Climate-dependent allocation of resources to secondary sexual traits in red deer

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Fitness in highly polygynous male ungulates is related both to body size, weight and antler size. Males must therefore allocate resources both to growth of the body and growth of the antlers, which may lead to tradeoffs whenever resource levels are in limited supply. Several studies have reported how (absolute) growth of antlers and horns are related to environmental conditions, but few have looked for the relative allocation patterns (i.e. relative to body size and weight). We analyzed how the influence of variation in climate (the North Atlantic oscillations, NAO) and population density affected the allocation of resources to antlers, based on data from 2720 red deer stags two years or older harvested during 1965–2002 along the west coast of Norway. Number of antler tines increased up to six years of age, remained stable until 12 years of age, and then decreased significantly (>12 years, n =45). The NAO was positively related to number of antler tines in prime aged males (6–12 years, n =629), also after controlling for both body size and weight. Our study thus suggests that deer have a higher allocation of resources to antlers relative to body weight during favorable environmental conditions.

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Sexual selection is widely accepted as the main evolutionary force of extravagant male ornaments (Darwin 1871, Andersson 1994). Among the most spectacular examples are antlers of Cervidae and horns of Bovidae, which have evolved as a result of intense inter-male competition for mates (Clutton-Brock et al. 1980, Coltman et al. 2002). That inter-male competition for mates is a key factor in the evolution of morphology in highly polygynous male ungulates is evidenced from the fact that both sexual body size dimorphism (Weckerly 1998, Loison et al. 1999b) and antler size (Clutton-Brock et al. 1980) is positively correlated with the level of polygyny. Males fight for access to females during a short rutting season to increase their reproductive success (Clutton-

Brock et al. 1982, 1988). Male quality is therefore closely correlated to fighting ability, which in turn is correlated with body size and age (Clutton-Brock 1982, Clutton-Brock et al. 1982). Even though antler fights can lead to severe injuries (Kitchen 1974, Geist 1986), such fights are often highly ritualised, and both antlers and horn are suggested to function both as a signal and a weapon (Goss 1983).

Antler size has a direct effect on fitness also after controlling for differences in body size (Kruuk et al. 2002), and antlers are believed to be an honest advertisement of male quality (Clutton-Brock 1982, Solberg and Sæther 1993, Ditchkoff et al. 2001b). For example, the number of parasites may influence antler symmetry

and development (Markusson and Folstad 1997, Ditchk-off et al. 2001a). In order to avoid cheating, a signal should bear some costs to the signaler (Zahavi 1975). According to a simulation model, the energy needed for growing antlers is about 50% compared to the energy used for building summer fat and protein deposition in moose (*Alces alces*) (Moen et al. 1999). Since antlers are costly to produce, their growth is affected by environmental conditions (Sæther and Haagenrud 1985, Schmidt et al. 2001). Density-dependent and density-independent factors such as climate may have profound effects on life history traits of ungulates, but less is known regarding similar effects on secondary sexual traits such as antler size.

In this study, we analyze how number of antler tines from 2720 red deer stags two years or older harvested during 1965–2002 along the west coast of Norway (Table 1), varies as a function of age, density and climate, before and after controlling for body size and weight. We test the following hypotheses:

H$_1$. Age-pattern

Ungulates go through juvenile, sub-adult, prime-age and senescent stages with performance typically peaking during the prime-age stage (Caughley 1966, Gaillard et al. 1998). Decline in performance traits with age after prime-age (i.e. senescence; Kirkwood and Austad 2000), has been documented for a number of ungulates for body weight (Mysterud et al. 2001c), reproduction (Ericsson et al. 2001) and survival (Loison et al. 1999a). We test specifically whether there is senescence in number of antler tines for which there are few accounts in the literature. The only record we could found was for moose, which antlers were larger for 7–9 years old when compared to older males pooled (Sæther and Haagenrud 1985). In a recent, very thorough analysis of red deer on Rum, Scotland, there was no evidence of senescence in antler size up to 16 years of age (Kruuk et al. 2002).

