CHANGES IN THE RELATIONSHIP BETWEEN PALMATE AND CERVINE ANTLERS IN MOOSE (*ALCES ALCES)* IN SOUTHEASTERN NORWAY

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ABSTRACT: Moose (*Alces alces*) have evolved 2 antler morphs; palmate and cervine. Using data from 1,186 antlers collected from moose harvested in southeastern Norway during 1950-1997, I tested the widely held hypothesis that the cervine morph has become the predominant antler type in Norway. The antlers were categorized according to palmate, intermediate, and cervine form. I also used quantitative measurements of tines (average length and number) to study trends in morphology. An adaptive landscape method was used to study a combination of the relative number of tines and relative tine length. Since 1950, the palmate morph decreased significantly by 0.52% per year ($P = 0.002$), while the cervine morph increased significantly by 0.39% per year ($P = 0.008$). Number of tines decreased in the palmate morph, but there was no trend in tine length. The intermediate morph increased in the number of tines and decreased in tine length, while the cervine morph showed no trends in morphology. Combined for all morphs in the adaptive landscape, the relative number of tines decreased and relative tine length increased throughout the time series, indicating a change toward more cervine antlers in southeastern Norway. The causes for this change are discussed in relation to frequency-dependent selection and density/social stress hypotheses.

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Moose (*Alces alces*) have evolved 2 main antler morphs (Collett 1912, Sckuncke 1949, Bubenik 1973, Rülker and Stålfelt 1986, Andersen and Saether 1996, Engan 1998). The cervine antler morph has few, rough, and long tines, but no palm (Bubenik 1973). It is distinguished by monopodic branching, with 2 real tines, a brow tine, and an eye tine (Bubenik 1973). The palmate morph has a distinct palm with many thin and short tines, and can have both monopodic and dichotonic branching.

Cervine antlers are common among young bulls, and it is difficult to separate a developing palmate antler from a cervine one (Rülker and Stålfelt 1986). An important difference is that the beam in a developing palmate antler is triangular, while the beam in a cervine antler is rectangular (Rülker and Stålfelt 1986).

The distribution of the morphs worldwide is interesting from an evolutionary biogeographical perspective. Cervine antlers are common in Manchurian moose (*A. a. cameloides* ; Jia et al. 1994) and European moose (*A. a. alces* ; Voippio 1952, Markgren 1982, Saether and Haagenrud 1985, Engan 1998). Cervine antlers are rare in North America, where mature bulls with cervine antlers are found in the subspecies *A. a. americana*, but are absent in the 3 subspecies *A. a. gigas, A. a. shirasi*, and *A. a. andersoni* (Gasaway et al. 1987). In moose from northern Siberia (*A. a.*

pfizenmayeri), only 5% of mature bulls exhibit cervine antlers (Egorov 1965). Thus, an important taxonomic difference between European and North-American moose is the high occurrence of cervine antlers in mature bulls (Geist 1998).

In the 20th century, hunters and zoologists in Norway debated the question of moose antler morphology with the prevailing view that cervine antlers were most common. Collett (1912) claimed that the cervine morph had become more common in some places in Norway. Lykke (1960) disagreed with this view, however, because many bulls with strong palmate antlers were killed in the 1950s. That debate lacked empirical evidence, thus, I aimed to investigate 2 main questions using data over a 47-year period: (1) has the cervine morph become the predominant moose antler type in Norway; and (2) what factors determine this feature?

STUDY AREA

The study area (79,344 km^2) encompasses 7 counties in southeastern Norway (Fig. 1): (1) Østfold; (2) Oslo; (3) Akershus; (4) Hedmark; (5) Oppland; (6) Buskerud; and (7) Vestfold (59°N to 62° 40' N, 7°30'E to 12° 35' E). Approximately 45-50% of all moose shot in Norway are harvested in this region yearly. For example, during the 1997 hunting season, 16,924 of 36,059 moose shot in Norway were harvested in this region. (Statistics Norway 1998).

