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Moose antler type polymorphism: age and weight dependent phenotypes and phenotype frequencies in space and time

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We provide the first detailed description of the phenotypic polymorphism of the European moose (*Alces alces*) bulls with three different antler types: cervina, intermediate and palmated. We assess how the frequencies of bulls with different antler types as well as antler spread and tine numbers are related to age, body weight, region and time. Our results indicate that antler type phenotypes are linked to other body and antler size characteristics. The cervina type had the smallest and the palmated the largest carcass weight, antler spread and tine numbers. The youngest age groups were predominantly of cervina type. At the prime age of 6.5–10.5 years, the prevalent types were intermediate and palmated. At an older age, the cervina type increased and the other types decreased. We propose that the penetrance of inherited antler type is best at prime age when it is important for a bull to be successful in mating competition. The cervina type was most prevalent in the southern zone and the palmated type in the northern zone. The mean age, mean carcass weight, antler spread and tine numbers all decreased from 1976–1986 to 1996–1999. The results were similar in the age-standardized prime age bulls. We hypothesize that intensive selective hunting as well as possible fitness differences between antler types in managed forests may have been involved in the decrease of the palmated antler type.

Introduction

In polygynous cervids, antlers are sexually selected organs important for the success of male mating (Clutton-Brock 1982, Lincoln 1992, Solberg & Sæther 1994). Antlers function as organs displaying rank and/or serve as weapons in intraspecific fighting among males (Bubenik 1973, Kitchener 1991). The size and shape of antlers vary greatly among and within species, but the variety of antlers has been subject to little systematic inquiry (Caro *et al*. 2003). Antler characteristics are influenced by both genetic and environmental factors (Harmel 1983, Geist

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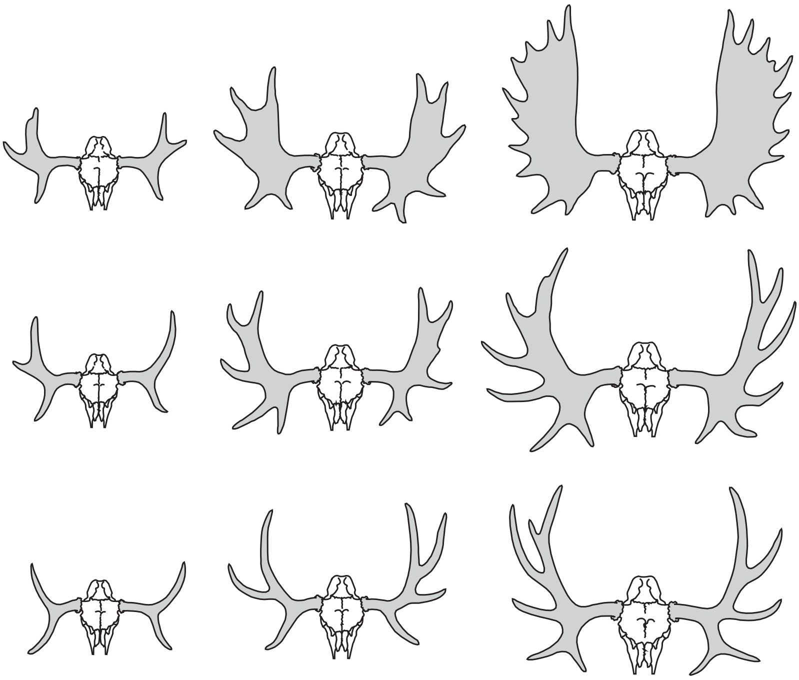

Fig. 1. Stylized drawing of typical palmate (top row), intermediate (centre), and cervina (bottom row) antlers on young (left) and middle-aged (centre) bulls, and on bulls at their prime breeding age (right). (Drawing by Maija Wallén).

1986, Hundertmark *et al*. 1998, Schmidt *et al*. 2001, Kruuk *et al*. 2002).

The moose (*Alces alces*) has morphologically variable antler types that can be classified according to palm breadth (Fig. 1). In North America, the typical antler type is palmated (Cringan 1955, Peterson 1955, Rülcker & Stålfelt 1986, Gasaway *et al*. 1987). In most North American moose subspecies, the deer-like cervina type is known only in bulls less than two years of age (Gasaway *et al*. 1987, Geist 1998). An exception is *A. a. americanus* in New Brunswick and Maine, where 7% of bulls at prime age (i.e., the age with the best overall signalling of reproductive maturity) have cervina type antlers (Gasaway *et al*. 1987). In the Old World, the small Manchurian moose (*A. a. cameloides*) has almost exclusively cervina type antlers (Bubenik 1973, Bromlei & Kucherenko 1983, Jia *et al*. 1999, Boeskorov & Puzachenko 2001) but only 9% of the Yakutian moose (*A. a. pfizenmeyeri*) living to the north of the Manchurian moose carry cervina type antlers (Egorov 1965). The distribution of antler types in the European moose (*A. a. alces*) is, however, highly variable (Boeskorov & Puzachenko 2001; Table 1). Three different antler types — palmate, intermediate and cervina (Fig. 1) — are usually distinguishable in all populations of the European moose. However, antler type is seldom permanent throughout the lifetime of a moose bull. An adult bull with intermediate or palmated antlers often has cervina type antlers in its youth and old age, as illustrated by the cast antler series of a bull moose in Skansen Zoo, Sweden (Skuncke 1949, Koivisto 1972).

Several authors have suggested that the number of tines is higher in palmated than in cervina type antlers (Radzevitch 1902–1903 [as cited in Heruvimov 1969], Lönnberg 1923, Skuncke 1949, Cringan 1955, Koivisto 1965, Markgren 1982, Sæther & Haagenrud 1985) and that cervina type bulls are larger than palmated bulls (Munsterhjelm 1937, Egorov 1965). Others have claimed that the cervina type moose has shorter legs (Schulz 1931 [as cited in Munsterhjelm 1937], Heruvimov 1969) or they are smaller (Lönnberg 1923) than the palmated type moose. It has even been suggested that palmated and cervina type bulls represent different moose strains with differences in body size, height and colour (Narushkin 1900, Munsterhjelm 1937, Bäckström 1948, Skuncke 1949, Kramer 1963). However, we were unable to find published data on the relationship between numbers of tines or body size and moose of different antler types.

Similarly, data on the frequency distribution of moose antler types are scarce (Table 2). Voipio (1952), Koivisto (1965), Nygrén and Nygrén (1976) and Nygrén (1997) published frequency data from Finland and Bäckström (1948) and Stålfelt (1974) from Sweden. Engan (2001) studied the frequencies of antler types in trophy bulls in Norway and found that the proportion of cervina type antlers slowly increased from 1950 to 1997. According to antler type statistics (Nygrén 1997) and the opinion of the majority of hunters (Nygrén & Tykkyläinen 2006), the proportion of palmated type antlers has also decreased in Finland.