H$_2$. Environmental variation

In bighorn sheep (*Ovis canadensis*), size of horns decreased with increasing density for males under four years of age (Jorgenson et al. 1998). In subadult males, horn growth for a given body mass became progressively smaller with decreasing resource availability, while adult rams grew slightly more horn for a given body mass as resource availability decreased (Festa-Bianchet et al. 2004). As antlers are cast each year in contrast to horns, patterns with regard to density dependence may be different. In moose, antler size did not display a density-dependent response despite a density dependent decline in body mass (Solberg and Sæther 1994),

suggesting a higher relative allocation to antlers at high density. Similarly, no density effect was found in elk, while both spring and winter climate affected antler size in elk (Smith 1998). Horn growth of alpine ibex (*Capra ibex*) was faster in years with early onset of plant growth (Giacometti et al. 2002). In red deer on Rum, Scotland, increasing population density and summer temperature negatively affected antler size in both yearling (Schmidt et al. 2001) and prime-aged males (Kruuk et al. 2002), but the allocation pattern was not assessed. For our population, we predict fewer antler tines with increasing environmental harshness; either due to H$_{2a}$ severe climate (low NAO values; Mysterud et al. 2000, 2001b) or H$_{2b}$ high density (Mysterud et al. 2001c, 2002). We specifically explored whether any relationship was simply due to climate or density affecting body size or weight, or whether there was different allocation of resources to antler growth for a given weight depending on environmental variation.

Material and methods

Study area

The study area is along the west coast of southern Norway, which is the main distribution range for red deer in Norway (Langvatn et al. 1996, Mysterud et al. 2000). The vegetation on the west coast of Norway is mostly in the boreonemoral zone (Abrahamsen et al. 1977). A more thorough description of the study area is given elsewhere (Mysterud et al. 2001a, 2002).

Red deer data

Data on number of points (or tines) from left and right antler were available from 5246 male red deer (of which 2720 were ≥2 years) sampled during the annual autumn (usually between 10 September and 15 November) harvest 1965–2002 (Table 1). These deer are a subset of the deer used in the extensive analysis of body weight in these populations (Mysterud et al. 2001b, 2002, Yoccoz et al. 2002), but the data on number of antler tines has never been analysed before. Hunting is controlled through licenses issued by local wildlife boards in each municipality. In addition to data on number of antler points, hunters provided mandibles from all animals shot, together with records of date of culling, locality (municipality) and body weight. Body weight is dressed weight (58% of live weight), i.e. live weight minus head, skin, viscera, bleedable blood and metapodials (Langvatn 1977). In cervids, the correlation between total weight and dressed weight is above 0.99 (Wallin et al. 1996). Most animals were aged using annuli in the cementum of the first incisor (Reimers and Nordby 1968, Hamlin et al. 2000), only younger animals

Table 1. Sample sizes (total also including size data), overall mean antler size (number of spikes) and body size (jawbone size in cm) for age classes of male red deer at the west coast of Norway.

Age	Antler size (no. of tines)															Mean	n	Body size
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16			
2	82	32	174	112	853	163	229	57	31	5	1					6.0	1739	26.88
3	3	3	27	37	237	116	208	99	129	43	30	2				7.8	934	28.10
4		2	5	11	55	31	78	64	105	58	64	6	1			9.1	480	28.74
5			4	5	36	23	41	33	69	49	71	6	5			9.6	342	29.11
6			7	5	7	6	17	22	33	41	60	12	2			10.2	212	29.46
7	1		2	1	10	6	12	14	38	23	39	6	5			10.1	157	29.47
8			1	1	7	9	12	5	10	20	23	8	2	1		10.1	99	29.54
9		1	1	2	2	4	3	6	15	10	20	9	3			10.4	76	29.63
10				2		1	3	5	6	4	4	2	3	2		10.6	32	30.15
11						6	4	1	4	5	7	4	2		1	10.5	34	29.83
12						1	1	3	4	4	2	1	3			10.8	19	29.59
13	1		1		1		1		3			1				7.9	8	28.24
14			1		2	2	1	1		1	3					8.5	11	29.91
15					1		1		2		1					9.2	5	28.27
16					1				1							8.0	2	30.10

(calves and yearlings) were aged by pattern of tooth eruption (Loe et al. 2004). We use jawbone length as a proxy for body size (Langvatn 1977).