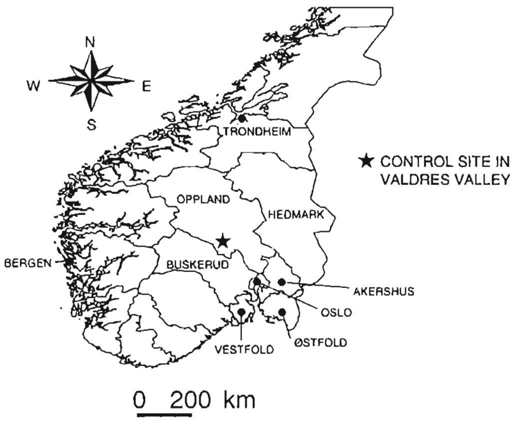

Fig. 1. Map of the study area, showing the 7 counties in southeastern Norway, and the control site in Valdres Valley.

The physical geography of southeastern Norway is diverse. The bedrock geology ranges from Precambrian to Permian in age (Sigmond et al. 1984). The climate ranges from temperate (C-climate, with unstable snow cover, coldest average month temperature above -3°C, and more than 4 months above 10°C in summer) around the Oslo fjord, through snowy forest (D-climate, with more permanent snow cover, coldest average month temperature below -3°C, and 1-3 months above 10°C in summer) in the interior, to an alpine climate (E-climate where the warmest month in the year is below 10°C) at higher elevations (Klemsdal 1983, Strahler and Strahler 1994). The landscape is split in major valleys in a northwest-southeast direction, with low mountains between the valleys. Eskers and tills are common, especially in the east (Thoresen 1990). In the western part of the region, there are more alpine mountains, with the highest point 2,469 meters above sea level. The human use of the area is intense, where forestry, agriculture, roads, railways, villages, and towns dominate the landscape.

The vegetation composition is diverse and mosaic. Major forest types are Bilberry forests and Cowberry forests (Tomter 1994). The vegetation zones range from boreonemoral, with mixed temperate deciduous and coniferous forests, to boreal regions dominated by coniferous forests, to alpine tundra zones above the timberline. The dominant tree species are pine (*Pinus sylvestris*), spruce (*Picea abies*), and birch (*Betula* spp.) (Nordisk Ministerråd 1977, Fremstad 1997, Moen 1998).

METHODS

I obtained antler measurements from the "gold, silver, and bronze" trophies in this region (*n* = 1,186) recorded by the Norwegian Association of Hunters and Anglers each hunting season during the period 1950-1997. I specifically chose those data in order to decrease a potential bias caused by age- specific antler development (Rülker and Stålfelt 1986). Descriptive antler characteristics and body weight (e.g., carcass weight) were recorded (Table 1). To test and control for the possible bias that hunters send in their best antlers, I measured 133 cast antlers from moose inhabiting Valdres Valley, within the study area and compared the occurrence of antler morphs in that population with the archived antler material from the same valley.

Antler measurements were based upon a standard protocol devised by the Conseil International de la Chasse (CIC), which differs from the standard system (i.e., Boone and Crocket, Pope and Young) used in North America (see Trense et al. 1981, Rameau and Rameau 1993). The CIC formula includes 6 measurements, with the first 3 measurements similar with respect to the 2 antler morphs: (1) circumference of the beam; (2) greatest span; and (3) length of the palm. For palmate antlers, the 3 final measurements are: (4) width of the palm; (5) the average length of the tines; and (6) number of tines above 10. For cervine antlers the final 3 measurements are: (4) circumference of the tines; (5) average

Table 1. Descriptive antler measurements and carcass weight (mean ± SD) of moose from southeastern Norway, 1950-1997.

