the newborn calf
July-September temp/rain in year of birth	September rain: fecundity in milk hinds, mean calving date, calf winter mortality (Clutton-Brock and Albon 1989)	Plant senescence, length of growing season – autumn body weight and early winter nutrition
Dec-February temp/ rain first winter	Temperature: stag body weight, calves/ 100 hinds in May (Clutton-Brock and Albon 1989)	Energy loss due to thermal requirements
March-May temp/ rain 10/11 month of age		Primary production, thermal requirements
May-July temp/ rain 11-13 month of age	May/June temperature: probability of conception in autumn for primiparous hinds (Langvatn et al. 1996)	Nutrient availability and length of growing season, thermoregulation of newborn calf

ed r . Yearling antler lengths are constrained to be ≥ 0 with many observations equal to zero. This causes the distribution of yearling antler lengths to be non-normal. The effects of environmental factors and phenotype characteristics on yearling antler length were therefore modelled using generalised linear mixed models (Littell et al. 1996) assuming a quasi-Poisson error distribution. Again, stochastic between-year variation and variation between mothers were taken into account by including year and mother as a random effects. The variance in the data increased more with the mean than expected assuming a Poisson distribution. This overdispersion with respect to the Poisson distribution was corrected for by scaling the deviance and variance by the ratio of the residual deviance to the residual degrees of freedom (Littell et al. 1996). The scale was estimated as around 4 in the different models. The predictor variables were assumed to affect yearling antler length multiplicatively through a log link function.

The Wald statistic was used to test for statistically significant effects, and was assumed to be distributed as χ^2 , except for year-dependent covariates for which the Wald statistic were tested against $F_{1,r}$ where r was the residual degrees of freedom of years.

The models were fitted using restricted maximum likelihood. The best model was considered the one where all predictor variables included were significant ($P < 0.05$), and where adding other variables or interaction terms would not improve the fit significantly. Sample sizes vary between years and predictor variables, thus residual degrees of freedom vary concomitantly. All analyses were performed in SAS (Anonymous 1996)

Results

Yearling antler length and body condition

To test whether yearlings that did grow antlers were in better body condition than yearlings which did not grow antlers at all (i.e. only pedicles) we looked for a possible connection between having grown antlers versus no antlers and survival through the second winter. There was a

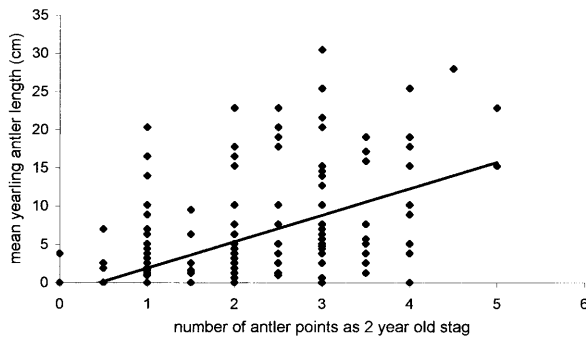


Fig. 2 Correlation between antler length of yearlings (mean of left and right beam for each individual) and number of antler points as 2-year-old stags ($n=581$)

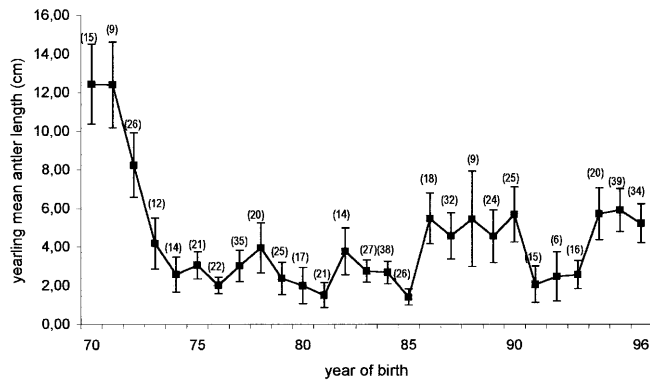


Fig. 3 Mean cohort yearling antler length (\pm SE, cm) for cohorts born 1970–1993 (numbers in parentheses sample size)

significant association between survival and antler growth (Fisher exact test, $P < 0.0001$): in yearlings that had grown antlers survival rate was 87% ($SE=0.03$, $n=137$) as compared to only 61% ($SE=0.05$, $n=85$) in yearlings that had not grown antlers. When the effect of between-year variability in survival were accounted for by fitting year as a random effect in logistic regression, the effect of whether yearlings grew antlers or not was still significant ($\chi^2=11.71$, $df=1$, $P=0.0006$). The main relationship between antler growth and over winter survival appeared to be captured in whether the yearlings grew antlers or not. Fitting yearling antler length as a continuous covariate to the model did not improve model fit significantly ($\chi^2=0.51$, $df=1$, $P=0.48$).

