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Variation in growth pattern of male moose *Alces alces* after two contrasted periods of hunting

Raisa Tiilikainen[1,*], Tuire Nygrén[2], Jyrki Pusenius[1] & Vesa Ruusila[3]

[1)] *Finnish Game and Fisheries Research Institute, Joensuu Game and Fisheries Research, Yliopistokatu 6, FI-80100 Joensuu, Finland (*corresponding author's e-mail: raisa.tiilikainen@rktl.fi)*
[2)] *Finnish Game and Fisheries Institute, Joensuu Game and Fisheries Research, Yliopistontie 4, FI-82900 Ilomantsi, Finland*
[3)] *Finnish Game and Fisheries Research Institute, P.O. Box 2, FI-00791 Helsinki, Finland*

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Exploitation by humans impacts wildlife in many ways. Selective harvesting regimes affect demography of the remaining population, and increased mortality shortens life expectancy affecting optimal life-history strategies. We studied this in a Finnish moose (*Alces alces*) population using harvest data on age, carcass weight, antler spread and tine number, and compared the growth in body weight and that of antlers in male moose after adult-biased and mixed age class harvesting. According to our results, both body weight and antler growth of young males increased after mixed age class harvesting. Changes in growth patterns were affected by population density and sex ratio, but as the period effect still remained in the growth patterns after removing the effects of density and sex ratio, we suggest that the change in male moose growth patterns might have resulted from the harvest-induced young-male age structure and higher harvest pressure among young male moose.

Introduction

There is growing concern regarding the consequences of human exploitation of wildlife species. Besides over-exploitation of populations, the potential evolutionary effects of selective harvesting have received attention of biologists. Especially adaptive changes in life histories have been in focus (e.g. Gordon *et al*. 2004, Proaktor *et al*. 2007, Coltman 2008, Fenberg & Roy 2008). Age and size at maturation are important life-history traits that influence survival, reproductive effort and growth, offspring survival and length of reproductive lifespan, and thereby expected lifetime fecundity (Roff 1992, Stearns 1994). Demographic pressure to mature early must be balanced by trade-offs with other fitness components that explain delayed maturity (Stearns 1994). Furthermore, life-history trade-offs are predicted to evolve in response to differences in extrinsic mortality rates (Gasser *et al*. 2000).

Majority of studies on the effects of size-selective harvesting on growth and age (size) at maturity have focused on fish (Fenberg & Roy 2008, and the literature therein). In fish, harvest pressure is indiscriminate of sex, yet in large terrestrial vertebrates (mostly ungulates), harvesting is usually both sex and size selective (Fenberg & Roy 2008), and it is still unclear if the evolutionary responses to harvesting observed in fish can be applied to terrestrial species. Different predictions can be made according to whether selection is positively or negatively size-selective. Evolutionary models suggest that size-dependent mortality among large individuals causes maturation size to decrease (in fish: Ernande *et al*. 2004), and mortality among small individuals is predicted to induce delayed maturation at larger sizes (in ungulates: Proaktor *et al*. 2007). Size-dependent mortality may also have more complex effects on maturation adaptations (in fish: Gårdmark & Dieckmann 2006). Evolutionary models for size-selective harvesting have also received empirical support both in fish (Conover & Munch 2002), and in ungulates (Coltman *et al*. 2003, Festa-Bianchet *et al*. 2004, Garel *et al*. 2007, Fenberg & Roy 2008).

Furthermore, elevated mortality induced by harvesting alone (whether size-selective or not) is expected to lead to a very small number of individuals surviving to old ages and attaining large sizes, leaving relatively young individuals to dominate the population (Gasser *et al*. 2000, Festa-Bianchet 2003, Proaktor *et al*. 2007, Milner *et al*. 2007, Fenberg & Roy 2008). Biased sex- and/or age-specific hunting may strengthen the selection for increased reproductive effort earlier in life, and for reduced body size and earlier maturation (Festa-Bianchet 2003, Proaktor *et al*. 2007). In fish, these factors have also been connected to population decline (Olsen *et al*. 2004).