Our main aim is to provide the first detailed description of moose bulls with different antler types. We present phenotype frequencies of killed moose bulls with cervina, intermediate or palmated antlers in Finland and assess how the frequencies of bulls with different antler types as well as their antler spread and tine number are related to age, body weight, geographical region and time. We determine age classes of bulls with prime antler characteristics and body size, and define the average phenotypes and spatial and temporal frequencies of prime bulls with different antler types. Finally, we discuss the temporal and spatial differences of the antler type phenotype distribution and present our hypothesis on the observed age dependence of antler types.

Table 1. Summary of available data on antler type distribution of the European moose (*Alces alces*).

Region/country	Antler types	Author
Irkutsk, Russia	Prevailing antler type is cervina	Skalon 1951 (acc. to Heruvimov 1969)
Pechora, Russia	Prevailing antler type is cervina	Yazan 1972
Tambov, Russia	No more than 1.5%–3.0% of the bulls have palmated antlers	Heruvimov 1969, Bromlei & Kucherenko 1983
Southwest Russia	Palmated and cervina antler types represented	Narushkin 1900
Southwest Russia	Prevailing antler type is cervina	Rusakov 1970 (acc. to Bromlei & Kucherenko 1983)
Southwest Russia	Prevailing antler type is cervina	Timofejeva 1974
Karelia, Russia	Prevailing antler type is palmated	Lampio 1946
The Baltic countries	Cervina type antlers more common than in Peterburg and Novgorod areas and in Finland	Narushkin 1900
Lithuania	Prevailing antler type is cervina (44.6% cervina, 25.0% intermediate, 27.7% palmated, 2.7% deformed)	Baleisis & Blusma 1982 (acc. to Danilkin 1999)
Finland	Prevailing antler type is cervina in south Finland; the proportion of palmated antlers increases to the north	Voipio 1948
Finland	Almost exclusively cervina type antlers in Parkano area in southwestern Finland	Voipio 1952
Finland	Ca. 20% palmated antlers; the proportion of palmated antlers increases to the north	Koivisto 1965
Finland	Prevailing antler type is cervina in southwest, intermediate type in the middle and palmated antlers in northern parts of Finland	Nygrén & Nygrén 1976
Sweden	Prevailing antler type is intermediate; the proportion of palmated antlers increases from south to north	Bäckström 1948
Sweden	29%–56% palmated antlers; the proportion of palmated antlers increases to the north	Stålfelt 1974
Norway	Prevailing antler type is cervina excluding North-Trøndelag	Munsterhjelm 1937
Norway	The proportion of palmated antlers increases from south to north	Sæther & Haagenrud 1985
Norway	31% palmated, 41% intermediate, 28% cervina antlers among trophy bulls	Engan 2001

Material and methods

Study area and the Finnish moose population

Finland is located between the 60th and the 70th northern parallels in the Eurasian continent's coastal zone, characterized by both maritime and continental climate, depending on the direction of the airflow (www.fmi.fi/weather/climate.html). Finland belongs to the temperate coniferous-mixed forest zone with cold and wet winters. Mean temperature of the warmest month is over 10 °C and of the coldest month is less than –3 °C, and rainfall is, on average, moderate in all seasons (www.fmi.fi/weather/climate.html). In coastal Finland, seasonality is less pronounced, climate is more windy and humid, and snow depth is lower. The average length of the growing season is 180 days in the southwestern archipelago, 140 to 175 days elsewhere in southern and central Finland, and 100 to 140 days in Lapland (www.fmi.fi/weather/climate.html). The most continental climate and the deepest snow layer are in eastern and northern Finland. Forest covers about 86% of Finland's land area, and forests are mainly (about 70% of all forest cover) seedling stands and thinning stands (Finnish Forest Research Institute 2001). Since the 1950s, intensive forest regeneration with pine plantations has dramatically increased the amount of moose forage but at the same time, it has restricted the distribution of other forage species.

Moose have inhabited Finland since the end of the last Ice Age. In the refuse fauna, it was a common species as early as 9000–8000 years ago (Ukkonen 1993). During its history, the population has experienced strong fluctuations but most probably it has never before been as numerous as during the period under study (Nygrén 1987, Nygrén *et al*. 2000), with an estimated size of the winter population around 50 000 to 100 000 animals (0.17–0.33 moose/km^2 on average). Since the 1970s, the population has been intensively exploited; during the period under study, 1976–1999, the number of annually killed moose varied from 17 000 to 69 000 animals (Nygrén & Pesonen 1989, Nygrén 1996, T. Nygrén, unpubl. data). At the same time, selective harvesting increased the productivity of the population until the end of the study period to the highest average level ever (Lavsund *et al*. 2003); annually 56 calves/100 adult moose and 97 calves/100 females were born (Nygrén *et al*. 2000).

Data

Two datasets were used: (1) data collected by hunters in 1976–1986 and 1991–1999 on antler type, number of antler tines, antler spread, carcass weight (weight), and the back fat thickness (BFI) of moose bulls older than 1.5 years of age (Appendix); and (2) data on moose bulls older than 1.5 years of age sent by hunters to the Finnish Game and Fisheries Research Institute (FGFRI) in 1976–1986 and 1997–1999. These

Table 2. Published frequency distributions of antler types in the European moose (*Alces alces*).

Author	Area	*N*	Antler type			Type of data
			cervina	interm.	palmated	
Bäckström 1948*	Sweden	129	35.7	44.2	20.2	> 6 year old bulls
Stålfelt 1974	Sweden, south	160	30.0	41.2	28.8	≥ 6 year old bulls
Stålfelt 1974	Sweden, central	135	39.2	34.1	26.7	≥ 6 year old bulls
Stålfelt 1974	Sweden, north	195	8.8	35.2	56.0	≥ 6 year old bulls
Engan 2001	Norway	1186	28.2	40.6	31.1	trophy bulls
Voipio 1952*	Finland	658	74.2	–	25.8	questionnaire to hunters
Koivisto 1965	Finland	> 2000	78.8	–	21.2	questionnaire to hunters
Nygrén & Nygrén 1976	Finland, southwest	186	40.9	37.6	21.5	bulls with more than 6 tines
Nygrén & Nygrén 1976	Finland, central	862	27.0	48.0	25.0	bulls with more than 6 tines
Nygrén & Nygrén 1976	Finland, northeast	663	18.7	33.2	48.1	bulls with more than 6 tines

* data recalculated.

data included jaws or front teeth for age determination and data on antler type, number of antler tines, antler spread, weight and BFI (Appendix). These data were merged and the observations were classified into four geographic zones from south to north (Fig. 2) and two time periods 1976–1986 (period I), and 1996–1999 (period II).

The classification of antlers into cervina, intermediate or palmated types rested on the experience of moose hunters. Since the 1970s, the FGFRI has requested hunters to annually report the weight, tine number, antler spread and antler type of killed bulls (Nygrén & Pesonen 1993, Lavsund *et al*. 2003). Finnish hunters show a particular interest in moose antlers and are well conversant with antler type qualities. Therefore no guidelines for the classification of antlers were given. Possible individual or regional inconsistencies in the classifications cannot be ruled out, but we found no actual reason to suspect the credibility of the hunters' classifications.