There was a high correlation of yearling antler length and the number of points as a two-year old stag ($r_s=0.67$, $n=317$, $P < 0.0001$) (Fig. 2.), and this relationship was also highly significant within the group that grew antlers as yearlings ($r_s=0.50$, $n=207$, $P < 0.0001$).

Variation between years

Mean yearling antler length varied from a minimum of 1.4 cm (1985 cohort) to a maximum of 12.9 cm (1970 cohort) ($SE=2.1$) (Fig. 3). Median yearling antler length

Table 2 Parameter estimates and standard errors (SE) for the best fitting generalised linear mixed model for yearling antler length using cohort specific predictors. The model was fitted using a log link function and year and mother's identity as random effects. The significance of terms was assessed using F -ratios with 1,19 df (t current year, $t-1$ previous year)

Term	Estimate	SE	P
Intercept	3.32	1.26	
1/Total density ($t-1$)	78.09	28.39	0.01
June temperature (t)	-0.23	0.10	0.03

varied from zero (1979, 1980, 1981, 1985, 1991 cohorts) to a maximum of 14 cm (1970 cohort). Maximum individual antler length was 30.5 cm (1972 cohort). The percentage of individuals with zero antler length varied from a minimum of 7% in the 1970 cohort to a maximum of 67% in the 1981 and 1991 cohorts.

The population densities in the year of birth and year as yearling were highly correlated ($r=0.90$, $P=0.0001$). This made it impossible to disentangle the effects of population density in the two years from each other. Yearling antler length was negatively correlated with total population density in both years, but a model with the inverse of population density at year of birth as a linear predictor described this relationship slightly better (deviance=1736.05, Table 2) than a model using density at year as yearling as linear predictor (deviance=1741.24).

The relatively long antlers the yearlings developed in 1971–1973 (Fig. 3), when the population density was low (less than one-third of the maximum population density during the study years), had a strong influence on this result. When these years were excluded from the analysis the effect of population density was not significant ($P=0.94$).

After correcting for the population density effect by fitting it as a covariate, cohort variation in yearling antler length was best explained by variation in temperature in June at 12 months of age. June temperature ranged from 10.3 to 15.3°C (averaging 12.1°C across study years), and was negatively correlated with mean yearling antler length (Fig. 4, Table 2). June temperature and population density showed a tendency to be positively correlated ($r=0.27$, $n=23$, $P=0.20$), but while the effect of population density on yearling antler length was mainly due to the effects of the low densities in 1971–1973, the effect of June temperature was significant also when fitted as the only predictor in the regression model and the years 1971–1973 were excluded ($F=4.61$, $df=1$, $20 P=0.04$). There was no evidence for a significant effect of April/May temperature ($F=0.01$, $df=1,18$, $P=0.92$) or rain ($F=0.01$, $df=1,18$, $P=0.91$) in year of birth in multiple regression models where density and June temperature were also fitted as predictors.

Variation within years

When population density at birth and June temperature at 12 months of age were fitted as covariates, yearling ant-

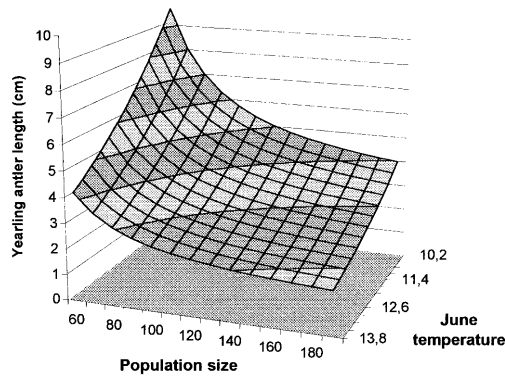


Fig. 4 Predicted mean cohort yearling antler length in relation to population density in year of birth and temperature in June ($^{\circ}\text{C}$) at 12 months of age (parameter estimates are given in Table 2). The model for the predicted yearling antler length was fitted using a log link function so the effect of one of the variables depends on the value of the other at the linear scale even though there was no significant interaction between the two predictors in the statistical model