Populations usually display sufficient genetic variation needed for age at maturation to evolve (Réale & Festa-Bianchet 2000, Roff 2000, Olsen *et al*. 2004, Charmantier *et al*. 2006). It is, however, difficult to separate environmental effects and genetic changes (Garel *et al*. 2007), and earlier maturation may simply reflect phenotypic plasticity (Olsen *et al*. 2004). Biased sex- and/or age-specific hunting often biases the sex ratio and age structure of a population (e.g. Ginsberg & Milner-Gulland 1994), and may thus cause several demographic side effects (Milner *et al*. 2007) and eventually affect population dynamics (Festa-Bianchet 2003). Consequently e.g. density-dependent changes in growth patterns may be observed. Growing number of examples of rapid evolution in long-lived organisms indicates that many species respond quickly to new selective pressures (Ashley *et al*. 2003, Svensson & Gosden 2007), and that selective pressures associated with human activity can be strong (Palumbi 2001).

Harvesting by humans does not necessarily select prey according to availability or vulnerability (Ginsberg & Milner-Gulland 1994), but is often guided by laws and/or hunter preferences (Coltman *et al*. 2003, Nilsen *et al*. 2006). Hunting effects can be particularly pronounced in licence harvesting and/or if the population size and structure are regulated by hunting (Ericsson 1999, Milner *et al*. 2007). Hunting imposes directional selection especially when the individuals targeted are selected based on heritable morphological traits (Coltman *et al*. 2003, Garel *et al*. 2007).

The intensively harvested moose *Alces alces* population in Fennoscandia (e.g. Lavsund *et al*. 2003) has very low natural mortality in near absence of natural predators (Ball *et al*. 1999, Stubsjøen *et al*. 2000, Ericsson & Wallin 2001, Nygrén 2003). The Finnish moose population has experienced dramatic changes in its numbers and structure (Lavsund *et al*. 2003; Fig. 1), and the population size and structure have been controlled by licence-based hunting (Nygrén & Pesonen 1993). Before the 1970s, population densities were low and harvesting focused mainly on adults (Fig. 1a), but since the mid-1970s harvesting has been targeted at individuals of low reproductive value (i.e. calves and young adults, mainly males) to ensure the productivity of the population (Nygrén & Pesonen 1993, Lavsund *et al*. 2003). Consequently, the proportion of females and their mean age has increased in the Finnish moose population and the proportion of males (Fig. 1b) and their mean age has decreased (Nygrén *et al*. 2000, Nygrén *et al*. 2007).

The moose has a rapid body growth rate, and its body size is positively correlated with reproduction (Sæther & Heim 1993, Sand 1996). There is also a trade-off between growth and reproduction especially in young individuals (red deer: Yoccoz *et al*. 2002, moose: Garel *et al*. 2006). A male moose matures at the age of 1.5 years but the prime age is usually reached at 6.5 years (Mysterud *et al*. 2005, Nygrén *et al*. 2007). Body masses of large ungulates vary accord-