All data were collected during the annual hunting season between 15 September and 15 December. The data were a representative samples of the killed adult bulls; due to selective hunting, the younger age groups were more common and the older age groups less common in the sample data than they were in the living male population. There were some changes in hunting methods, hunting recommendations and sampling instructions during the sampling period from 1976 to 1999, but we did not see any notable bias that might have resulted from these changes. Age was determined from the root of the first or the second incisor according to the method of Sergeant and Pimlott (1959). The FGFRI laboratory determined the age of bulls of period I and Matson's Lab, Montana, USA determined the age of bulls of period II. We could not rule out minor differences between determinations for period I and II.

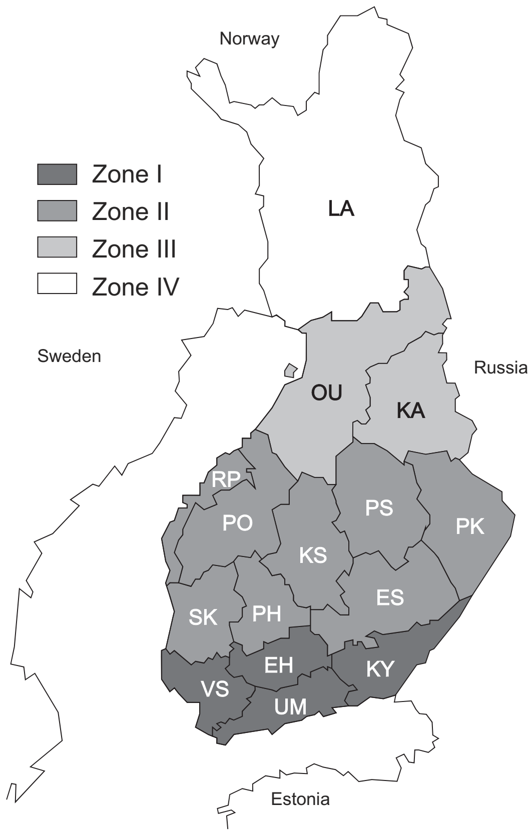

Fig. 2. The study area was divided into four geographic zones from south to north. Data and samples were collected from 15 game management districts (*see* Nygrén 2003).

Analyses

The credibility of the data was checked before the analyses were carried out. Clear misinterpretations and outliers were rejected. Outliers were identified using box-and-whiskers plots. A limit of 1.5 times the interquartile range above the 75th percentile or below the 25th percentile was chosen as the limit for an acceptable observation. As a result, 0.5%–1.5% of the values of the variables investigated was excluded.

Carcass weight is the fresh weight of the animal after the skin, viscera, head, and lower legs have been removed. Hunters reported carcass weights as measured or estimated weights in kilograms. In period I, the majority of the data were estimated weights. Later, the proportion of measured data increased; 2647 moose had both estimated (mean = 182.85 kg) and measured (mean = 182.23 kg) weights, which were strongly correlated ($r = 0.880$) and did not differ from each other ($t = -1.772$, df = 2646, $P = 0.077$). Mean carcass weight ± SD for all data — including estimated and mean weight

— was 182.78 ± 36.36 kg (range 60 to 380 kg, N = 84 334).

The number of tines was counted separately for each antler. A tine was defined when larger than 2-cm long. The numbers of left and right antler tines were totalled and all animals without one or both antlers were excluded. Antler spread is the maximal vertical width of antlers measured in centimetres (Trense *et al*. 1981, Gasaway *et al*. 1987). Back fat thickness (BFI) was measured in millimetres according to the method of Riney (1955).

The relationship between the frequencies of different antler type categories and the covariates of age, weight and BFI, and the categorical independent variables of geographic zone and period were analysed using multinomial logistic regression. The model included the interactions between the categorical variables and those between categorical variables and each of the covariates. However, the interactions with two or more continuous variables were omitted. The initially fitted model was then simplified according to the procedure described by Crawley (2002). Thus after fitting the factor, covariates and interactions of interest, the non-significant terms starting from the highest order interaction, were removed. The fit of the reduced model was then assessed. A term was excluded from the model if the change in model log-likelihood was non-significant ($P \geq 0.05$); otherwise, it was retained.

The relationships between antler characteristics (the number of tines and antler spread) and the covariates of age, weight and BFI, and the categorical variables of antler type, geographic zone and period were analysed using ANCOVA. All main effects and interactions (except those with two or more covariates) were included into the model. The number of tines and the covariates of age and BFI were log-transformed prior to the analyses.

Prime-age classes were defined using the results of antler type frequencies and antler and body size qualities. To find the age classes with the highest mean weight, antler spread or the number of tines for the different antler types, we graphically determined the age with the highest mean value of these three variables. Then we searched for the age classes with mean values no smaller than that of the age class with the maximal mean value. This was done using the Dunnett pairwise post hoc comparison test of the General Linear Model. The youngest age class with the mean value (of weight, antler spread or number of tines) not significantly smaller ($P \geq 0.05$) than the maximum mean value was then considered as the age at which the maximum mean value was attained. Weight classified into 40-kg intervals was used as an independent variable in the analysis.

The average measures of weight, antler spread and number of antler tines were determined from the prime-age bulls. We performed ANOVA to analyse whether there was variation in weight, BFI, tine number and antler spread among prime bulls from different geographic zones and periods and with different antler types. The models included all interactions between these variables. All statistical analyses were performed using the SPSS 12.0.2 software.

Results

Age distribution

The mean age ± SD of the 8256 bulls was 3.79 ± 2.17 years (range 1.5 to 19.5 years). A total of 7122 (86.3%) of the bulls were younger than 6.5 years. Only 138 (1.3%) bulls were at least 10.5 years old. Mean age increased from zone I to IV ($F_{3,8248}$ = 29.36, P < 0.001) and decreased from period I to II ($F_{1,8248}$ = 307.52, P < 0.001) (Fig. 3).

Antler type frequencies

Two-thirds (68.6%) of the studied bulls (N = 84 370) had antlers classified as cervina whereas 9.3% had antlers classified as palmated. The remaining 22.1% of the bulls were classified into the intermediate type. The multinomial regression (N = 4215) indicated that antler type frequencies varied among the combinations of geographic zones and periods (zone × period interaction: χ^2 = 20.66, df = 6, P = 0.002). Moreover, antler type frequencies depended on the age (χ^2 = 105.24, df = 2, P < 0.001) and weight of