Table 3 Parameter estimates and SEs for the best fitting generalised linear mixed model for yearling antler length including cohort and individual specific predictors. The model was fitted using a log link function and year and mother's identity as random effects. The significance of terms were assessed using F -ratios with 1,19 df for the cohort-specific variables population density in year of birth and June temperature at 12 months of age, and the χ^2 statistic with 1 df for birth weight and each element of the polynomial model for the effect of birth date

Term	Estimate	SE	P
Intercept	-0.53	1.66	
1/Total density ($t-1$)	80.7	31.8	0.02
June temperature (t)	-0.143	0.096	0.15
Birth date	0.103	0.044	0.02
Birth date \times Birth date	-0.0014	0.0005	0.008
Birth weight	0.151	0.062	0.02

ler length was related to birth date and birth weight (Table 3). Birth date and birth weight were not strongly correlated ($r=0.10$, $P=0.09$). Birth date was fitted as a second-order polynomial, and yearling antler lengths showed an increase and then a decrease with increasing birth date (Table 3, Fig. 5a). Yearling antler lengths increased with increasing birth weight (Table 3, Fig. 5b). June temperature at 12 months of age was not significant when birth weight was included in the model ($P=0.15$). Average birth weight and June temperature the next year were not confounded ($r_s=-0.07$, $P=0.73$) suggesting that the effect of birth weight on the significance of June temperature was mainly due to the reduced sample size when birth weight was included in the model (going from 391 observations with estimates of day of birth to 291 observations with estimates of day of birth and birth weight).

We investigated the effect of maternal phenotype variables by adding them to the model presented in Table 3, but both with and without birth weight as a covariate since including birth weight reduced sample size con-

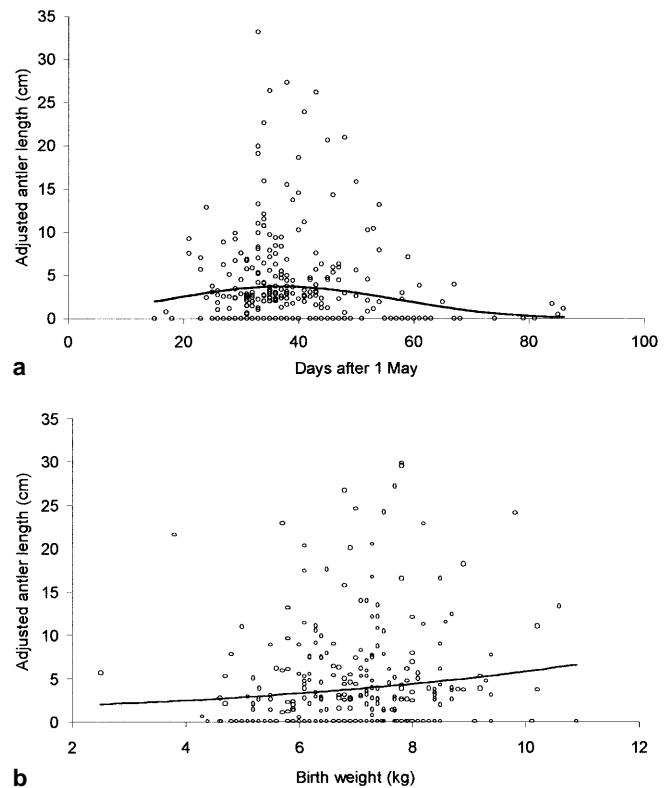


Fig. 5 Yearling antler length in relation to **a** birth date (days after 1 May) and **b** birth weight. Observations plotted are adjusted for the fixed effects of population density at year of birth and June temperature at 12 months of age and **a** birth weight, **b** birth date. The lines give the predicted values for the mean values of the other fixed effects in the model (parameter estimates for the model are given in Table 3)

siderably. None of the maternal phenotype variables – mother's age fitted as a second-order polynomial (with birth weight: $P=0.82$, without birth weight: $P=0.33$), mother's home range area (with birth weight: $P=0.37$, without birth weight: $P=0.13$), local population density around the mother's home range (with birth weight: $P=0.07$, without birth weight: $P=0.11$), sex of previous offspring (with birth weight: $P=0.79$, without birth weight: $P=0.66$) or whether the mother had a calf in October before conception (with birth weight: $P=0.72$, without birth weight: $P=0.18$) – had a significant effect on yearling antler length. Of these maternal phenotype variables, the strongest and most consistent effect across models was a negative effect of local population density around the mother's home range (estimate=-0.0091, SE=0.0049). This suggests that within-year variation in yearling antler lengths is affected by the local population density around the mother's home range when the effect of overall population density has been controlled for.