To validate whether number of tines reflect total volume of antler or not, we explored the relationship between the two size variables based on detailed data on size measurements of antlers from 148 males (2 to 10 years of age) derived from Songli research station (Langvatn and Hanley 1993) in Sør-Trøndelag, Norway. There was a linear relationship between (ln) number of tines and (ln) total antler volume for males aged between 6 and 10 years (n = 76, Fig. 1, $r^2 = 0.322$), whereas the sample size for 2-year-old males (n = 13) were too limited to provide a certain assessment. Also on Rum, Scotland, was a close correlation between several aspects of antler size and the number of antler points in red deer reported (Clutton-Brock et al. 1982). It is therefore likely that the total number of antler points is a good proxy for antler size. We exclude yearlings that usually have

Fig. 1. The relationship between number of antler points and total volume for males aged between 6 and 10 years old (dotted lines indicates 95% confidence intervals).

spikes, since spike length is a better measure of size for yearlings (Schmidt et al. 2001).

Environmental and other covariates

Other covariates used in the present study are similar to those reported in analyses of body weight (Mysterud et al. 2001a, 2001b, 2001c, 2002, Yoccoz et al. 2002), and only a brief description is given here.

Current density is total number of red deer harvested each year divided by the so-called "qualifying area" in each municipality (used area for 2000 for all years; Statistics Norway 1977–2000; as in Mysterud et al. 2001a, 2001b, 2001c, Yoccoz et al. 2002), and reflects both spatial and temporal variation in density. The "qualifying area" is the area of suitable red deer habitat within each municipality, constituting the basis for harvest quotas as approved by the management authorities (Statistics Norway 2002). The red deer population has been increasing steadily, and the harvest has increased 10-fold from 1965 to 2002. The density increase is also evident from the number of deer killed in traffic, even after controlling for increase in traffic (Mysterud 2004). It has therefore likely been under-harvesting in the sense that the harvest is smaller than the annual production. The body weights are still decreasing (R. Langvatn, unpubl.), indicating that the population size is still increasing, i.e. we have not yet reached a situation of overharvesting. This index is therefore likely a reliable measure of density for the study period due to a fairly similar harvesting regime. We also calculated density for the year of birth, called cohort density. This is correlated with current density so we did not use both in the same model (6–12 yr olds: r = 0.892).

As an index for winter weather, we used the North Atlantic oscillation (NAO; Hurrell 1995, Hurrell et al. 2003, Stenseth et al. 2003) for the previous winter
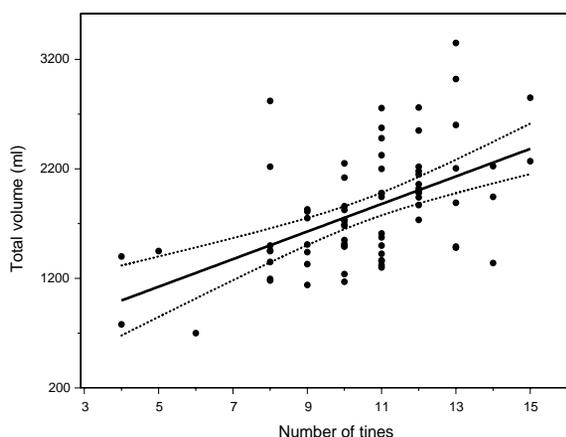
(NAO-previous winter) and in year of birth (cohort NAO). The NAO is positively correlated with precipitation and temperature during winter (Dec-Mar) along the west coast of Norway. Since temperatures in coastal, low land regions often are around 0°C during winter, and since temperature declines with altitude, altitude is a key factor determining whether precipitation comes as rain or snow. There is a negative correlation between the NAO and snow depth at low altitude (below 400 m a.s.l.), whereas there is a positive correlation between the NAO and snow depth at high altitude (Mysterud et al. 2000). Forage in the field layer is thus more easily available during winters with a high NAO index. Further, more snow in the high-elevation summer areas will lead to a prolonged period of access to high quality forage during summer (Mysterud et al. 2001b). A high NAO value is in general correlated positively with body weight (Mysterud et al. 2001b).

Geographic or topographic covariates were proportional to high altitude habitat, diversity of altitudes and aspects, distance from the coast and degree of latitude (Langvatn and Albon 1986, Mysterud et al. 2001a), and the categorical covariate "population" (Forchhammer et al. 1998, Mysterud et al. 2002). Counties Rogaland and Hordaland are referred to as population "P1", Sogn og Fjordane as population "P2", Møre og Romsdal and Sør-Trøndelag as population "P3", and Nord-Trøndelag as population "P4". The island Hitra is referred to as population "P5". We also included the proportion of "high calcium" bedrock (i.e. containing soluble and consisting of up to 56% CaO) in each municipality (a number ranging from 0 to 0.92) (Loe et al. 2004), since possibly, mineral content may affect antler development.

