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# Sexual dimorphism and intercorhort variation in reindeer calf antler length is associated with density and weather

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**Abstract** We analysed intercohort variability of live weight and antler length of 5,123 reindeer calves. We further assessed the influence of climate and density on the interannual variation in antler length, and discussed sex-specific resource allocation and response to climate variability. Antler length varied significantly among years and between sexes, with interaction between year and sex. Body weight and antler length were highly positively correlated, showed similar intercohort variability, and had a strong allometrical link, suggesting that antler length could be an equally reliable measure of calf condition as live weight. We found a relative measure of antler length (i.e. antler length corrected for the allometric effect of body mass) to be positively influenced by increasing density and May–June precipitation, and also decreasing May–June temperature. We attributed the effect of early summer weather to its influence on forage availability and quality as well as the level of parasitic insect harassment. Gender difference in both the allometric exponents and the interannual variability suggest that young males and females may have different tactics for relative resource allocation towards growth of antlers as compared to body mass. Because antlers are costly to produce, they may be an honest signal of individual quality for both sexes. However, we found gender-specific allometry, as female calves more than males appear to prioritize their antler growth over body mass, especially when resources are limited. Thus, our results suggest that environmental variation may influence the extent of sexual dimorphism in antler length.

**Keywords** Body mass · Environmental variation · *Rangifer tarandus* · Resource allocation · Trade-off

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## Introduction

There is increasing evidence of both density-dependent and density-independent factors, as well as their interaction, affecting life history parameters, and thus population dynamics of northern ungulates (see reviews by Putman et al. 1996; Sæther 1997; Post and Stenseth 1999; Gaillard et al. 2000; Stenseth et al. 2002; Weladji et al. 2002). While density-independent effects (being either direct or indirect) are highly variable in terms of directions or trends (see review by Weladji et al. 2002), studies of density dependence in mammals suggest that increasing population density has an adverse impact on most life history parameters (Fowler 1987; Weladji 2003). However, most studies have focused on body mass, reproductive performance, survival and more recently sex ratio (see review by Weladji et al. 2002: Tables 1, 2).

Secondary sexual traits such as the horns and antlers of ungulates that are particularly costly to grow and maintain (Andersson 1994) year after year have received little attention in this context. Yet, antler length or horn length can be easily measured in the field from both live and dead individuals, and requires less handling than, for example, live body weights. Importantly, antler and horn growth are dependent on and reflect the condition of the animal during the year of growth. To our knowledge, only one study has analyzed the influence of density and climate on antler length (Schmidt et al. 2001); and a few others have assessed the influence of environmental factors (e.g. Giacometti et al. 2002 and von Hardenberg et al. 2004) or resource availability (Festa-Bianchet et al. 2004) on horn growth.

It has been argued that individuals that develop larger antlers may have a better ability to buffer developmental stress than individuals that develop smaller antlers (Markusson and Folstad 1997), and antler length is functionally related to body mass. Because antler size can be related to food availability, as there are large mineral costs as well as energetic costs associated with growing them (e.g. Suttie and Kay 1982; Ullrey 1982), it is likely that factors affecting body mass variation, such as density and climate, will also affect antler length. Indeed, Schmidt et al. (2001) recently showed that density and June temperature best explained variation in antler length in yearling red deer (*Cervus elaphus*) on the Isle of Rum, Scotland. We therefore predict that environmental conditions might also affect antler length variation in reindeer (*Rangifer tarandus*), even after correcting for the allometric effect of body mass.

*Rangifer* are unique among Cervids, with both sexes carrying antlers that begin to grow within weeks after birth (Blake et al. 1998). Antlers presumably provide a selective advantage for female reindeer in intraspecific competition, primarily during foraging, and especially during winter (Skogland 1989), allowing them to have higher dominance status (Holand et al. 2004) than antlerless males during winter and spring. Indeed, males shed their antlers after the rut in October when they use their antlers in competition for mates, whereas reproductive females shed their antlers around calving. Antlers in female reindeer can also be employed in defending newborn calves from predators (Suttie and Webster 1998). It is therefore important in an evolutionary perspective to investigate sex differences in the response of antler development to environmental variation.

We address these questions using 8 years of data from 5,123 reindeer calves of known body mass, sex and antler length in Østre-Namdal (Norway). More specifically, we (1) investigated cohort-specific variation in antler length of both sexes, (2) assessed the allometric relationship between body mass and antler length, (3) tested the hypothesis that antler length is influenced by density and climate, and (4) discussed sex-specific resource allocation (antler growth vs. body growth) and response to environmental variation (antler length). We used a relative measure of antler length, that is, corrected for the allometric effect of body mass, when assessing the influence of climate and density.