Character	Palmate (*n* = 335)	Antler morph Intermediate (*n* = 482)	Cervine (*n* = 369)
Carcass weight (kg)	284.4±31.8	281.1±29.6	279.1±29.9
Circumference of the beam (cm)			
Right:	16.9±1.4	16.7±1.4	16.6±1.6
Left:	16.8±1.4	16.7±1.5	16.6±1.5
Overall spread (cm)	107.5±9.2	106.1±8.9	103.4±9.4
Palm/Beam length (cm)			
Right:	89.9±8.1	89.4±7.0	88.8±8.0
Left:	90.1±8.3	89.5±7.3	89.0±7.9
Palm width (cm)			
Right:	21.4±3.3	18.1±2.7	NA
Left:	21.9±3.0	17.8±2.2	NA
Circumference of tines (cm)			
Right:	NA	9.2±2.0	9.3±1.1
Left:	NA	9.2±2.3	9.3±1.2
Tine length (cm)			
Right:	13.8±3.0	16.3±3.5	21.5±3.7
Left:	13.7±2.9	16.4±3.5	21.6±3.8
Number of tines			
Right:	8.6±1.4	7.3±1.3	5.2±0.9
Left:	8.7±1.5	7.4±1.3	5.2±0.9

length of the tines; and (6) number of tines up to 10.

Antlers from European moose are smaller than antlers from North American and Siberian moose (Gasaway et al. 1987, Geist 1998), therefore, I subjectively assigned my own criteria. A palmate antler had at least 2 out of 3 of these characters: palm width > 20.0 cm; average tine length < 17.5 cm; and/or number of tines > 16. A cervine antler displayed at least 2 out of 3 of the following characteristics: palm width < 20.0 cm; average tine length > 17.5 cm; and/or number of tines < 12. Antlers that did not match those properties were classified as intermediate morphs.

I used quantitative measurements of tines (average length and number) to study trends in morphology. For all temporal analyses, I chose 4-year periods to get enough data for the first section of the time series. I combined the relative number of tines and relative tine length through use of an adaptive landscape, also called a fitness surface (Ridley 1993, Futuyma 1998). In a population, a trait has a mean (z) and a standard devation (SD). A change in a trait is called Dz (Futuyma 1998, Wolf and Broodie III 1998), and this can be expressed mathematically as (z_{t1}-z_{t2} / SD), where z_{t1} and z_{t2} are mean values of z at time t_1 and t_2, and SD is the standard deviation for trait z. As z-values, I used tine length and number of tines because of the strong negative phenotypic correlation (r = - 0.70, J. H. Engan, unpublished data) between these traits. Furthermore, I arranged these combinations in a 2-dimensional coordinate system and defined a plot as a 4-year period. If a population "walks" within a quadrate, there was a selection event; if the population "jumps" from one quadrate to another, there is a random event, or drift (Futuyma 1998). When changes were detected, I explored possible causal factors by testing for the effects of following types of selection: naturally induced, hunting-induced, frequency-dependent, and/or social stress.

I studied trends in morphology and quality characteristics by using linear regression. In morphology, an increase in tine length and/or decrease in number of tines over time indicated a cervine influence, while a decrease in tine length and/or increase in number of tines indicated a palmate influence. For natural selection, I calculated fitness, Z, (Ridley 1993) for the antler morphs in the period before 1950 (e.g., antlers in the period 1900-1950). Expected frequencies of morphs were estimated as if a single, codominant locus was controlling antler morphs, with palmate and cervine morphs representing homozygotes and the intermediate morphs representing heterozygotes. Random mating was assumed. Ratios of observed / expected frequencies (Z') were calculated, and fitness of morph i was estimated as the ratio of Z'_i / Z'_{max}. I simulated the frequency for all morphs by putting the fitness values and initial proportions of morphs in the Hardy-Weinberg equilibrium equation. Finally, I used a linear regression between the simulated and observed values to compare the simulated and observed values under natural selection. A strong relation between the simulated and the observed values may indicate natural selection.

To test for hunting selection, I used the relationship between the frequency of killed bulls and the frequency of antler morphs. I assumed a Type 2 functional response, expressed as $Pe = a' \; T_s N$, where Pe is number of prey items (occurrence of the antler morphs) harvested by a predator (hunters) during a searching time T_s (number of hunting days and I assumed an equal number of days for all antler morphs), were N is the density of prey items, and a' is the attack rate of the predator (Begon et al. 1996). Finally this was put in a linear regression where the model (Type 2 functional response) was the independent variable and observed values were the dependent variable.