Statistical analyses

We used a combination of linear models (LM), linear mixed-effects models (LME) and additive models (AM; Hastie and Tibshirani 1990) to analyze variation in number of antler tines. A logarithmic transformation of number of antler tines (ln[no. of antler tines]) was used in order to get residuals with constant variance when using LM and LME. AM with smoothing splines was used to explore possible non-linear relationships graphically.

After initial analysis of the full dataset to describe age pattern, we considered in more detail all ages from 6 to 12 yr of age as prime-age (no age effect was detected within these age classes), and from 12 yr and older to test for senescence (H_1). The reason for this split is partly because of a strong correlation between age and body size, and partly because data are from the rutting season in which males of different ages loose weight at different rates (Yoccoz et al. 2002). It is therefore not sufficient to enter body weight, but also date of culling to control for this decrease in condition. When pooling too many age

classes in one model, there are expected rather complex interactions between predictor variables "age", "date of culling" and "body weight" (Yoccoz et al. 2002), and modeling attempts with a global model showed that models were sensitive to what factors were included.

We standardized (mean 0, variance 1) the relevant predictor variables to facilitate the interpretation of the interaction and polynomial terms (Mysterud et al. 2000, 2001c). The NAO index is already standardised (it is defined as a normalised pressure difference, and standardized over a longer time period than our study; Hurrell 1995). When variables are standardised, the coefficient for a variable included in an interaction term is the strength of this variable when the other variables in the interaction are average (because the interaction term is then zero). For a second-order polynomial, the linear term represents the slope at the average, and the quadratic term the curvature at the average.

We used the Akaike's information criterion (AIC; Burnham and Anderson 1998, Johnson and Omland 2004) to find a parsimonious model, i.e. a compromise between explaining most of the variation and simultaneously using as few parameters as possible. Automatic selection procedures are not necessarily reliable as, for example, a third-order polynomial may give a much better fit than a first-order (i.e. linear) polynomial, but a second-order may not. We therefore explored models with higher-order polynomials, as well as interaction terms systematically. The detailed strategy of model selection is given in the electronic appendix (O14197 at www.oikos.ekol.lu.se). The choice of models used in the selection procedure was partly based on biological reasoning, as we expect part of any environmental effect on antler size to operate through body size and weight. We therefore first analyzed variation in number of antler tines without body size or weight included, and we then added first body size and then weight to the most parsimonious model without body size or weight.

With hunter collected data, it is always important to consider the possibility for biases in the sampling procedure. Before 1990, we had antler data from as much as 92.4% of the males for which we have data on body weight. Collection of antler data were close to zero between 1991 and 2001, before we reentered this into data schemes in 2002, but only 55.9% reported antler data from 2002. Overall, there was no difference in weight between animals with and without antler size reported at age two. However, for prime-aged animals it was a consistent pattern that hunters reported antler data from on average somewhat larger individuals (on average about 5 kg difference). For prime-aged males, we therefore rerun the final models excluding data after 1990 to see whether this affected parameter estimates notably. As results were qualitatively identical, we have

no reason to believe that bias affected our results (electronic appendix).

Analyses were performed in S-Plus 6.1 and 6.2 (Venables and Ripley 1994, Crawley 2003).

Results

The number of antler points (tines) increased markedly from two to six years of age, and then remained stable until 12 years of age (Fig. 2). After this, number of antler tines decreased significantly (Table 2), in support of H_1. There was large variation in number of antler tines within age classes (Table 1). Number of tines varied between 2 and 12 in 2 yr old males and between 2 to 16 for prime-aged males (Table 1).

Prime-aged males (6−12 yr of age)

Number of antler tines was positively correlated with the NAO and negatively with density in year of birth (Table 3, Fig. 3). Average number of tines was 10.4 and 11.6 respectively, after low (−2) and high (4) NAO index winters for males born at low density in population "P1". For males born at high density, number of tines was 9.5 and 10.6, respectively, after low and high NAO index winters (in population "P1"). The most parsimonious model included only body size up to third order and body weight up to second order, i.e. number of antler tines increased with body size and weight, but at a diminishing rate. The interaction between st(date) and st(ln[body weight]) was also significant, which reflects that animals loose condition during the rutting season (Yoccoz et al. 2002). Number of antler tines increased with a high NAO-index the previous winter also after controlling for both body size and weight. The effect of the NAO (previous winter) also remained significant
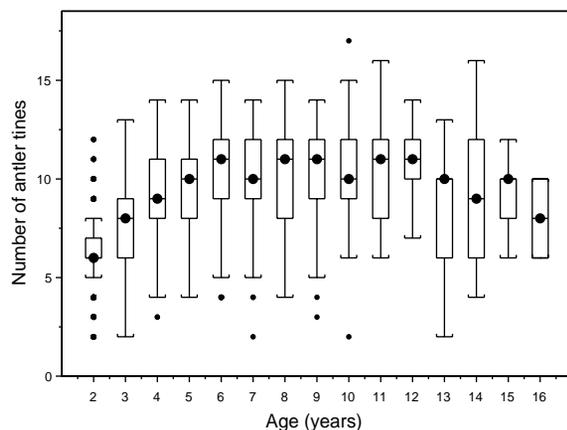