## Materials and methods

### Reindeer data

We used data from a semi-domestic reindeer population in Østre Namdal reindeer-grazing area, Nord-Trøndelag County, West coast of Central Norway. The local Reindeer Husbandry Administration Office in collaboration with local reindeer herders collected these data during a project aiming at investigating condition-dependent calf mortality (Ansgar Kosmo, unpublished data). The data are available in the records of the regional reindeer administration office of Snåsa, Nord-Trøndelag, and is described in details elsewhere (Weladji and Holand 2003a, b). Previous analyses tested the effect of winter weather and density on calf live weight and growth (Weladji and Holand 2003a), and on calf sex ratio (Weladji and Holand 2003b), but did not investigate influence of weather and density on antler length. Our dataset included 2,503 male and 2,620 female calves with known antler length, live weight and date of measurement (see Fig. 1 for sample size by year and sex). This is a managed population as all semi-domesticated reindeer population throughout Norway, Sweden, Finland and Russia as they belong to the reindeer herders. However, the density varies greatly between years due to environmental stochasticity (climate) and predators influencing calf survival. This environmental unpredictability in addition to the between year variation in the herders success to gather the herd and hence slaughter according to their plans, imply an adaptive harvesting strategy where density varies greatly.

Following the calving period in the middle of May, reindeer are gathered for calf marking (ear tagging), and live body weight, antler length and sex of calves were recorded, in addition to 'weighing dates' or 'dates of antler length measurement' (hereafter referred to as 'date'). Recorded dates were mainly from mid-July.

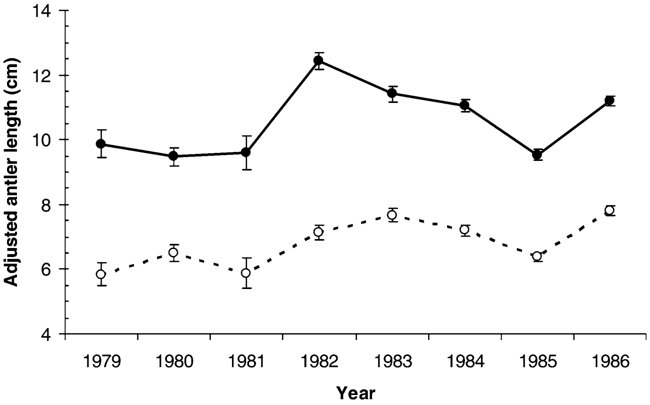

**Fig. 1** Inter-annual variation in mean antler length adjusted for the date of measurement (with error bars) for male (*filled circles* and *solid lines*) and female (*open circles* and *dotted lines*) reindeer calves in Østre-Namdal Norway, during 1979 through 1986. Sample size for each year in sequential order: males, 95, 194, 58, 240, 275, 429, 650 and 562; females, 98, 209, 60, 250, 304, 421, 684 and 594

Antler length is the mean length (cm) of the left and right antler. In order to obtain an index for density, the population size (estimated from a yearly census at the end of March during a round up) was divided by total available range (Reindriftsforvaltningen 1998). During the study period, the density varied between 0.27 animal/km$^2$ and 0.57 animal/km$^2$ (mean = 0.40, SD = 0.10), with no temporal trend.

### Climatic data

Based on previous work relating weather to northern ungulate phenotypic traits (review in Weladji et al. 2002), climatic variables affecting fitness, energetic requirement, and plant phenology were selected (Langvatn et al. 1996). We used mean snowfall from December to March as a winter condition index, and monthly mean temperature and precipitation from May to June as our early summer indices (e.g. Hewison and Gaillard 2001). We considered the winter index in the wintering area, and the summer indices in the summer area as reindeer display migratory patterns within the study area. Values are calculated from Namdalseid weather station (~80 m asl) for the winter area and from Nordli-Holand station (~433 m asl) for the summer area. The meteorological data were obtained from the Norwegian Meteorological Institute, Oslo.