To test frequency-dependent selection, I calculated fitness (Z) for each antler morph in every period in the same way as in natural selection. Frequency-dependent selection means that a genotype or phenotype has variable fitness, and this fitness is dependent on the genotype's (and phenotype's) proportion within the population. The fitness can show variation in time and/or in space. If the fitness fluctuates, this should indicate frequency-dependent selection.

For examining social stress (Bubenik 1973), which is a component of the complex concept of intra-specific competition, I used a quadratic regression ($y = a + b_1*x + b_2*x^2$) with average moose density (measured as number of bulls killed per 10 km^2 forest and bog area; Hohle and Lykke 1986, Statistics Norway 1987-98) in a time period as independent variable x versus frequency of the antler morph as dependent variable y; b_1, b_2 are regression values and a is a constant.

Statistical tests were done in S-plus 4.0 (Mathsoft Engineering & Education, Inc., Surrey, U.K.) and significance levels were set at $\alpha = 0.05$ (2-tailed).

RESULTS

Frequency of occurrence of the antler morphs in the archive material and the cast antler data from Valdres Valley were not significantly different, ($\chi^2 = 3.92$, df = 2, $P = 0.20$). The frequency of the palmate morph increased through the 1950s, declined during the following decade, and then remained stable for next 25-30 years (Fig. 2). Throughout the time series, the palmate antler morph decreased by 2.08% per 4-year period (0.52% per year, y = 2.08*period + 48.44, R^2= 0.599, df = 11, $P = 0.002$). The intermediate morph increased from the end of the 1950s to the middle of the 1970s. Throughout the time series, the intermediate morph increased, but this trend was not statistically significant (0.14% per year, y = 0.55*period + 36.51, R^2= 0.079, df = 11, P = 0.355). The cervine antler morph increased from the end of the 1960s to the middle of the 1980s, and throughout the time series the cervine antler morph increased by 1.55% per 4- year period (0.39% per year, y = 1.55*period + 14.99, R^2=0.492 P = 0.008).

With respect to the palmate antler morph, the average number of tines decreased significantly during the time series (y = -0.11*period +18.34, df = 11, R^2 = 0.315, P= 0.045; Fig. 3). Tine length did not display any significant trend (y = 0.06*period + 13.04, df = 11, R^2= 0.106, P = 0.277). For the intermediate morph, the average number of tines decreased significantly throughout the time series (y = -0.18*period +16.18, df = 11, R^2= 0.417, P = 0.018; Fig. 3) and average tine length increased significantly (y = 0.15*period + 15.14, df = 11, R^2 = 0.311, P = 0.048; Fig. 3). With respect to the cervine morph, none of the morphological traits showed significant trends (number of tines: y = -0.01*period + 12.40, df = 11, R^2= 0.002, P = 0.891, and tine length: y = -0.12*period + 23.19, df = 11, R^2= 0.137, P = 0.213).

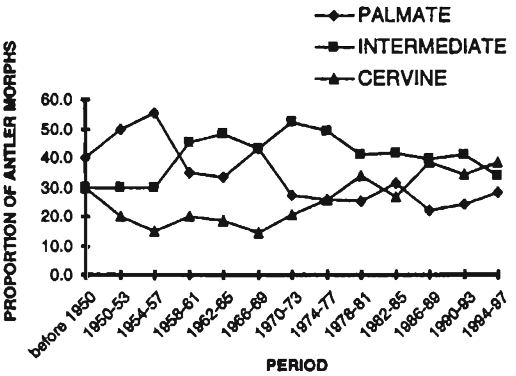

Fig. 2. Variation of the antler morphs among moose in southeastern Norway, during 1950-97.