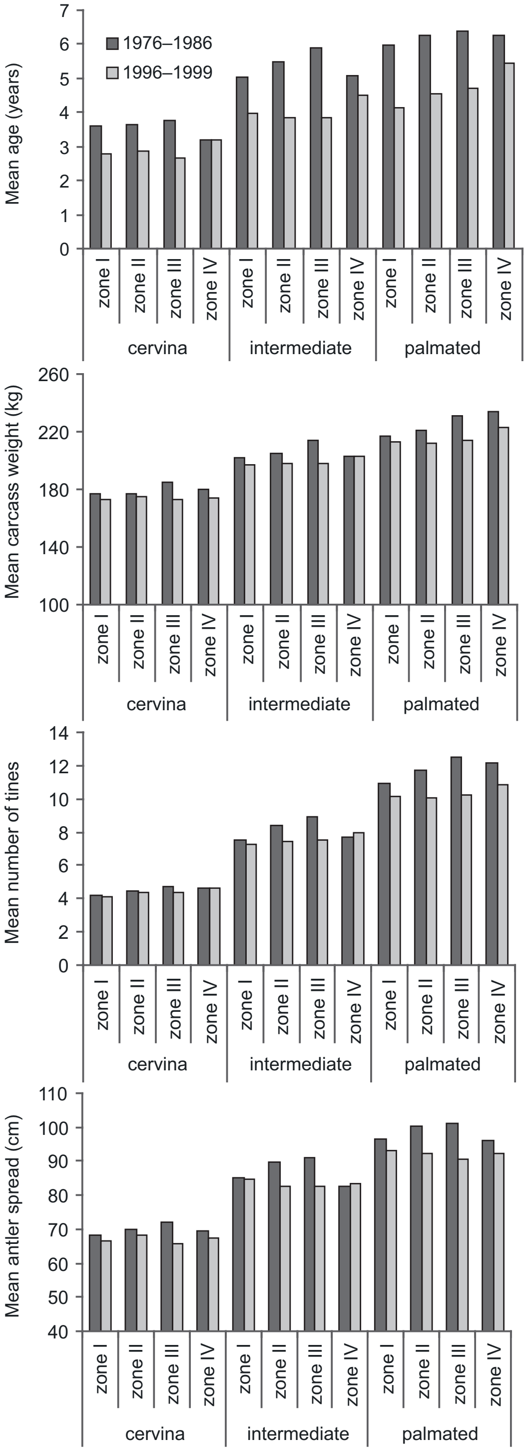

Fig 3. Average age (N = 8594), carcass weight (N = 42 334), number of tines (N = 46 258) and antler spread (N = 46 308) of the cervina, intermediate and palmated antlered bulls in four geographic zones in 1976–1986 and 1996–1999.

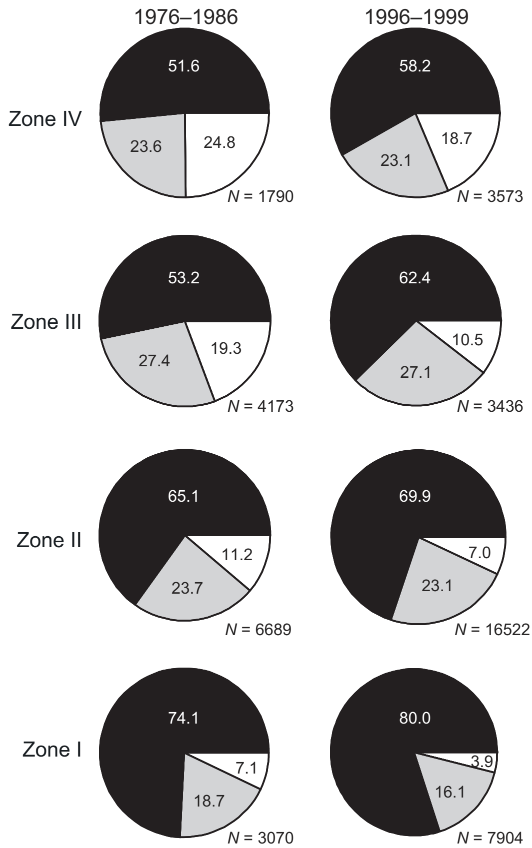

Fig. 4. The distribution of cervina (black), intermediate (grey), and palmated (white) antlers in four geographic zones in 1976–1986 and 1996–1999 (N = 47 157).

the bulls. The relationship between weight and antler type frequency changed from period I to II as indicated by the significant weight × period interaction (χ^2 = 19.43, df = 2, P < 0.001).

The proportion of palmated antlers increased from south to north (Fig. 4). From period I to II, the proportion of palmated antlers decreased and the proportion of the cervina type antlers increased in all geographic zones. The significant zone × period interaction was due to the pronounced temporal change in the proportions of palmated and cervina antlers in zone III. The frequency of bulls classified into intermediate type did not change much between the two periods for all zones.

The distribution of the antler type frequencies changed rapidly with age (Fig. 5a). The youngest age groups were predominantly of cervina type. At the age of 6.5–10.5 years, the proportion of

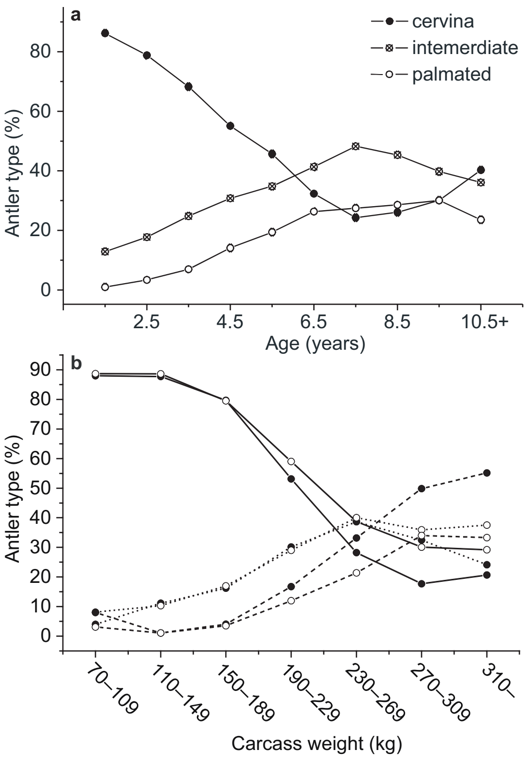

Fig. 5. (**a**) Change in the percentage of cervina, intermediate and palmated antlers with age in 1976–1999 (N = 8362). (**b**) Change in the percentage of cervina (solid line), intermediate (dotted line), and palmated (dashed line) antlers (N = 78 051) with weight in 1976–1986 (black dots) and 1996–1999 (circles).

cervina type bulls was lowest and the proportion of intermediate and palmated type bulls was the highest. Among these age classes, the intermediate type was most prevalent. In the age classes older than 10.5 years, the proportion of cervina type antlers again increased and that of the palmated antlers decreased.

The distribution of the antler type frequencies also depended on carcass weight. The frequency of palmated and intermediate type antlers increased and the frequency of cervina antlers decreased with increasing weight (Fig. 5b). The cervina type was the prevailing antler type when weight was ≤ 220 kg, the intermediate type was the most frequent when weight was between 220–250 kg but when weight was ≥ 280 kg, the prevailing antler type was palmated. The frequency of the palmated antlers increased with weight at a higher rate in period I than in period II.

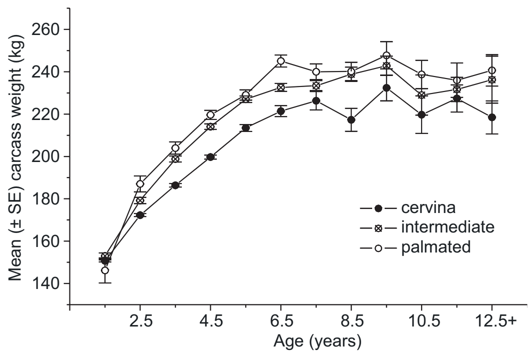

Fig. 6. Mean age-dependence of carcass weight in cervina, intermediate, and palmated antlered bulls in 1976–1999 (N = 7485).