### Data analysis

We used linear models (GLM procedure; SAS 1999) to test the effects of year (cohort effect in this case), and sex as well as their interaction, on the variation in antler length, while including 'date' of measurement, the only continuous independent variable in the models, to account for temporal changes in antler length. From these models, we also generated least square means (lsmeans) of antler length by year and sex (Fig. 1). We compared inter-cohort variability between lsmeans body mass and antler length using the Levene's test that fit any continuous distribution (Levene 1960). Since antler size and body mass are functionally related (see also Fig. 2), we assessed their allometric relationship by applying allometric regression ($y = bx^a$; or log–log regression) separately for male and female, between antler length (the response) and body mass (the predictor) of calves. As we found evidence of an allometric relationship (see Results section), we then used the residuals of each individual from the preceding models when testing the effect of environmental conditions as a measure of relative antler length (RAL), that is, antler length corrected for the allometric effect of body mass.

Environmental effect on antler length was analyzed by mixed linear models with both fixed and random effects (Littell et al. 1996) using the *Mixed* procedure in SAS (1999), version 8 with a 95% level of significance. Because of repeated sampling within a year, 'year' was fitted as a random effect in the model (see e.g. Weladji and Holand 2003a). The following fixed and continuous independent variables were included in the model: 'date', density, winter snowfall, May–June temperature and precipitation. Different models were performed for each sex. There was no correlation between the climatic variables (May–June temperature and May–June precipitation: $r = 0.22$, $P = 0.6$; May–June temperature and winter snowfall: $r = -0.16$, $P = 0.7$; May–June precipitation and winter snowfall: $r = -0.22$, $P = 0.6$). We used the parameter estimates of the models (i.e. comparison of the 'effect size') to discuss the eventual sex-specific effect of weather on the RAL.

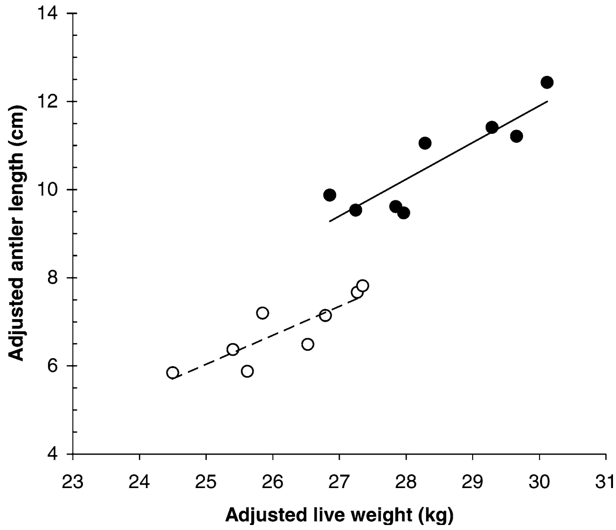

**Fig. 2** Scattergram displaying the relationship between live weight (adjusted for the weighing date) and antler length (adjusted for the date of measurement) for male (*filled circles* and *solid lines*) and female (*open circles* and *dotted lines*) reindeer

## Results

### Cohort and sex-specific variation, and allometric relationship

Antler length varied significantly among cohorts ($F_{7,5106} = 27.71$, $P < 0.001$; Fig. 1) and between sex ($F_{1,5106} = 726.47$, $P < 0.001$; Fig. 1). The interaction between sex and year was also significant ($P < 0.001$), suggesting a gender specific pattern of variation in antler length. Males had on average 3.8 cm (SE = 0.22) longer antlers than female calves. Adjusted yearly mean of body mass and antler length showed similar inter-cohort variability (Levene's test statistic = 0.02, $P = 0.9$), also reflected by the high correlation between the two phenotypic traits (male: $r = 0.89$, $P = 0.003$; female: $r = 0.86$, $P = 0.007$; Fig. 2). Accordingly, we found the relationship between antler length and body mass to be allometric [i.e. allometric exponent *a* expected to be 3 as it relates a volume (here body mass with power of 3) to a length (here antler length with a power of 1); Huxley

1932] for both male ($2.72 \pm 0.04$, df = 2501, $P < 0.001$, $R^2 = 0.70$) and female ($3.11 \pm 0.05$, df = 2614, $P < 0.001$, $R^2 = 0.60$) calves. RAL also varied significantly between years for both male ($F_{7,2494} = 18.05$, $P < 0.001$) and female ($F_{7,2607} = 21.24$, $P < 0.001$) calves.