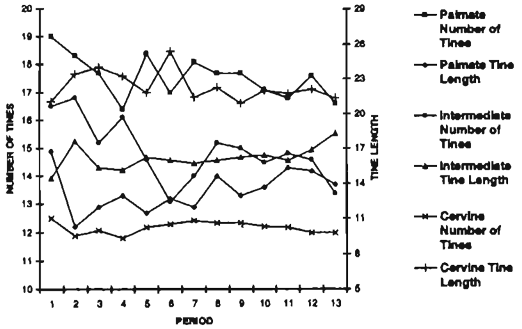

Fig. 3. Variation in average number of tines and average tine length (in cm) in 3 antler morphs among moose in southeastern Norway 1950-97; period 1 = prior to 1950, 2 = 1950-53, 3 = 1954-57, and so on, with each period representing a 4-year period.

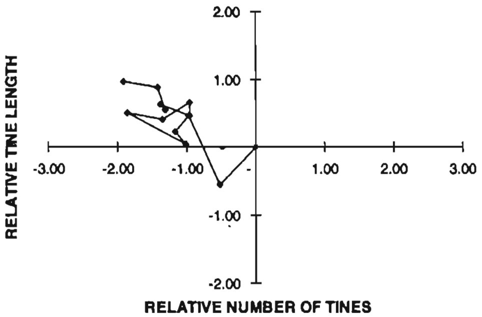

Fig. 4. An adaptive landscape with the relative change in number of tines and relative tine length for antlers of moose in southeastern Norway, 1950-97. The "zero-point" is the period prior to 1950, the first point is the period 1950-53, and each point thereafter represents the next 4-year period.

In the adaptive landscape, there was an overall increase in tine length and a decrease in number of tines except for the first plot (the beginning of the 1950s). This indicated a trend for an increase in cervine morphs in southeastern Norway throughout the time series (Fig. 4).

Under natural selection, the cervine antler morph had the highest relative fitness calculated prior to 1950 (Z = 1.00), the palmate morph was next (Z = 0.89), and the intermediate morph was lowest (Z = 0.41). The linear regression between simulated and observed values for the degree of palmate antlers was: observed value = 2.76*simulated value –92.11, (R^2 = 0.523, df = 11, P = 0.005), indicating natural selection.

None of the morphs showed a significant functional response, indicating a lack of hunting selection. The linear regression statistics between model (Type 2 functional response) and observed values were non-significant for palmate morph (y = 47.11 – 0.235*model, R^2 = 0.008, df = 11, P = 0.781), intermediate morph (y = 13.16 + 0.481*model, R^2 = 0.073, df = 11, P = 0.402), and cervine morph (y = 39.07 – 0.234*model, R^2 = 0.011, df = 11, P = 0.740).

The quadratic regression was significant for the palmate morph (y = 56.04 – 18.27*density + 2.46*density^2, R^2 = 0.65, df = 9, P = 0.02) and the cervine morph (y = 11.63 + 7.69*density – 0.59*density^2, R^2 = 0.81, df = 9, P = 0.01), but not for the intermediate morph (y = 32.38 + 10.57*density – 1.87*density^2, R^2 = 0.28, df = 9, P = 0.24). The palmate morph decreased with high densities and the cervine morph increased with high densities. The intermediate morph was insensitive to density.

The antler morphs show fluctuations in fitness throughout the time series (Table 2). This may indicate a trend toward frequency-dependent selection.

DISCUSSION

I revealed a trend in the relationship between the palmate and cervine antler morphs in southeastern Norway. Similar trends have not been found in other regions of Norway (Engan 1998). Kramer (1963) claimed that there could be a genetic basis for the 2 antler morphs in East Prussia, a region in Poland, where there was a shift toward more cervine morphs when these were protected and palmate morphs were hunted. When they protected palmate morphs and harvested more cervine morphs,

Table 2. Variation of fitness in 3 antler morphs of moose in southeastern Norway, 1950-1997.