Antler type and weight

Results suggest weight differences between bulls with different antler types. To further describe this relationship, we performed an analysis of covariance by examining the weight differences among bulls with different antler types at different ages (covariate) and combinations of geographic zone and period. The analysis revealed significant variation among the geographic zones ($F_{3,7399}$ = 4.42, P = 0.004) and between periods ($F_{1,7399}$ = 17.36, P < 0.001). Overall, carcass weight increased from south to north and decreased from period I to II (Fig. 3). A highly significant age × antler type interaction ($F_{2,7399}$ = 24.89, P < 0.001) indicated that the weight differences between bulls with different antler types varied with age (Fig. 6). Between the ages of 2.5–6.5 years, palmated bulls were the heaviest and cervina bulls the lightest. The significant difference between palmated and intermediate bulls disappeared at older ages (Tukey HSD: P < 0.05). Weight rose with increasing age, and full size was attained at the age of 6.5 years (Fig. 6). Post hoc comparisons of the weights at different ages against the weight at age with the highest mean (*see* Fig. 6) indicated that weight did not change between the ages of 6.5 and 12.5 years in any of the antler types. There was also a significant four way geographic zone × period × antler type × age interaction ($F_{6,7399}$ = 2.34, P = 0.029). Thus, age specific differences in weight among antler types depended on the combination of the geographic zone and period although the spatial and temporal variation was not very pronounced (data not shown).

Antler type and the number of tines

The cervina type antlers only rarely had more than 12 tines (Fig. 7a). The mean number ± SD of antler tines was 4.3 ± 2.3 in the cervina antlers, 7.5 ± 3.5 in the intermediate antlers and 11.0 ± 4.1 in the palmated antlers. One-fourth of all bulls (N = 84 370) had 4 tines, the highest number of antler tines recorded was 29, and the number of even tines was more prevalent than the number of odd tines.

ANCOVA results (Table 3) indicated that the number of tines varied among the combination of geographic zones and periods. In period I the number of tines increased from geographic zone I to II to IV to III, but in period II the order was I to II to III to IV. The number of tines decreased from period I to II, except in zone IV where there was no change between the periods. The decrease was largest in zone III (Fig. 3).

The number of tines increased with age and varied among bulls with different antler types. Overall, the highest number of tines occurred in palmated antlers and the lowest in cervina type antlers (Fig. 7b), but the magnitude of the differences between the antler types depended on age (Table 3). The differences between the antler types increased until 7.5 to 8.5 years. After 10.5 years, the significant difference between palmated and intermediate types disappeared (Tukey HSD: $P < 0.05$; Fig. 7b). The number of tines received their highest values from 6.5 to 11.5 years in the cervina type, from 7.5 to 12.5 years in the intermediate type and from 5.5 to 12.5 years in the palmated type.

The number of tines also increased with increasing weight, and the relationship between the number of tines and weight varied somewhat among the combination of geographic zones and periods (data not shown). In period I, the order of the zones, when assorted according to the slope between weight and the number of tines in a decreasing order, was II to I to III to IV. In period II, the order was II to I to IV to III. The slope of the relationship decreased from period I to II, except in zone IV where there was no change due to period. In the data pooled across zones and periods, the maximum number of tines of all antler types occurred at weights ≥ 270 kg (Fig. 7c).

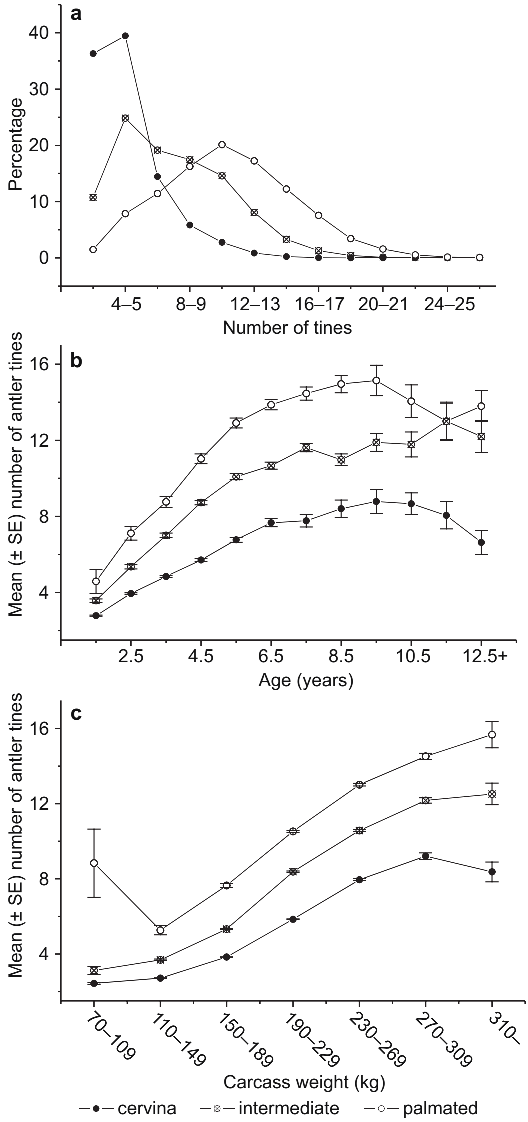

Fig. 7. (**a**) Percentage distribution of the number of tines on cervina, intermediate and palmated antlered bulls in 1976–1999 (N = 76 987). Right and left antler tines and successive even and odd tines are summed up. (**b**) The relationship between mean number of antler tines and age in cervina, intermediate and palmated bulls in 1976–1999 (N = 8362). (**c**) The relationship between carcass weight and number of antler tines in cervina, intermediate and palmated bulls in 1976–1999 (N = 76 637).

Antler type and antler spread

The ANCOVA results (Table 3) showed that antler spread decreased from period I to II (Fig. 3). It rose with increasing age and weight and varied among bulls with different antler types. Overall, the widest antlers occurred in the palmated type and the narrowest in the cervina type (Fig. 8). However, the differences in antler spread between antler types depended on both age and weight (Table 3). Moreover, age and weight dependent differences between the antler types varied somewhat among the combinations of geographic zones and periods (Table 3, data not shown). The palmated antlers were the widest and cervina antlers the narrowest until 6.5 years of age. Thereafter, the statistical difference between palmated and intermediate antlers disappeared (Tukey HSD: $P < 0.05$). The spread of intermediate type antlers increased most rapidly with age. The largest spread was observed from 6.5 to 12.5 years of age, independent of antler type (Fig. 8a). Maximum antler spread was observed at weight ≥ 270 kg in the cervina type and at weight ≥ 230 kg in the intermediate and palmated types. In the data pooled across periods and zones, the difference between intermediate and palmated antlers decreased with increasing

Table 3. ANCOVA results showing the relationship between dependent variables: the number of tines (log transformed; N = 4121) and antler spread (N = 3315), and covariates: age (log transformed), carcass weight and BFI (log transformed), and the categorical variables antler type, geographic zone, and period. Initially a model with all main effects and interactions (except those with two or more covariates) was fitted.