### Effect of environmental condition

Decreasing early summer temperature (male: $F_{1, 2496} = 18.20$, $P < 0.001$; female: $F_{1, 2609} = 18.26$, $P < 0.001$; Table 1, Fig. 3a), and increasing early summer precipitation (male: $F_{1, 2496} = 3.73$, $P = 0.05$; female: $F_{1, 2609} = 6.04$, $P = 0.014$; Table 1, Fig. 3b) had a positive effect on RAL. Density-dependence was expressed through a positive effect of density on RAL (male: $F_{1, 2496} = 5.25$, $P = 0.02$; female: $F_{1, 2610} = 8.79$, $P = 0.003$; Table 1). Although not significantly different, the effects of environmental variation (i.e. early summer weather and density) on RAL were, on average, higher on females than on males (parameter estimates and standard errors in Table 1). The effect of ‘date’ was positive and significant, whereas the effect of winter snowfall was not significant (Table 1).

## Discussion

Antler lengths of calves were highly variable among cohorts. The variability in antler length was induced by the combined effect of density-dependent and density-independent factors experienced by cohorts in utero and during their postnatal period of early summer. Indeed, even after the allometric effect of body mass was removed, variation in RAL was sensitive to environmental conditions. Increasing population density while calves were in utero, increasing May–June precipitation and decreasing May–June temperature all positively influenced the relative measure of antler length for both male and female calves. Several other studies have shown effects of environmental conditions on inter-cohort variation in life history traits and population dynamics of large herbivores (see review by Putman et al. 1996; Sæther 1997; Gaillard et al. 2000; Weladji et al. 2002; Stenseth et al. 2002), including reindeer (Weladji 2003).

**Table 1** Parameter estimates and standard errors (SE) from the mixed model describing the response of the relative measure of antler length of males and females to density and weather variables. Significant parameters ($P \leq 0.05$) are from the model excluding non-significant terms (reduced model). Denominator degrees of freedom were 2,496 for males and 2,609 for females

| Dependent variables | Estimate | SE | *P* |
|---|---|---|---|
| Males | | | |
| Date | 0.00151 | 0.0002 | < 0.001 |
| Density the winter calves were in utero | 0.26070 | 0.1158 | 0.025 |
| December–March snow fall | 0.00003 | 0.0002 | 0.853 |
| May–June precipitation | 0.00028 | 0.0001 | 0.040 |
| May–June temperature | −0.02326 | 0.0049 | < 0.001 |
| Females | | | |
| Date | 0.00178 | 0.0003 | < 0.001 |
| Density the winter calves were in utero | 0.40600 | 0.0867 | < 0.001 |
| December–March snow fall | 0.00030 | 0.0002 | 0.204 |
| May–June precipitation | 0.00048 | 0.0002 | 0.005 |
| May–June temperature | −0.03393 | 0.0061 | < 0.001 |

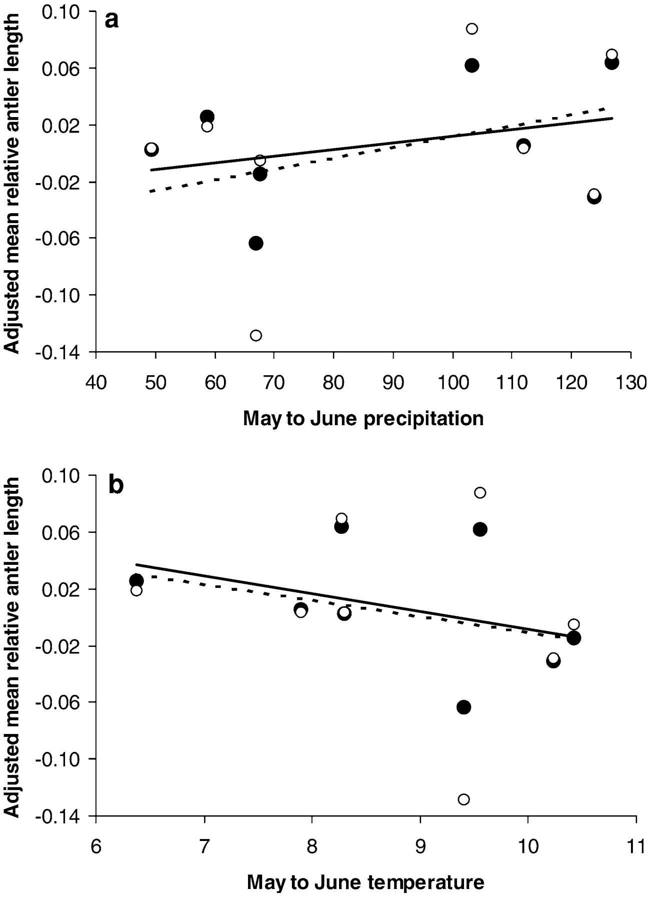

**Fig. 3** Variation in mean relative antler length (RAL) (adjusted for calf sex and the date of measurement) for male (*filled circles* and *solid lines*) and female (*open circles* and *dotted lines*) reindeer calves in relation to (**a**) May–June precipitation (mm) and (**b**) May–June temperature (°C)