	Fitness		
Period	Palmate	Intermediate	Cervine
Before1950	0.89	0.41	1.00
1950-53	0.72	0.40	1.00
1954-57	1.00	0.26	0.63
1958-61	1.00	0.81	0.99
1962-65	0.68	1.00	0.76
1966-69	1.00	0.48	0.63
1970-73	0.98	1.00	0.91
1974-77	1.00	0.96	0.99
1978-81	0.78	0.69	1.00
1982-85	1.00	0.50	0.66
1986-89	0.99	0.69	1.00
1990-93	0.88	0.71	1.00
1994-97	1.00	0.49	0.91

the trend was reversed and the palmate became more common. In my study, the frequency of the palmate morphs declined 0.52% per year from 1950 to 1997, and began stabilizing in the 1970s. The palmate morph may be reaching a selection plateau or limit. However, no clear explanation for this can be provided without further investigation. In an adaptive landscape, the relative tine length increased, and the relative number of tines decreased. This covariation between the relative number of tines and relative tine length indicated a change toward more cervine antlers since 1950. The hypothesis that there is a change occurring in the relationship between palmate and cervine antler morphs in southeastern Norway cannot be rejected.

The results indicated natural selection. The assumption of a single locus may be simple and unrealistic, but a number of loci controlling antler development could be so closely linked that they act as a supergene, similar to a single locus (Ridley 1993, Futuyma 1998). Fitness is difficult to estimate (Caswell 2001), so the estimates could be uncertain and need further investigation.

The results showed no trend for hunting selection, and in light of this, I rejected the hypothesis of hunting selection. This is not surprising, because moose hunting in Scandinavia is primarily for meat and harvesting is mostly random. However, effects of hunting selection are found in other studies. For example, Hundertmark et al. (1993) simulated genetic effects of selective harvesting in Alaskan moose (*A. a. gigas*) where the most negative effect was seen when harvesting bulls with an antler spread above 36 inches (91.4 cm). In red deer (*Cervus elaphus*), Dubas et al. (1989) claimed that antler quality declined during the period 1975-1981 in northeastern Poland because of hunting selection. This is not surprising because trophy hunting is more common on the European Continent than in Scandinavia (Engan 1998). For the Forelhogna reindeer (*Rangifer tarandus*) herd, Skogland (1988) claimed that the body mass declined 10% during the 1980s as a result of harvesting large males and females in all age classes. In France, Hartl et al. (1991) studying the relationship between allozymes, heterozygosity, and morphological characters in red deer found that selective hunting could lead to changed gene frequencies and gene extinction.

My results indicate that the frequency of the palmate morphs decreased as population size increased. A possible explanation for this may entail the energy demand for producing palmate antlers. At higher moose densities, the transcription (protein synthesis) of the palmate morph may be reversed into an earlier evolutionary morph, i.e., the cervine morph (Geist 1998). Hundertmark et al. (1998) maintained for cervids that in population densities below the nutritional carrying capacity, an individual should exhibit larger age-specific body and antler size because of the greater availability of nutritious forage available to individuals. Little is known about the genetic basis of moose antlers (Bubenik 1973), but it is plausible there are important genetic factors influencing the development and frequency of morphs (Rülker and Stålfelt 1986, Haagenrud 1995). In this context, Robert Collett's explanation from 1912 is relevant: "The reason for this degeneration, that can be shown in all ages is unknown... This phenomenon seems to increase in districts where the population size has been large and then declined...perhaps because of lack of an important nutrient substance, and then an influence of the testicles" (Collett 1912, my translation). If this is correct, the moose population should be relatively small today, however, it has never been larger (Engan 1998), thus my results cannot support Collett's explanation.

My results showed that the fitness of antler morphs varied throughout the time series. Therefore, I suggest that this variation indicates frequency-dependent selection. Benkman (1996) showed that variation in the rate of mandible crossing direction in Crossbills (*Loxia* spp.) was a result of frequency-dependent selection. Interesting are the 2 observations in 1962-1965 and 1970-1973, where the intermediate morph showed the highest fitness of these 3 morphs. In light of this, the hypothesis of frequency-dependent selection cannot be rejected.