	Number of tines				Antler spread			
Source	df	MS	*F*	*P*	df	MS	*F*	*P*
zone (z)	3	0.12	1.92	0.124	3	51.52	0.35	0.788
period (p)	1	0.47	7.41	0.007	1	577.31	3.95	0.047
antler type (t)	2	0.97	15.46	< 0.001	2	1037.01	7.09	0.001
weight (w)	1	13.61	216.17	< 0.001	1	24412.09	166.89	< 0.001
age (a)	1	20.96	332.81	< 0.001	1	43844.81	299.74	< 0.001
fat (f)	1	0.02	0.28	0.597	1	187.83	1.28	0.257
z × p	3	0.21	3.33	0.019	3	118.02	0.81	0.490
z × t	6	0.07	1.08	0.370	6	19.07	0.13	0.993
z × w	3	0.12	1.94	0.121	3	178.69	1.22	0.300
z × a	3	0.05	0.82	0.480	3	152.10	1.04	0.374
z × f	3	0.05	0.79	0.501	3	154.09	1.05	0.368
p × t	2	0.06	0.97	0.378	2	67.44	0.46	0.631
p × w	1	0.16	2.49	0.115	1	235.14	1.61	0.205
p × a	1	0.04	0.65	0.420	1	40.06	0.27	0.601
p × f	1	0.00	0.00	0.949	1	44.49	0.30	0.581
t × w	2	0.12	1.95	0.143	2	635.39	4.34	0.013
t × a	2	0.47	7.42	0.001	2	722.52	4.94	0.007
t × f	2	0.09	1.44	0.237	2	264.87	1.81	0.164
z × p × w	3	0.21	3.38	0.018	3	182.94	1.25	0.290
z × p × a	3	0.10	1.60	0.188	3	146.64	1.00	0.391
z × p × f	3	0.07	1.11	0.344	3	5.58	0.04	0.990
z × t × w	6	0.08	1.35	0.231	6	54.12	0.37	0.898
z × t × a	6	0.09	1.38	0.221	6	116.81	0.80	0.571
z × t × f	6	0.03	0.46	0.838	6	161.48	1.10	0.357
p × t × w	2	0.02	0.38	0.681	2	164.05	1.12	0.326
p × t × a	2	0.10	1.56	0.210	2	252.01	1.72	0.179
p × t × f	2	0.04	0.58	0.559	2	193.74	1.32	0.266
z × p × t × w	6	0.09	1.40	0.209	6	382.22	2.61	0.016
z × p × t × a	6	0.10	1.56	0.155	6	323.02	2.21	0.040
z × p × t × f	6	0.05	0.80	0.570	6	135.83	0.93	0.473
Error	4031	0.06			3225	3225.00	146.28	

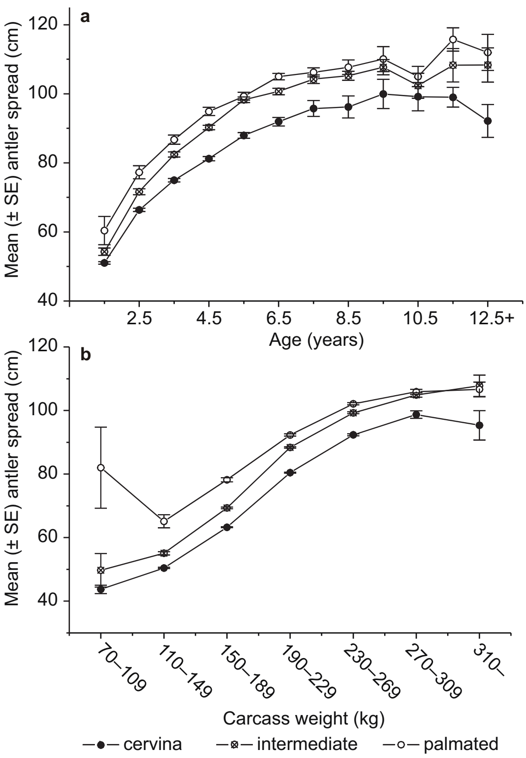

Fig. 8. (**a**) The relationship between antler spread and age in cervina, intermediate and palmated bulls in 1976–1999 (N = 6523). (**b**) The relationship between antler spread and carcass weight in cervina, intermediate and palmated antlered moose in 1976–1999 (N = 49 973).

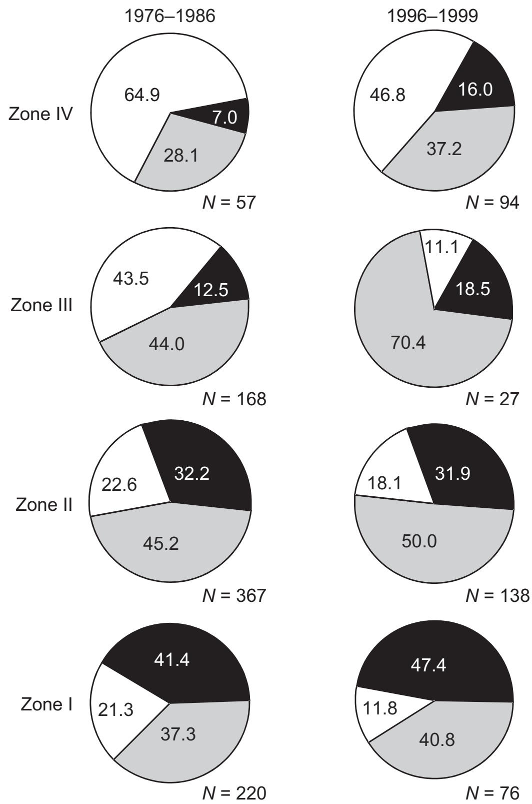

Fig. 9. The distribution of cervina (black), intermediate (grey) and palmated (white) type antlers of 6.5–10.5 year old prime bulls in four geographic zones in 1976–1986 and 1996–1999.

weight and was non-existent among bulls with carcass weight greater than 270 kg (Fig. 8b).

Characteristics and frequencies of prime bulls with different antler types

We defined the prime age of bulls based on antler type frequencies and antler and body size qualities (for the rationale, *see* Discussion). The frequency of palmated bulls was highest at 6.5 to 10.5 years (Fig. 5a), which we considered as prime age.

The frequencies of the different antler types among the prime bulls varied among the combinations of zones and periods (multinomial logistic regression: $\chi^2 = 21.78$, df = 9, $P = 0.01$, $N = 1051$). During both study periods, the proportion of prime bulls with cervina type antlers decreased from south to north. The proportion of palmated bulls increased from south to north during period I. However, the proportion of palmated bulls decreased rapidly from period I to period II in geographic zone III to a level lower than in zones I and II (Fig. 9).