As expected in *Rangifer*, a highly sexual size dimorphic species, male calves had longer antlers (e.g. Wika 1980; Blake et al. 1998) than females. Overall and for both sexes, live weight and antler length were positively correlated and showed similar intercohort variability. Indeed, both phenotypic traits showed a strong allometric relationship. Because male calves are heavier (Weladji and Holand 2003a, b) and have longer antlers than females (this study) in this population, and as sexual dimorphism in antler length was largely explained by the difference in body mass, RAL did not differ between sexes. This supports the view that body size is one of the most important life history traits (Calder 1996).

That the effect of density on RAL was positive might seem surprising, but this may also reflect differential tactics of individuals towards various phenotypic traits like body mass and antler length. Indeed, a negative effect of increasing population density on live body mass of this population have been shown (Weladji and Holand 2003a), and was attributed to increased intra-specific, winter competition resulting in reduction of the per capita food availability while in utero (through the mother by affecting foetal growth: see e.g. Skogland 1984 for *Rangifer*) and after birth (neonatal resource limitation) (see e.g. Reimers et al. 1983 and Skogland 1983 for *Rangifer*). Given the high correlation between live weight and antler length in this population, the effect of density on antler length is also expected to be negative. Indeed, reduced resource availability has been reported to negatively affect antler growth or length (Wika 1980; Scribner et al. 1989; Schmidt et al. 2001), as well as horn growth (Festa-Bianchet et al. 2004). The reported positive effect of density on RAL could be caused by the removal of the allometric effect of body mass on antler length. Indeed, live weight was, largely, a linear function of population density (Weladji and Holand 2003a) and increased population density would certainly lead to increased competition. That the relative allocation of resource towards antler growth (in comparison to body growth as measured by the RAL) is higher at high density suggests a real investment into antler, leading us to argue that antlers are important for both male and female calves. Longer antler is reflected in higher social rank in this population (see Holand et al. 2004), beneficial in both intrasexual and intersexual competition.

The effect of early summer weather variables on RAL could partially be attributed to variation in forage quality and quantity. Increased precipitation is expected to favor plant growth, that is, increased biomass, while temperature changes have potentially more influence on the forage quality. That both precipitation and temperature were important predictors of variation in RAL suggests that a combination of both quality and quantity of the forage determine the relative growth of antlers in summer. Indeed, appropriate proportion of nutrients, water, light and heat are necessary for optimal plant growth (Jurïsson and Raave 1984). We found increased temperature to significantly reduce RAL, most likely through its influence on the phenological development of forage plants. This is in accordance with recent findings by Schmidt et al. (2001) for red deer. Several other studies have shown a relationship between ungulate condition and the conditions of the summer range (Reimers et al. 1983; Sæther et al. 1996; Hjeljord and Histøl 1999), with cool early summers being favorable for weight gain (Langvatn et al. 1996) and antler growth (Schmidt et al. 2001; this study). During cool summer weather, lignification of the vegetation is delayed; thereby extending the period when high quality forage is available by increasing the crude protein:dry matter ratio (Jonasson et al. 1986; Laine and Henttonen 1987). Another potential, but not mutually exclusive, explanation is an increase in parasitic insect harassment towards reindeer, and especially calves, with increasing temperature and moisture. Insect harassment would have a similar effect through decreasing time spent feeding (reduced intake) and increasing an individual's energy expenditure (Colman et al. 2002; Weladji et al. 2003), thus decreasing growth (of e.g. antlers). Calves are especially susceptible to the negative effects of insect harassment through direct losses, but also indirectly through a potential decrease in their mother's lactation and allocated suckling time.

Antler length inter-cohort variability confirms the potential for a cohort effect caused by physical condition experienced by pregnant females. Antler size is important for breeding success for males and winter and spring foraging success for females (Prichard et al. 1999). Moreover, it has been shown that the conditions under which individuals are born may have important long-term consequences for the cohort's life history (Albon et al. 1992; Forchhammer et al. 2001; Gaillard et al. 2003 for a review on deer; see also Solberg et al. 2004). These suggest that the conditions experienced by female reindeer during pregnancy, and thereby their offspring, could persist throughout a calf's life span (see e.g. Adams and Dale 1998), as we show for antler length in reindeer (see electronic appendix S1).