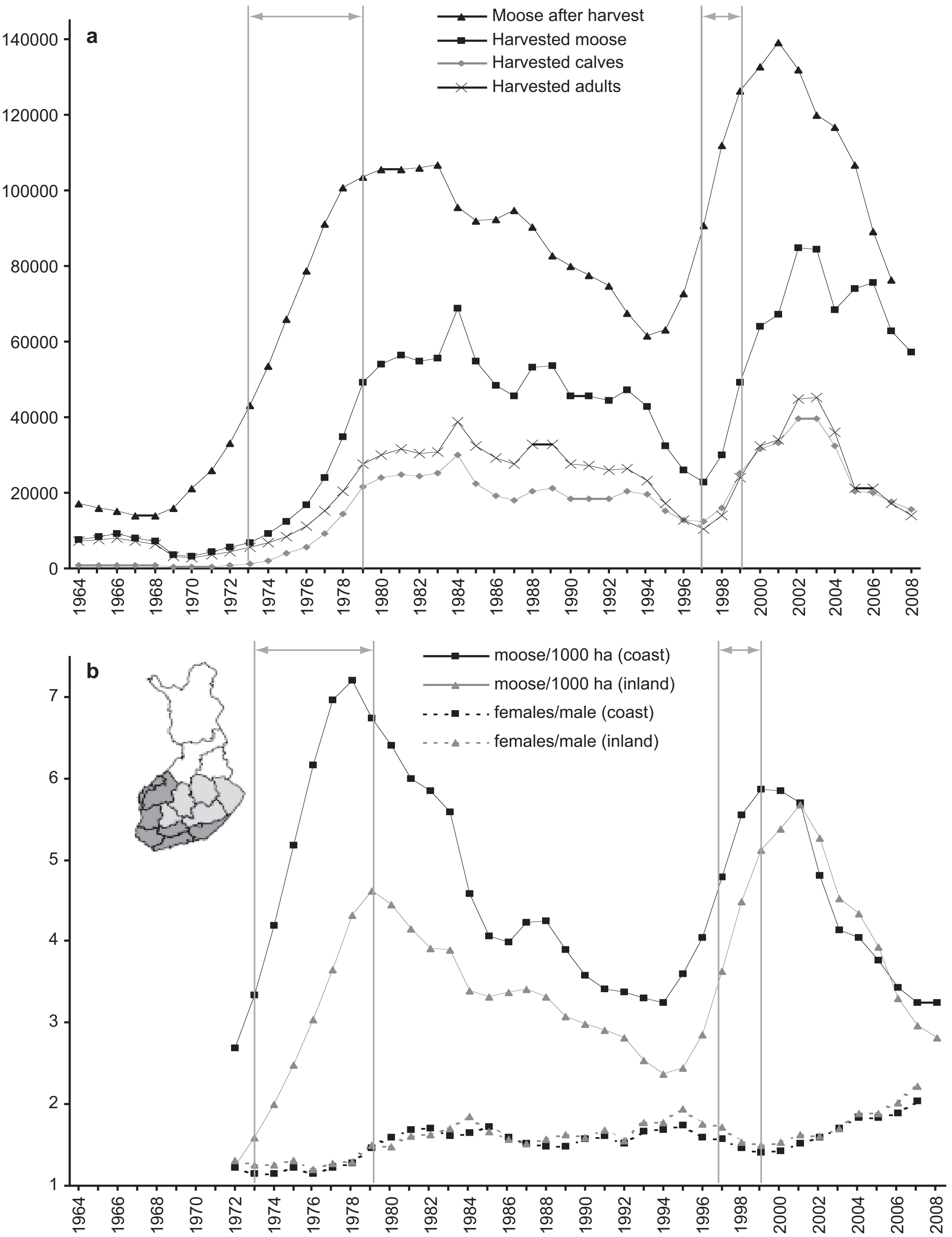

Fig. 1. — **a**: Total harvest numbers and moose numbers after harvest during 1964–2008 in Finland. — **b**: Moose density (moose/1000ha) and sex ratio (females/males) during 1973–2008. The study periods are indicated with grey vertical lines and arrows. The study area (map in the lower panel) was divided by the median of the length of the growing season in 1965–1999 in southern Finland according to game management district borders: ≥ 165 days (coast; dark grey) and ≤ 165 days (inland; light grey).

ing to density-dependent food availability and stochastic environmental variation (Sæther *et al.* 1996, Sæther 1997), and indirectly according to hunting as a response to changes in density or structural composition of a population (Ginsberg & Milner-Gulland 1994, Solberg & Sæther 1994, Langvatn & Loison 1999, Solberg *et al.* 1999, 2000, Laurian *et al.* 2000, Coltman *et al.* 2003, Sæther *et al.* 2003). Both hunting pressure and hunting selectivity against young has increased in Finland (Fig. 1a). While increasing hunting pressure is expected to favour early and lightweight reproduction, high mortality among young is expected to favour late and heavyweight reproduction in females (Proaktor *et al.* 2007).