We then performed univariate ANOVA to study variations in weight, BFI, antler spread and the number of tines in relation to geographic zones, periods, antler types and all their interactions among the prime bulls. The results indicated variation in weight ($F_{3,884} = 4.52$, $P = 0.004$), number of tines ($F_{3,994} = 4.11$, $P = 0.007$) and antler spread ($F_{3,805} = 2.98$, $P = 0.031$) among zones. Carcass weight and the number of tines increased from south to north. Antler spread increased from zone I to III; antler spread in zone IV was as low as that in zone I. There were also differences between bulls with different antler types in weight ($F_{2,884} = 5.42$, $P = 0.005$), number of tines ($F_{2,994}$ = 70.89, P < 0.001) and antler spread ($F_{2,805}$ = 15.12, P < 0.001). For all these traits, all antler types differed significantly from each other; palmated bulls had the highest, intermediate bulls intermediate and cervina bulls the lowest values (Tukey HSD: P < 0.05) (Table 4). There was also a significant period × antler type interaction ($F_{2,994}$ = 6.12, P = 0.002) for the number of tines. This was because the number of tines in cervina type tended to increase from period I to II, but no change occurred in the other antler types (results not shown). None of the studied factors or their interactions influenced the amount of fat in the prime bulls.

Discussion

Our aim was to describe the phenotypic polymorphism of the Finnish population of the European moose with different antler types. The main results were: (1) Antler type frequencies change with age. Most young bulls have cervina type antlers. Cervina type decreases and intermediate type increases until the age of 7.5 years, while the proportion of palmated type increases until the age of 10.5 years. Thereafter, the proportion of bulls with palmated or intermediate antlers decreases while the frequency of cervina type increases. (2) The palmated bulls are larger, have more antler tines and a wider antler spread than intermediate or cervina type bulls until the age of 6.5 years. Thereafter, the significant differences in weight and antler spread between palmated and intermediate bulls disappear. However, the palmated bulls have the highest number of tines irrespective of age. (3) Carcass weight increases from south to north in all antler types. (4) Antler spread and number of antler tines in all antler types increase from south to north until zone III but in the northernmost zone IV, they are somewhat smaller than in zone III. (5) The proportion of palmated antlers increases from south to north and has decreased from 1976–1986 to 1996–1999.

Antler type frequencies change when bulls grow older and gain weight. The simultaneous attainment of full size and the culmination of the high incidence of palmated and intermediate antler types at the age of 6.5–7.5 years suggest that the antler type of a bull is closely related to its reproductive maturity and physical condition. Supposing that antler type is an inherited trait, we suggest that age-dependent antler type frequencies are a result of changing penetrance of the antler type genotype. Penetrance is best at the age with the best overall signalling of reproductive maturity. In younger as well as in very old or weak bulls, the penetrance of the palmated or intermediate antler types will be incomplete and the expressivity of the true genotype will be weaker than in the strongest bulls. As a result, the proportion of intermediate or palmated phenotypes will be smaller in these younger, smaller, weaker or older bulls than is the proportion of the intermediate or palmated genotypes in the population. However, in the strongest bulls, the penetrance of the antler type genes is best and the proportions of antler type phenotypes is similar or nearly similar to the proportions of antler type genotypes. According to Bubenik (1973), the cervicorn (cervina) antler type has to be considered as a construction form precedent to palmicorn (palmated) antler types. Therefore, any palmated population can produce a variable number of specimens with cervina antlers if the environmental or social pressure inhibits the hypertelical growth between the tines necessary for palmation. The hypothesis of Bubenik (1973) is supported here.

When a male moose ages, its size and antlers grow larger and the number of tines increases (e.g. Sæther & Haagenrud 1985). Males at their prime have the largest, strongest and architecturally optimally modelled antlers (Bubenik 1983). Later, when the best reproductive years are over, the size of antlers begins to decline (Narushkin 1900, Kramer 1963, Timmerman 1972, Stålfelt 1974, Markgren 1982, Sæther & Haagenrud 1985). The age of bulls with prime antlers seems to differ between studies from 6–8 years to 10–13 years (Collett 1911–1912, Skuncke 1949, Cringan 1955, Yazan 1961, Kramer 1963, Lange 1970 [as cited in Markgren 1982], Timmerman 1972, Prieditis 1979, Sæther & Haagenrud 1985, Gasaway *et al.* 1987, Bowyer *et al.* 2001). Because of the strong relationship between the frequency variation of different antler phenotypes and the variables indicating condition (weight, antler spread, the number of tines), we defined the prime age of the studied bull population to be from 6.5 to 10.5 years on the basis of the maximum frequency of palmated antlers. Most of the studied characteristics reach their maximum value at the age of 6.5 years. Many of these traits also retain high values at 10.5 years, especially among bulls with intermediate and palmated antlers. However, these traits may be of lower value for determining the initiation of senescence than is the frequency of palmated bulls. If only males in good condition maintain palmated antlers, the trait values of these males are expected to stay high as long as they express the palmated type. However, the mere decline in the proportion of palmated antlers after 10.5 years is indicative of senescence.

The fact that antler type frequencies are age-dependent stresses the importance of analysing antler type frequencies from age-standardized populations only. Some authors (Bäckström 1948, Stålfelt 1974, Nygrén & Nygrén 1976) tried to avoid classification difficulties by removing all bulls younger than six years of age or with less than six tines from their data. Despite the poor comparability between studies, some of the earlier results are consistent with ours. The proportion of palmated antlers increases from south to north (Stålfelt 1974, Nygrén & Nygrén

Table 4. Mean carcass weight, number of antler tines, and antler spread among prime bulls (6.5 to 10.5 years old) in relation to geographic zone and antler type.

Character	Antler type	Zone	*N*	Mean	SD	Min	Max
Carcass weight (kg)	cervina	I	114	216.61	30.85	145	287
		II	133	224.22	32.40	130	314
		III	22	240.05	28.88	177	280
		IV	15	238.13	38.82	150	292
	intermediate	I	102	230.91	26.38	150	291
		II	211	232.65	25.42	153	321
		III	79	240.37	27.34	160	315
		IV	46	242.24	32.10	150	310
	palmated	I	49	233.14	23.91	170	293
		II	90	236.87	28.62	170	350
		III	60	245.22	28.22	180	307
		IV	73	254.11	35.36	180	340
Number of tines	cervina	I	119	7.04	2.74	2	16
		II	156	8.34	2.74	2	19
		III	26	8.96	2.52	5	15
		IV	19	8.95	3.03	2	14
	intermediate	I	109	10.17	2.56	4	16
		II	233	11.30	2.63	4	20
		III	92	11.58	2.67	5	19
		IV	50	11.90	3.07	7	25
	palmated	I	51	13.53	2.58	9	21
		II	102	13.91	3.46	4	23
		III	71	14.99	3.55	5	25
		IV	81	14.78	3.02	8	22
Antler spread (cm)	cervina	I	86	92.44	17.07	41	127
		II	125	95.93	16.36	40	135
		III	24	97.71	13.71	66	120
		IV	17	90.41	16.83	60	118
	intermediate	I	88	102.86	14.08	66	130
		II	190	104.01	11.14	72	133
		III	81	104.33	14.11	48	139
		IV	46	98.22	12.82	66	135
	palmated	I	39	106.74	12.22	85	135
		II	79	107.27	12.15	75	140
		III	67	107.96	11.49	75	130
		IV	71	103.38	10.70	70	124