The allometry between antler length and body mass was gender specific, being positive for females (i.e. antler length increased proportionally faster than body mass; $a > 3$) and negative for males (i.e. body mass increased proportionally faster than antler length; $a < 3$). Indeed, compared to male calves, female calves likely prioritize antler growth over body mass, as shown by their significantly higher allometric exponent (especially in poor years with reduced resources). This is likely caused by male calves having higher body mass threshold for winter survival than females, and may therefore have a more risky allocation strategy (Loison et al. 1999; see also Clutton-Brock et al. 1982). Our study therefore demonstrates significant sexual dimorphism in allometry. This suggests that female calves may be directing proportionally more resources to antler growth, as compared to other nutritional costs related phenotypic traits such as body mass. They may thereby enhance their competitive ability for food (in winter/spring), and when sexually mature secure their access to dominant males through intrasexual competition, and/or their attractiveness to males, be more successful in intersexual competition and, lastly be able to provide security to their offspring after calving. Indeed, in semi-domestic reindeer, antlers provide females a social advantage during rut, winter and calving (Espmark 1964, 1971) and, thus, have an important social function (Reimers 1993; Holand et al. 2004). Female reindeer need larger antlers to aggress and repel young bulls during the rut, and to secure access to feeding craters during winter for themselves and their offspring (Reimers 1993). This suggest a sexual difference in the resource allocation strategy for growth of various life history traits and for reproduction (see LeBlanc et al. 2001). Accordingly, Festa-Bianchet et al. (2004) found that as resources become scarce, young bighorn rams allocate an increasing proportion of those resources to body growth rather than to horn growth, thereby increasing their probability of survival. Solberg et al. (2004) recently reported sex-specific difference in the magnitude of the effects of environmental conditions at birth on adult body mass, being more influential on males than females. Timing of antler growth differs between reindeer sexes (see Blake et al. 1998), so any environmental influence on condition/growth that operates seasonally might also influence the sexes differently for this trait (see Solberg et al. 2004 for evidence on body mass). Our results lend support to the hypothesis that environmental variation influences the extent of sexual dimorphism (Post et al. 1999) in antler size. Indeed, the cohort variation in antler length was gender specific.

Finally, our analysis suggests that antler length is a phenotypic trait as good as live body mass for signalling individual quality for male and female reindeer, and that antler length is hence an indicator of viability (Kokko 1997; Ditchkoff et al. 2001). This has already been proposed for several large herbivore populations (reindeer: Markusson and Folstad 1997; red deer: Schmidt et al. 2001; white-tailed deer *Odocoileus virginianus*: Ullrey 1982; Rasmussen 1985; Ditchkoff et al. 2001; moose *Alces alces*: Solberg and Sæther 1993). Horn size has also been proposed to be an 'honest' signal of individual quality (Festa-Bianchet et al. 2004; von Hardenberg et al. 2004). Because factors affecting antler growth and length are important for breeding success (Prichard et al. 1999), because cohort effects are widespread in deer populations (Gaillard et al. 2003), and because intra-specific competition favor individuals with large antlers (e.g. Clutton-Brock 1982; Barrette and Vandal 1985), we suggest that antler length, which is easily recorded in the field, could be used when selecting superior animals for future reproduction. Indeed, we also found antler length to increase with increasing age, and show that on average, individuals with long antlers as a calf also have long antlers as an adult (see Fig. S1 in electronic appendix S1). This has important implications for the semi-domestic reindeer husbandry and slaughtering practices, as well as wild reindeer population assessments and management decisions. Trophy hunters should be aware that removals of superior animals might have undesirable evolutionary consequences (see Coltman et al. 2003).