Fig. 2. The relationship between total number of antler points and age viewed as box plots not controlling for other factors.

Table 2. Parameter estimates for analysis of antler size (ln[no. of tines]) of red deer males aged 12 years and older ($r^2 = 0.348$).

	l.s. estimate	SE	T	P
Intercept	−19.6006	6.59		
Age	−0.0962	0.0465	−2.0679	0.0468
ln(jawbone size)	4.0501	1.1522	3.5151	0.0013

when using a LME model with year as a random effect (l.s. estimate = 0.0191, SE = 0.0080, df = 23, T = 2.384, P = 0.026), providing evidence for a higher relative allocation of resources to antler growth during favorable climatic conditions. After controlling for both body weight and size (set to average), number of tines was 10.2 vs 11.2 respectively after low and high NAO winters, for low density in population "P1"). The effect of cohort density was no longer significant after entering both body size and weight (average number of tines was 10.2 and 9.9 respectively at low and high density, at low NAO index in population "P1"), suggesting that the decreased number of antler tines with increasing density worked through body condition.

Thus, environmental variation related to the NAO and population density both affected absolute number of antler tines, lending support to H_2, while only the NAO affected the relative allocation to antlers.

The proportion of calcium rich bedrock within each municipality did not enter the most parsimonious models, except for one model and it was not significant when running the model (Table 3).

Discussion

Antlers are regarded as reliable indicators of quality and are costly to produce, and it was therefore not surprising that they were affected by environmental variation (H_2; Sæther and Haagenrud 1985, Solberg and Sæther 1994, Schmidt et al. 2001, Kruuk et al. 2002). More interesting is the relative allocation of resources to body size, weight vs antler size. In prime-aged red deer, the effect of climate (the NAO) remained even after controlling for both body size and weight. This provides evidence for a greater allocation of resources to antler growth during favorable climatic conditions. In contrast, there was a negative effect of population density only on absolute number of antler tines, and not on number of antler tines relative to body weight (Table 3). If there are tradeoffs, one may expect a negative relationship between body weight and antler size. However, in our case, since we do not have longitudinal data, large individuals also have large antlers.

The pattern of antler size development with age was largely different than that for conspecifics on Rum, Scotland (Kruuk et al. 2002). There was no further increase in number of antler tines after six years of age in

Table 3. Parameter estimates (least-square estimates and standard errors) and test statistics from the model analyzing variation in ln(antler size) for prime aged (6–12 yr old) males in Norway (A: model excluding body size and weight; $r^2 = 0.224$; B: model with size but without weight included; $r^2 = 0.381$; C: model including both size and weight; $r^2 = 0.466$). The reference level for population is 'P1'. Other parameters are given as the differences between levels.