Discussion

Our analysis corroborates the assumption that yearling antler length was an honest indicator of viability (Kokko

1997): the probability of dying during the second winter was 3 times higher in yearlings that had not grown antlers than in yearlings that had grown antlers. Also, antler length as a yearling was positively correlated with the number of points as a 2-year-old stag.

Yearling antler length was affected both by density-dependent and density-independent effects, and, at the individual level, by birth date and birth weight. Total population density strongly affected variation between cohorts, but only while rapidly increasing after culling had ceased in the area. However, at carrying capacity total density had no effect; only local density around the mother's home range showed a weak tendency to influence antler length.

Contrary to our expectations, cohort variation in yearling antler length was not affected by spring weather in the year of birth, which is known to affect mean cohort breeding success (Rose et al. 1998) and birth weight (Albon et al. 1983; Coulson et al. 1998). The only discernible weather variable affecting yearling antler length was June temperature at the onset of antler growth: mean cohort antler length was higher after a cool June at 12 months of age. An increase in body condition after relatively low early summer temperatures has already been shown for the probability of conception for first breeding hinds on Rum as well as in Norway (Langvatn et al. 1996) and for autumn body mass in moose (Solberg and Saether 1994; Saether 1985) and roe deer fawns (Gaillard et al. 1996). This effect of cool summer weather can best be explained by delayed lignification of the vegetation and a prolonged availability of high quality forage (Wilson 1982; Deinum 1984; Hay and Heide 1984), which enhances weight gain (Langvatn et al. 1996) and in yearling stags concomitantly antler growth. The effect of summer foraging conditions on antler length gives a potential explanation of why during years of high population densities local, but not total, density affects yearling antler length. In the study area, local densities are higher and food competition is more severe during summer than during winter, which also explained why local density had a stronger effect on calf winter survival than total population density (Coulson et al. 1997).

At the individual level, birth date and birth weight most strongly affected antler length in yearlings, with light and late-born individuals growing shorter antlers. This indicates a strong persistence of early life disadvantages, as the males which we had analysed were only those which had survived the strong selection of neonatal and first-winter mortality which is high for light or late-born calves, especially at high densities (Clutton-Brock et al. 1987a). This is less surprising for birth weight, which has a lasting effect on male (Rose 1995; Kruuk et al. 1999a) and female (Albon et al. 1987) lifetime reproductive success.

Under controlled conditions with ad libitum food supply, birth date did not affect weight gain or the onset of puberty in female red deer (Sibbald et al. 1993). The persistent and pervasive influence of birth date on yearling

antler length, a secondary sexual characteristic, shows that the potential for compensatory growth is limited under natural circumstances. In bison, late birth date reduced adult body weight and size, dominance rank and fecundity (Green and Rothstein 1993). Calf growth is significantly affected by summer nutrition (Loudon et al. 1984), so late-born individuals are at a disadvantage due to their smaller body reserves at the onset of winter. For late-born calves the period of milk intake is shorter and milk protein content might be lower, because peak energy requirements, which occur 5–6 weeks after parturition (Loudon and Brinklow 1992), occur at an advanced stage of plant phenology, with lower protein content of the forage. In reindeer, restricted maternal dietary protein:energy intake reduced milk lactose and protein content and consequently calf growth, because lactating reindeer do not mobilise body protein for lactation in order to ensure future fetal investment (Chan-McLeod et al. 1994), a strategy that might also apply to red deer.

In this study we found no effects of maternal phenotypic characteristics on yearling antler length. Maternal phenotypic characteristics were either too weak to measurably influence yearling antler length, or maternal effects were masked by their effect on birth date. Previous studies have shown that reproductive status at conception (lactating vs. yeld) affected birth date (Clutton-Brock et al. 1989) but did not influence yearling antler length (Clutton-Brock et al. 1983; this study). Alternatively, high population densities might have levelled the effects of maternal characteristics on maternal investment, just as high densities reduced the effects of maternal phenotype characteristics on reproductive success (Clutton-Brock et al. 1987b; Kruuk et al. 1999b). At low population densities and a higher variance in antler length, variation in individual yearling antler length might be more strongly related to maternal effects. Part of the variation in yearling antler length within cohorts can also be expected to be based on genetic differences, as this is the case for adult antler length (Williams et al. 1994; Hartl et al. 1995; L.E.B. Kruuk, J.M. Pemberton, J. Slate and T.H. Clutton-Brock, unpublished work) and birth weight (Coulson et al. 1998).

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