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## References

Adams LG, Dale BW (1998) Reproductive performance of female Alaskan Caribou. J Wildl Manage 62:1184–1195

Albon SD, Clutton-Brock TH, Langvatn R (1992) Cohort variation in reproduction and survival: implications for population demography. In: Brown RD (ed) The biology of deer. Springer, Berlin Heidelberg New York, pp 15–21

Andersson M (1994) Sexual selection. Princeton University Press, Princeton

Barrette C, Vandal D (1985) Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. Behaviour 97:118–146

Blake JE, Rowell JE, Suttie JM (1998) Characteristics of first-antler growth in reindeer and their association with seasonal fluctuations in steroid and insulin-like growth factor 1 levels. Can J Zool 76:2096–2102

Calder WA (1996) Size, function, and life history. Dover Publication Inc., Mineola

Clutton-Brock TH (1982) The function of antlers. Behaviour 79:108–125

Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of the two sexes. University of Chicago Press, Chicago

Colman JE, Pedersen C, Hjermann D, Holand Ø, Moe SR, Reimers E (2002) Do wild reindeer exhibit grazing compensation during insect harassment? J Wildl Manage 67:11–19

Coltman DW, O'Donoghue P, Jorgenson JT, Hogg JT, Strobeck C, Festa-Bianchet M (2003) Undesirable evolutionary consequences of trophy hunting. Nature 426:655–658

Ditchkoff SS, Lochmiller RL, Masters RE, Hoofer SR, van den Bussche R (2001) Major-histocompatibility-complex-associated variation in secondary sexual traits of white-tailed deer (*Odocoileus virginianus*): evidence for good-genes advertisement. Evolution 55:616–625

Espmark Y (1964) Rutting behaviour in reindeer (*Rangifer tarandus* L.). Anim Behav 12:159–163

Espmark Y (1971) Antler shedding in relation to parturition in female reindeer. J Wild Manage 35:175–177

Festa-Bianchet M, Coltman DW, Turelli L, Jorgenson JT (2004) Relative allocation to horn and body growth in bighorn rams varies with resource availability. Behav Ecol 15:305–312

Finstad GL, Prichard AK (2000) Growth and body weight of free-range reindeer in western Alaska. Rangifer 20:221–227

Forchhammer MC, Clutton-Brock TH, Lindström J, Albon SD (2001) Climate and population density induce long-term cohort variation in a northern ungulate. J Anim Ecol 70:721–729

Fowler CW (1987) A review of density dependence in populations of large mammals. Curr Mammal 1:401–441

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31:367–393

Gaillard J-M, Loison A, Toïgo C, Delorme D, Van Laere G (2003) Cohort effects and deer population dynamics. Ecoscience 10:312–320

Giacometti M, Willing R, Defila C (2002) Ambient temperature in spring affects horn growth in male alpine ibexes. J Mammal 83:245–251

Hewison AJM, Gaillard JM (2001) Phenotypic quality and senescence affect different components of reproductive output in roe deer. J Anim Ecol 70:600–608

Hjeljord O, Histøl T (1999) Range-body mass interactions of a northern ungulate—a test of hypothesis. Oecologia 119:326–339

Holand Ø, Gjøstein H, Losvar A, Kumpula J, Smith ME, Røed KH, Nieminen M, Weladji RB (2004) Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. J Zool 263:365–372

Huxley JS (1932) Problems of relative growth. Methuen, London

Jonasson OW, Bryant JP, Stuart Chapin FS III, Andersson M (1986) Plant phenols and nutrients in relation to variations in climate and rodent grazing. Am Nat 128:394–408

Jurïsson T, Raave L (1984) Influence of climatic conditions on the yield and quality of grassland in Estonia. In: Riley H, Skjelvåg AO (eds) The impact of climate on grass production and quality. Proceedings of the 10th general meeting of the European grassland federation, Ås-Norway, 26–30 June 1984, pp 339–350

Kokko H (1997) Evolutionary stable strategies of age-dependent sexual advertisement. Behav Ecol Sociobiol 41:99–107

Laine KM, Henttonen H (1987) Phenolics/nitrogen ratios in the blueberry *Vaccinium myrtillus* in relation to temperature and microtine density in Finnish Lapland. Oikos 50:389–395

Langvatn R, Albon SD, Burkey T, Clutton-Brock TH (1996) Climate, plant phenology and variation in age at first reproduction in a temperate herbivore. J Anim Ecol 65:653–670

Leblanc M, Festa-Bianchet M, Jorgenson JT (2001) Sexual dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. Can J Zool 79:1661–1670

Levene H (1960) Robust tests for the equality of variance. In: Olkin I (ed) Contributions to probability and statistics. Stanford University Press, Palo Alto, pp 278–292

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS system for mixed models. SAS Institute Inc., Cary

Loison A, Langvatn R, Solberg EJ (1999) Body mass and winter mortality in red deer calves: disentangling sex and climate effects. Ecography 22:20–30

Markusson E, Folstad I (1997) Reindeer antlers: visual indicators of individual quality? Oecologia 110:501–507

Post E, Stenseth NC (1999) Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339