1976, Sæther & Haagenrud 1985, Nygrén 1997). In adult bulls the intermediate antler type is most prevalent (Bäckström 1948, Nygrén & Nygrén 1976, Engan 2001). The average number of tines in cervina type antlers is smaller than in palmated type antlers (Radzevitch 1902–1903 [as cited in Heruvimov 1969], Lönnberg 1923, Skuncke 1949, Koivisto 1965, Markgren 1982). Cervina type antlers seldom have more than 12 tines (Radzevich 1902–1903 [as cited in Heruvimov 1969], Lönnberg 1923, Koivisto 1965). Moreover, antler type literature includes numerous notes on body size, height or colour differences between cervina and palmated types of moose (Narushkin 1900, Collett 1911–1912, Lönnberg 1923, Schulz 1931 [as cited in Munsterhjelm 1937], Munsterhjelm 1937, Skalon 1951 [as cited in Heruvimov 1969], Egorov 1965, Heruvimov 1969). Our results indicate that phenotypic dissimilarities between antler types exist in weight and body size measurements (results of body height, body length and body circumference not shown) but the observed differences are much too small to support the notion of strain differences in European moose.

Antler spread as well as the number of antler tines is regarded as a good indicator of antler size (Clutton-Brock 1982, Gauthier & Larsen 1985, Solberg & Sæther 1994). Most cervid studies show a strong correlation between antler size and body weight (Hyvärinen *et al.* 1977, Priediti s 1979, Sæther & Haagenrud 1985, Bowyer *et al.* 2001). Our results also provide evidence for the strong dependency between antler size and body weight. However, Sæther and Haagenrud (1985) noted that body weight variation could not explain the latitudinal differences in the number of antler tines. Solberg and Sæther (1994) found only a weak relationship between the number of antler tines and body weight and concluded that antler size seemed to vary independently of body mass. It is possible that the Norwegian results came from incomplete data, where no information about antler types and their weight differences was available.

Bergmann's rule states that races of warm-blooded animals from cooler climates tend to be larger than races of the same species from warmer climates (Mayr 1963). The validity of the rule has been debated, but Ashton *et al.* (2000) found broad support for it: 78 of 110 species (including *Alces alces*) showed a positive correlation between size and latitude. Sand *et al.* (1995) found that moose are larger at higher latitudes. According to Bubenik (1998), the general north-to-south decline in antler weight may follow the rule that antler weight in large deer showed a positive correlation with body weight (Huxley 1931 [as cited in Bubenik 1998]). Our results are consistent with these findings.

Average age, carcass weight, tine number and antler spread were higher in 1976–1986 than in 1996–1999, irrespective of antler type. The majority of these differences can be explained by changes in hunting practices. During the study period, moose hunting legislation and hunting goals changed (Nygrén 1998). Both changes successfully strived for better productivity. The proportion of bulls and calves in the bag increased rapidly and hence the proportion of cows and their mean age increased and the proportion of bulls and their mean age decreased (Nygrén *et al.* 2000). Consequently, the mean age of the killed bulls also decreased (Nygrén *et al.* 1999) and their carcass weight, antler spread and number of tines decreased as demonstrated by our data.

Zone III was optimal for producing large body and antler sizes in 1976–1986. The best antlers of the Finnish trofé exhibitions of CIC (International Council for Game and Wildlife Conservation) since the 1980s originated from this zone (K. Nygrén pers. comm.). However, in 1996–1999 the bulls in zone IV had the largest body and antler sizes. This is probably a result of the exceptionally intensive selective hunting that until the later period (1996–1999) caused a drastic decrease in the mean age of bulls in zone III. The average body and antler sizes as well as the frequency of palmated antlers quickly decreased with decreasing age. The decrease in mean age was less dramatic (Nygrén *et al.* 1999), and the temporal change of carcass weight, antler spread and number of tines was less obvious in zone IV where hunting was less intensive and selective hunting less reproduction oriented.

Several comments on the increase of cervina type antler frequencies in different moose populations have been published (Collett 1911–1912, Schulz 1931 [as cited in Munsterhjelm 1937], Munsterhjelm 1937, Skuncke 1949, Voipio 1948, Koivisto 1965), but data on the temporal change in antler type frequencies have only been published in Finland (Nygrén 1997) and Norway (Engan 2001). The results were consistent with our data on all age classes presented. The frequencies of the cervina type had increased and the frequencies of the palmated type had decreased during the periods under study. Moreover, a questionnaire addressed to Finnish hunters (Nygrén & Tykkyläinen 2006) gave parallel results; 57% of the respondents answered that the proportion of palmated antlers had decreased in their hunting grounds. However, age structures can be involved when temporal differences between antler type frequencies have been observed. When temporal frequency differences exist between age-standardized prime-age bulls as well — as was the case in our study between 1976–1986 and 1996–1999 — a change in age structure cannot explain the observed differences between antler type frequencies. This is a challenge for future studies.

In conclusion, our results indicate that antler type phenotypes are linked to other body and antler size characteristics and possibly with different speeds in somatic growth and the beginning of senility. Age is the most important variable regulating the development of a bull's size and antlers. We hypothesize that in 6.5–10.5 year-old prime-age bulls, the penetrance of inherited antler type is the strongest. The mean body and antler sizes of all antler types, as well as the proportion of the palmated antler type, increased to the north in Finland. However, the proportion of palmated antlers decreased during the study period. The decrease was also apparent in the age-standardized prime aged bulls. We hypothesize that intensive selective hunting as well as possible fitness differences between antler types in intensively managed forests may have been involved.

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Appendix. Number of data points and age determination samples from 1976 to 1999.

Year	Antler type	Antler tine number	Antler spread	Carcass weight	BFI	Sample for age determination	Number of bulls
1976	1315	1301	15	1372	1031	640	1484
1977	1678	1676	1288	1673	1284	952	1837
1978	1794	1818	1375	1751	1314	730	1978
1979	1801	1784	1333	1695	1261	723	2043
1980	1621	1689	1268	1642	1063	572	1956
1981	693	739	535	670	490	326	810
1982	1128	1163	846	995	670	198	1293
1983	1344	1381	1007	1157	719	201	1558
1984	1536	1632	1201	1239	938	319	1800
1985	1316	1396	977	1121	885	114	1506
1986	1520	2524	2069	2323	739	999	2679
1991	7401	7644	4645	7239	4219	0	7870
1992	8429	8708	4823	8289	4386	0	9056
1993	8459	8810	4959	8259	4496	0	9057
1994	8007	8312	4947	7952	4501	0	8556
1995	6221	6481	3712	6228	3503	0	6709
1996	4962	5158	3020	4984	2859	0	5317
1997	6494	6570	4428	6311	2298	1342	6766
1998	7876	8055	5279	7691	3870	1416	8329
1999	12103	12465	7614	11744	4969	1755	12858
1976–1999	85698	89306	55341	84335	45495	10287	93462