	l.s. estimate	SE	T	P
A. Excluding body size and weight				
Intercept	2.4488	0.0793		
st(cohort density)	−0.0441	0.0163	−2.701	0.007
NAO (previous winter)	0.0183	0.0072	2.535	0.012
Latitude	−0.0245	0.0157	−1.558	0.120
Population P2-P1	0.0691	0.0656	1.052	0.293
Population P3-P1	0.0973	0.1101	0.883	0.378
Population P4-P1	0.1510	0.1725	0.875	0.382
Population P5-P1	−0.0368	0.1276	−0.289	0.773
B. Including body size, excluding weight				
Intercept	2.4048	0.0726		
st(ln[body size])	0.1173	0.0188	6.240	0.000
st(ln[body size])^2	−0.0422	0.0100	−4.197	0.000
st(ln[body size])^3	−0.0078	0.0040	−1.937	0.054
st(cohort density)	−0.0301	0.0149	−2.022	0.044
NAO (previous winter)	0.0198	0.0065	3.052	0.002
Latitude	−0.0142	0.0142	−0.998	0.319
Population P2-P1	0.0682	0.0590	1.157	0.248
Population P3-P1	0.0117	0.0998	0.118	0.907
Population P4-P1	0.0655	0.1617	0.405	0.686
Population P5-P1	0.0306	0.1150	0.266	0.790
C. Including body size and weight				
Intercept	2.3780	0.0772		
st(ln[body size])	0.0530	0.0217	2.437	0.015
st(ln[body size])^2	−0.0148	0.0108	−1.376	0.170
st(ln[body size])^3	−0.0026	0.0042	−0.616	0.539
st(ln[body weight])	0.0844	0.0189	4.461	0.000
st(ln[body weight])^2	−0.0408	0.0094	−4.329	0.000
st(date)	0.0434	0.0125	3.470	0.001
st(date) × st(ln[body weight])	−0.0245	0.0116	−2.114	0.035
st(cohort density)	−0.0172	0.0150	−1.144	0.254
NAO (previous winter)	0.0163	0.0067	2.427	0.016
Latitude	−0.0057	0.0153	−0.374	0.709
Population P2-P1	0.0130	0.0622	0.210	0.834
Population P3-P1	−0.0699	0.1076	−0.650	0.516
Population P4-P1	−0.0491	0.1689	−0.291	0.771
Population P5-P1	−0.0070	0.1221	−0.058	0.954

Norway (Fig. 2), while antler size peaked at 10 yr of age on Rum (Kruuk et al. 2002). Further, on Rum there was no significant decrease in antler size after prime age up until 16 yr of age. In contrast, number of antler tines decreased significantly and quite markedly after 12 yr of age in Norway (Fig. 2). While red deer on Rum live in open habitat with females forming large parties, party sizes in the forested areas in Norway (and France, Bonenfant et al. 2003) are much smaller averaging around 1.5 (Loe et al. 2005). From this pattern, we would expect stronger sexual selection on Rum than in Norway, and therefore likely earlier senescence on Rum, which is opposite of what was observed. Possibly, this is related to an earlier age of maturation in the Norwegian populations, which may be related to a better habitat and/or that populations are heavily harvested (Mysterud et al. 2005). However, although we regard it as less likely, we cannot fully exclude the possibility that our results are due to hunter selectivity, if hunters preferentially shot the largest males first thus biasing results.
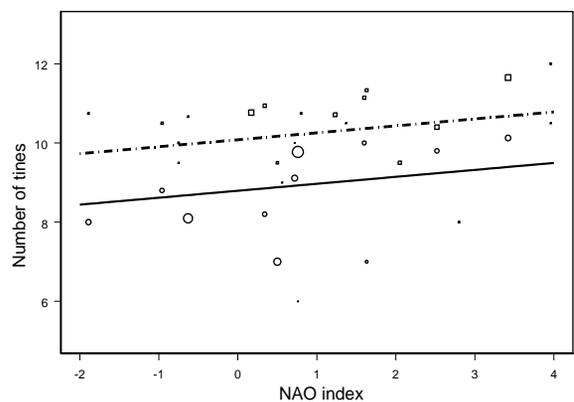

Fig. 3. The relationship between number of antler points and the North Atlantic oscillation for male red deer born at low (squares) and high (circles) density along the west coast of Norway. The size of squares and circles are directly proportional to the number of observations for a given value. Note that the analyses were done on ln-transformed values, and the figure is not adjusted for other factors affecting number of tines such as "population" and body weight.

We also found marked geographical differences (populations) in number of antler tines after controlling for a number of factors such as body weight and density. Geographical variation in antler size in moose were not reflecting variation in body weight (Sæther and Haagenrud 1985). Regional differences in antler size were also reported in white-tailed deer (*Odocoileus virginianus*), and were suggestively due to soil fertility (Strickland and Demarais 2000). If vegetation indeed contains different amounts of the minerals necessary to produce antlers or horns, there may therefore be substantial spatial variation in costs of producing secondary sexual traits such as antlers and horns. We may therefore expect variation in antler sizes even when the social environment (i.e. party sizes) is similar. However, we failed to find that the average calcium content in bedrock in each municipality affecting number of antler tines. Whether this reflect that minerals are not that important in our area, or that our measure is too coarse scale (Loe et al. 2004), remains to be determined.

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