We used harvest data to study both direct and indirect harvest effects on male moose growth patterns in Finland after adult biased hunting in 1973–1979 and mixed-age structure harvest in 1997–1999. First, we hypothesised that stronger harvesting pressure during the period from yearling to prime age (Table 1 and Fig. 1) might lead to a population where sexual maturation is attained early in life because animals which reproduce before others will be positively selected. Second, as compared with the adult-biased harvest before the 1970s, the female-biased sex ratio and the younger age structure of males of the second period would encourage increased growth at a younger age due to reduced competition from older males (but *see* Mysterud *et al.* 2003, Garel *et al.* 2006). Further, assuming that a rapid growth rate involves costs, we hypothesised a decrease in age and size when prime age is reached. We measured the body and antler growth of male moose, and tested if they differed between the two harvest patterns under different population density and structure.

Material and methods

Study area

Finland is located between 60°N and 70°N in the coastal zone of Eurasia. It is characterised by both a maritime and a continental climate, depending on the direction of airflow (Nygrén *et al.* 2007). Our study area covered 12 game management districts in southern Finland whose total size was ca. 152 960 km^2 (land area), comprising mainly (> 70%) managed forests (Finnish Forest Research Institute, national forest inventory data).

Environmental seasonality has been found to affect the moose growth (Garel *et al.* 2006, Herfindal *et al.* 2006a, Herfindal *et al.* 2006b), therefore, we studied the effects of winter (temperature and snow depth during January–March

Table 1. Numbers of moose in age classes in two study periods: low, adult-biased harvest (1973–1979) and intensive, mixed age structure harvest (1997–1999) in both regions (coast and inland). Numbers given separately for body weight (W), antler spread (AS) and tine number (TN).

Age		1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5+
1973–1979													
Coast	W	410	566	697	616	350	199	119	64	39	12	8	23
	AS	141	176	234	179	152	74	61	26	13	5	5	7
	TN	294	328	381	314	212	129	81	39	19	8	7	10
Inland	W	155	208	227	220	169	87	52	36	14	7	6	10
	AS	25	40	53	72	68	43	34	19	4	2	1	1
	TN	92	122	134	147	121	71	39	27	9	5	2	6
1997–1999													
Coast	W	694	469	328	197	98	51	34	13	5	5	5	1
	AS	597	358	361	201	103	52	30	12	4	2	5	2
	TN	715	437	312	231	108	58	34	15	6	3	5	2
Inland	W	381	340	253	173	81	37	36	18	9	7	8	10
	AS	333	281	247	166	87	36	31	17	8	4	6	8
	TN	383	302	275	181	91	37	33	18	10	5	8	9

on the year of harvest) and growing season conditions (length as well as heat and rain summations on the year of harvest) on the carcass mass regionally, as well as between our study periods 1973–1979 and 1997–1999 (*see* Data analysis). The yearly climate variables were obtained from the Finnish Meteorological Institute and they were fit at game management district level so that information from the observation station best to describe the area in question was used.

Commercial forestry practices shape Finnish forest landscape possibly providing better forage to moose. Indeed, young forest stands have been found to increase forage by moose (Kálen & Bergquist 2004). During winter, when other food resources are scarce, small and advanced seedling stands of Scots pine (*Pinus sylvestris*) are mainly exploited by moose (Heikkilä & Mikkonen 1992, Heikkilä & Härkönen 1998), Scots pine being also the most abundant tree species in Finland (Finnish Forest Research Institute, national forest inventory data). Thus we compared the area of small and advanced seedling stands regionally between the study periods (*see* Data analysis). This data was obtained from the national forest inventories (VI 1971–1976, VII 1976–1984 and VIII 1996–2003) carried out by the Finnish Forest Research Institute.