IMPLICATIONS FOR MANAGEMENT

An important question is whether we could regulate the occurrence of these morphs with hunting. Voippio (1952) proposed that in an area of low moose density in central Finland, migrating cervine bulls from southern Finland could be eliminated through hunter selection, such that bulls with palmate antlers could become more common. However, this suggestion was never undertaken. Wilhelmson and Sylvén (1980) questioned whether it was possible to effectively select for larger bulls with higher body weight and larger antlers, and they concluded this was impossible. I tentatively support their claim, since moose hunting in Scandinavia is primarily for meat harvest, and our knowledge of population genetics and population structure are inadequate for such application. My study reveals that the changes in antler morphs could be influenced by frequency-dependent selection and social stress. The first factor could be difficult to manage. However, if population size is reduced, there may be less social stress, and more palmate antlers.

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REFERENCES

ANDERSEN, R., and B. E. SAETHER 1996. Elg i Norge. Teknologisk forlag, Oslo, Norway.

BEGON, M., J. L. HARPER, and C. R. TOWNSEND. 1996. Ecology. Third edition. Blackwell Scientific Publications, London, England.

BENKMAN, C. W. 1996. Are the ratios of bill crossing morphs in crossbills a result of frequency- dependent selection? Evolutionary Ecology 10:119-126.

BUBENIK, A. B. 1973. Hypothesis concerning the morphogenesis in moose antlers. Proceedings of the North American

Moose Conference and Workshop 9:195-231.

Caswell, H. 2001. Matrix population models, construction, analysis, and interpretation. Second edition. Sinnauer Associates, Sunderland, Massachusetts, USA.

Collett, R. 1912. Norges Pattedyr. Aschehough and co. forlag, Kristiania.

Dubas, J. W., K. Olsztyn, and O. Jerzierski. 1989. Effekte der jagdlichen Auslese beim männliche Rotwild. Z. Jagdwiss 35: 192-197.

Egorov, O. V. 1965. Wild ungulates of Yakutia. Izdatel'stvo "Nauka", Moscow.

Engan, J. H. 1998. Har det skjedd en endring i forholdet mellom palmat og cervin gevirtype i ulike deler av Norge 1950-1997. Candidate Thesis, University of Oslo, Norway (with English summary).

Fremstad, E. 1997. Vegetasjonstyper i Norge. NINA-temahefte, Trondheim.

Futuyma, D. 1998. Evolutionary Biology. Third edition. Sinnauer Associates, Sunderland, Massachusetts, USA.

Gasaway, W. C., S. D. Dubios, D. J. Reed, and D. D. Roby. 1987. Comparative antler morphology and size of North American Moose. Swedish Wildlife Research Supplement 1:311-326.

Geist, V. 1998. Deer of the World. Their Evolution, Behavior, and Ecology. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Haagenrud, H. 1995. Elgjakt. Aschehough og co. forlag, Oslo, Norway.

Hartl, G. B, G. Lang, F. Klein, and R. Willing. 1991. Relationship between allozymes, heterozygosity and morphological characters in red deer (*Cervus elaphus*) and the influence of selective hunting on allele frequency distributions. Heredity 66:343-350.

Hohle, P., and J. Lykke. 1986. Elg og Elgjakt i Norge. Gyldendal Norsk Forlag.

Hundertmark, K. J, T. H. Thelen, and R. T. Bowyer 1998. Effects of population density and selective harvest on antler phenotype in simulated moose populations. Alces 34: 375-383.

______,______, and C. C. Schwartz. 1993. Population and genetic effects of selective harvest in moose: a modeling approach. Alces 29:225-234.

Jia, J., K. Nygren, and X. Yu. 1994. Biological features of Manchurian moose (*Alces alces cameliodes*) with special reference to comparative research. Alces 30:137-152.

Klemsdal, T. 1983. Nordens Klima. Det bestes store Norgesatlas. Forlaget Det Beste A/S, Oslo, Norway.

Kramer, A. 1963. Elchwald. Bayensicher Landwirtschaft Verlag, München.