Post E, Langvatn R, Forchhammer MC, Stenseth NC (1999) Environmental variation shapes sexual dimorphism in red deer. Proc Natl Acad Sci USA 96:4467–4471

Prichard AK, Finstad GL, Shain DH (1999) Factors affecting velvet antler weights in free-ranging reindeer in Alaska. Rangifer 19:71–76

Putman RJ, Langbein J, Hewison AJM, Sharma SK (1996) Relative roles of density-dependent and density-independent factors in population dynamics of British deer. Mamm Rev 26:81–101

Rasmussen GP (1985) Antler measurements as an index to physical condition and range quality with respect to white-tailed deer. NY Fish Game J 32:97–113

Reimers E (1993) Antlerless females among reindeer and caribou. Can J Zool 71:1319–1325

Reimers E, Klein DR, Sørumgård R (1983) Calving time, growth rate and body size of Norwegian reindeer on different ranges. Arctic Alp Res 15:107–118

Reindriftsforvaltningen (1998) Ressursregnskap for reindriftsnæringen. Reindriftsforvaltningen. Alta, Norge (Report in Norwegian)

Sæther BE (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends Ecol Evol 12:143–149

Sæther BE, Andersen R, Hjeljord O, Heim M (1996) Ecological correlates of regional variation in life history of a large herbivore, the moose *Alces alces*. Ecology 77:1493–1500

SAS Institute Inc (1999) The SAS system for Windows, release 8.01. SAS Inst. Inc., Cary, NC, USA

Schmidt KT, Stien A, Albon SD, Guinness FE (2001) Antler length of yearling red deer is determined by population density, weather and early life-history. Oecologia 127:191–197

Scribner KT, Smith MH, Johns PE (1989) Environmental and genetic components of antler growth in white-tailed deer. J Mammal 70:284–291

Skogland T (1983) The effect of density dependent resource limitation on size of wild reindeer. Oecologia 60:156–168

Skogland T (1984) The effects of food and maternal condition on fetal growth and size in wild reindeer. Rangifer 4:39–46

Skogland T (1989) Comparative social organisation of wild reindeer in relation to food, mates and predator avoidance. Z Tierpsychol [Suppl] Advances in ethology, vol 29. Parey, Berlin

Solberg EJ, Sæther BE (1993) Fluctuating asymmetry in the antlers of moose (*Alces alces*)—does it signal male quality? Proc R Soc Lond Ser B 254:251–255

Solberg EJ, Loison A, Gaillard J-M, Heim M (2004) Lasting effects of conditions at birth on moose body mass. Ecography 27:677–687

Stenseth NC, Mysterud A, Ottersen O, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. Science 297:1292–1296

Suttie JM, Kay RNB (1982) The influence of nutrition and photoperiod on growth of antlers of young red deer. In: Brown RD (ed) Antler development in Cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, pp 61–71

Suttie JM, Webster JR (1998) Are arctic ungulates physiologically unique? Rangifer 18:99–118

Toïgo C, Gaillard J-M, Michallet J (1999) Cohort affects growth of males but not of females in alpine ibex (*Capra ibex ibex*). J Mammal 80:1021–1027

Ullrey DE (1982) Nutrition and antler development in white-tailed deer. In: Brown RD (ed) Antler development in Cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, pp 49–59

Von Hardenberg A, Bassano B, Aranz Md-PZ, Bogliani G (2004) Horn growth but not asymmetry heralds the onset of senescence in male Alpine ibex (*Capra ibex*). J Zool 263:425–432

Weladji RB (2003) Climatic Influences on the Life History and Population Dynamics of a Northern Ungulate, *Rangifer tarandus*. PhD Thesis, Agricultural University of Norway

Weladji RB, Holand Ø (2003a) Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. Oecologia 136:317–323

Weladji RB, Holand Ø (2003b) Sex ratio variation in reindeer: a test of the extrinsic modification hypothesis. Wildl Biol 9:29–36

Weladji RB, Klein DR, Holand Ø, Mysterud A (2002) Comparative response of reindeer/caribou and other northern ungulates to climatic variability. Rangifer 22:33–50

Weladji RB, Holand Ø, Almøy T (2003) Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. J Zool 260:79–85

Wika M (1980) On the growth of reindeer antlers. In: Reimers E, Gaare E, Skjennberg S (eds) Proceedings of the 2nd international Reindeer/Caribou symposium, Røros, Norway, 1979. Direktoratet for vilt og ferskvannsfisk, Trondheim, pp 416–442