Population variables

The yearly estimates of population size were calculated retrospectively for each game management district as the number of moose after harvest. We used the following simple model of population growth of a harvested population:

$$N_{t+1} = (1 + R_t) \times N_t - H_{t+1},$$

where N_t is the minimum number of moose present after harvest in year t, H_{t+1} is the harvest in year $t + 1$, and R_t ia the reproductive rate in year t, estimated as the ratio of the number of calves to the number of adults observed during the first week of hunting season. The proxy for N_{t+1} was the number of moose left after hunting given by the hunters (e.g. Solberg & Sæther 1999, Ericsson & Wallin 1999). The value of N_{t+1} was subsequently corrected using the relationship between the estimate of hunters and the calculated population size in a constructed time series. As an estimate for the population sex-ratio, we used the hunters' estimate females/males index in each year for each game management district.

During both study periods, the moose population was in a growth phase (Fig. 1b). However, the first period followed several years of relatively low density, while the second period followed a period of higher density, although declining (Fig. 1; Lavsund *et al*. 2003). The moose densities were higher in coastal Finland, where the higher densities were found during the first study period (1973–1979). Inland, the densities were higher during the second period (1997–1999; Fig. 1 and Table 2). In both areas the sex ratios (females/males) were higher during the second period (Table 2).

Moose data

Two data sets were used: (1) data on male calf weights in 1976–1979 (n = 1339) and 1997–1999 (n = 9680); and (2) data on weight, antler spread and antler tine number in adult (≥ 1.5 year old) bull moose in 1973–1979 (n = 4659) and 1997–1999 (n = 3450). In both data sets, the data were collected during the hunting seasons of 1973–1979 (from 15 October to 15 December) and 1997–1999 (from the last saturday of September to 15 December). Hunters made all measurements of the carcass weight (kg), the number of antler tines and the antler spread (cm). During the second study period, hunters reported the carcass weight as measured (n = 1961) or estimated (n = 1448) weights in kilograms (Nygrén *et al*. 2007). When both were available (n = 156), estimated and measured weights were strongly correlated (r = 0.905) with measured weights being slightly higher than estimated weights (measured mean ± SD = 187.19 ± 39.869; estimated mean ± SD = 184.58 ± 34.337; t = 1.914, df = 155, p = 0.057).

The antler spread is the maximal width of the antlers measured between the outermost tines. The total tine number is the count of tines of both antlers. In the age sample data, age was determined using the method of Sergeant and Pimlott (1959), i.e. from the root of the first or the second incisor. From 1973 to 1979, the age was determined by the Finnish Game and Fisheries Research Institute, and from 1997 to 1999 by Matson's Lab in Montana, USA.

The moose-hunting season overlaps with the rut, and males participating in the rut generally lose some weight (Miquelle 1990, Mysterud *et al*. 2005). Weight increases with age and males of different ages invest and participate differently in the rut (e.g. Mysterud *et al*. 2005), and therefore male moose body weight is generally corrected for a possible effect of shooting day on weight (e.g. Garel *et al*. 2006). Because of the possible effect of harvest date on carcass weight and the effects of estimated carcass masse first we adjusted the carcass weight to that on 15 October, the first killing date available in both study periods. We calculated the adjusted body weight from the regression of carcass mass after splitting the data on age.

Data analysis

Environmental variables

First, we made scatterplots of all different environmental variables (*see* Study area) against the adjusted carcass mass with linear regression fit line for all data and also separately for each age group. As they all were insignificant and yet environmental seasonality has in other studies (Garel *et al*. 2006, Herfindal *et al*. 2006a, Herfindal *et al*. 2006b) been found to influence moose growth, we divided the study area (12 game management districts in southern Finland) further into two regions (Fig. 1) according to the length of the median growing season in 1964–1999 being ≥ 165 days on the coast and ≤ 165 days inland and used these regions in our further analyses to account for the possible environmental effects.

The growth period of moose

Moose has a distinct growth period and a more stable prime-age phase, whilst body and/or trait size may fluctuate according to factors such as season, forage conditions and ageing (Sand *et al*. 1995, Garel *et al*. 2006). While density may affect moose body size through density-dependent food limitation (Sæther 1997), population sex ratio may influence antler size and male

Table 2. Differences in the mean environmental variables: length (days), effective heat sum (°C per day) and total rainfall (mm) of the growing season, mean (January–March) winter temperature (°C) and snow depth (cm), and population variables: sex ratio (females/males) and density (moose/1000ha) in the study regions in coastal and inland Finland between the study periods 1973–1979 and 1997–1999. The standard deviations (± SD) are also given.