Lykke, L. 1960. Elgen og elgjakten. Pages 197-225 *in* P. Hohle, K. Rom, R. Frislid, and P. Søilen, editors. Jakt i Norge. Norsk arkivforskning, Bedrifthistorisk instittutt og forlag A/S, Oslo, Norway.

Markgren, G. 1982. Moose populations along a climatic gradient across Sweden. Naturvårdsverket, Protect Board Pm 1571.

Moen, A. 1998. Nasjonalatlas for Norge: Vegetasjon. Statens kartverk, Hønefoss.

Nordisk Ministerråd 1977. Naturgeografisk regioninndeling av Norden (with English summary). NUB 1977: 34, Gotab, Stockholm.

Rameau, J., and S. C. Rameau. 1993. Records of North American Big Game. Tenth edition. The Boone and Crockett Club, Old Milwaukee Depot, Missoula, Montana, USA.

Ridley, M. 1993. Evolution. Blackwell Scientific Publications, London, England.

Rülker, J., and F. Stålfelt. 1986. Das Elchwild. Paul Parey verlag, Hamburg, Berlin.

Saether, B. -E., and H. Haagenrud. 1985. Geographical variation in the antlers of Norwegian moose in relation to age and size. Journal of Wildlife Management 49:984-986.

Sckuncke, F. 1949. Älgen, studier, jakt och vård. P. A. Nordstedt & Söners forlag, Stockholm.

Sigmond, E. M. O., M. Gustavson, and D. Roberts. 1984. Bed Rock Map, Norway. Scale: 1:1,000,000, Norges Geologiske Undersøkelse.

Skogland, T. 1988. Bestandsdynamisk analyse av villreinstammen i Forelhogna: Tellinger og produksjon, vektutvikling og darwinisme, effekten av tannslitasje på livshistorie. Villreinen 2:14-22.

Statistics Norway 1987. Hunting Statistics 1986. Kongsvinger, Oslo, Norway.

_______. 1988. Hunting Statistics 1987. Kongsvinger, Oslo, Norway.

_______. 1989. Hunting Statistics 1988. Kongsvinger, Oslo, Norway.

_______. 1990. Hunting Statistics 1989. Kongsvinger, Oslo, Norway.

_______. 1991. Hunting Statistics 1990. Kongsvinger, Oslo, Norway.

_______. 1992. Hunting Statistics 1991. Kongsvinger, Oslo, Norway.

_______. 1993. Hunting Statistics 1992. Kongsvinger, Oslo, Norway.

_______. 1994. Hunting Statistics 1993. Kongsvinger, Oslo, Norway.

_______. 1995. Hunting Statistics 1994. Kongsvinger, Oslo, Norway.

_______. 1996. Hunting Statistics 1995. Kongsvinger, Oslo, Norway.

_______. 1997. Hunting Statistics 1996. Kongsvinger, Oslo, Norway.

_______. 1998. Hunting Statistics 1997. Kongsvinger, Oslo, Norway.

Strahler, A. H., and A. N. Strahler. 1994. Introduction to Physical Geography. John Wiley & Sons, New York, New York, USA.

Thoresen, M. K. 1990. Quaternary map of Norway. Scale: 1:1,000,000, Norges Geologiske Undersøkelse.

Tomter, S. M. 1994. Skog-94. Statistikk over skogforhold og – ressurser i Norge, Statistics of forest conditions and resources in Norway. NIJOS, Ås.

Trense, W., A. J. Hettier De Boislamert, and G. K. Whitehead. 1981. Die Jagdtrophäen der Welt / Les Trophées de Chasse du Monde / The Game trophies of the World. Paul Parey Verlag, Hamburg, Berlin.

Voippio, P. 1952. How shall we get our moose population palmated in type? Soumen Riista 7:52-59.

Wilhelmson, M., and S. Sylvén. 1980. Är ett effektivt avelutval möjligt att genomföra i älgstammen? Viltnytt 11:22-34.

Wolf, J. B., and E. D. Broodie III. 1998. The co-adaptation of parental and offspring characters. Evolution 52:299-308.