	Length		Effective heat sum		Total rainfall	
	1973–1979	1997–1999	1973–1979	1997–1999	1973–1979	1997–1999
Coast	165 ± 21.1	175 ± 15.4	1238 ± 159.5	1369 ± 160.6	319 ± 80.8	359 ± 94.5
Inland	147 ± 10.1	163 ± 14.3	1107 ± 106.4	1222 ± 99.1	326 ± 96.1	316 ± 75.6
	Winter temperature		Snow depth			
	1973–1979	1997–1999	1973–1979	1997–1999		
Coast	–5.1 ± 2.8	–4.5 ± 1.3	25 ± 16.7	21 ± 10.2		
Inland	–6.7 ± 3.1	–7.8 ± 1.3	41 ± 18.3	36 ± 12.7		
	Females/males		Moose/1000 ha			
	1973–1979	1997–1999	1973–1979	1997–1999		
Coast	1.23 ± 0.158	1.47 ± 0.107	6.56 ± 2.296	5.03 ± 1.182		
Inland	1.31 ± 0.161	1.54 ± 0.145	3.49 ± 1.341	4.28 ± 0.777		

body size through different levels of intraspecific competition among males (e.g. Solberg & Sæther 1994, Festa-Bianchet 2003, Mysterud *et al*. 2005, Garel *et al*. 2006). Hence, we first tested whether density and sex ratio affected growth using a univariate analysis of variance (ANOVA). We performed ANOVA for each of the dependent variables (harvest date adjusted carcass mass, antler spread and tine number). The independent covariates were density during the year of harvest (year t), density of the previous year (year $t - 1$), sex ratio during the year of harvest (year t) and their interactions at the game management district level. We used logarithmically transformed tine number to account for a normal distribution.

The residuals of these first analyses were used in another ANOVA to find the age class when the prime age was attained separately for both periods and regions. The dependent variables were the residuals of adjusted body weight, antler spread or antler tine number and age class as a categorical independent variable. We chose the age class when the prime age was reached to be the first age class for which the mean of the dependent variable did not statistically ($p > 0.05$) differ from the mean of its preceding age class. We compared the successive age classes using *a priori* 'repeated' contrasts. This contrast compares the mean of each level (except the last) to the mean of the subsequent level. Males being ≥ 9.5 years old were all pooled because of small sample sizes of the older age classes (Table 1).

The oldest age class when the prime age was reached in all combinations of period and region was 6.5 years. Therefore, we analysed growth from 1.5 to 6.5 years using age as a continuous covariate. Also in this analysis we used the residuals of the first analyses to test whether period still explained any variation in growth rate of body weight, antler spread and tine number after the effects of density and sex ratio had been accounted for. Other independent variables in this last ANOVA were the two time periods studied, region and all interactions between the covariate age, period and region. A significant interaction between age and period would indicate differential growth between the periods studied.

Results

Environmental variables and habitat

During the second study period (1997–1999), the snow depth decreased in both regions, and in coastal Finland winters were warmer. Also during the second period, in both regions the growing season was longer and warmer, and coastal Finland received more rainfall (Table 2). The area of small and advanced seedling stands in southern Finland decreased from 1971 to 2003 by ca. 20% (from 33 470 km^2 to 26 970 km^2).

Based on the existing knowledge (Garel *et al*. 2006, Herfindal *et al*. 2006a, Herfindal *et al*. 2006b), the observed changes in the environmental conditions (*see* Table 2) would most likely have caused growth changes opposite to those hypothesised in the present study. Thus, we did not consider the changes in environmental conditions as likely causes of the observed changes in growth patterns between the study periods, and therefore did not include the environmental effects in the analyses of male moose growth pattern.

Body weight

The harvest-date adjusted body weight of a male moose was affected by both density in year $t - 1$, that is the year before the harvest ($F = 6.306$, df = 1, MS = 8519.278, $p = 0.012$) and the sex ratio in the year of harvest ($F = 3.881$, df = 1, MS = 5243.291, $p = 0.049$) of the population, as well as by their interaction ($F = 6.133$, df = 1, MS = 8284.752, $p = 0.013$). The results for the population density in the year of harvest was a borderline ($F = 2.739$, df = 1, MS = 3699.546, $p = 0.098$). The results of ANOVA with 'repeated' contrasts over 1.5 year olds indicated that the increase in body weight levelled off at the age of 6.5 years in the combinations of period and region (Fig. 2). When the effects of density and sex ratio were removed, the residuals of harvest-date adjusted body weight (body growth) between 1.5 and 6.5 years revealed statistically significant interaction between period and age (Table 3). The results indicated that the growth

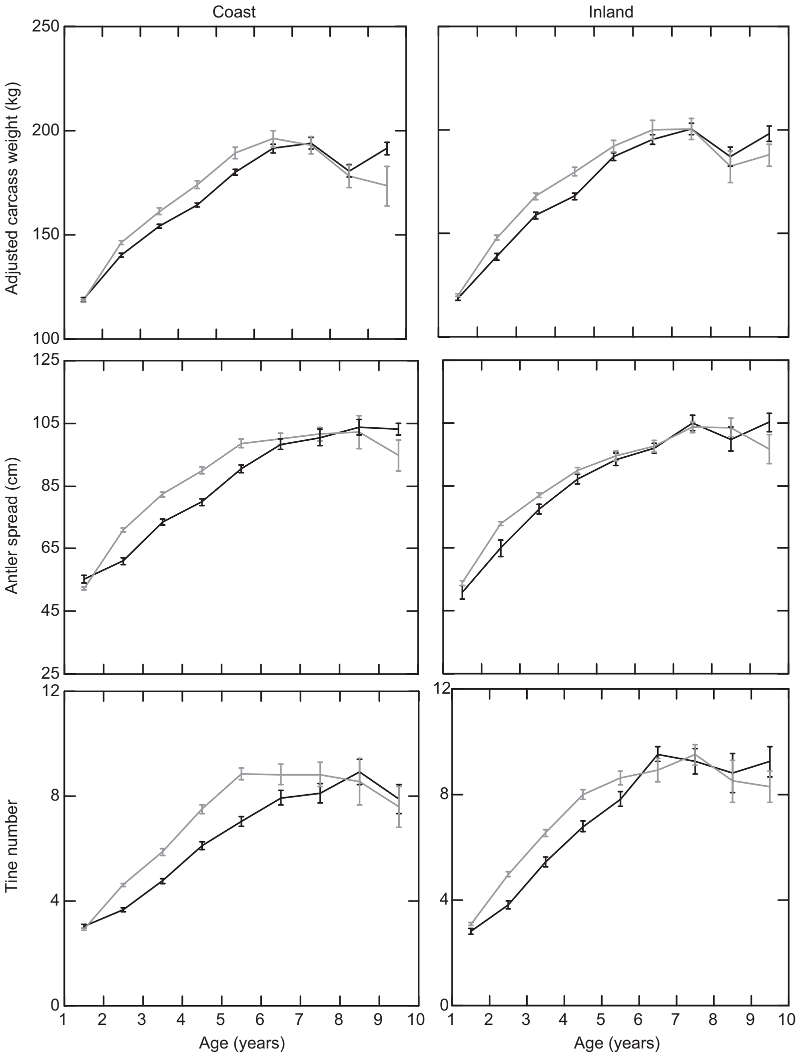

Fig. 2. The mean ± SE killing date adjusted carcass weight (kg), antler spread (cm), and antler tine number in relation to male age from actual data sets of the adult-biased harvest structure in 1973–1979 (black) and of mixed age harvest structure in 1997–1999 (grey) on the coast and in the inland. The ≥ 9.5 years old are all pooled because of small sample sizes in the older age classes.

Table 3. The results of an ANOVA analysing the effects of period, region, age and all their interactions on standardised residuals for killing date adjusted body weight (df = 6517), antler spread (df = 4115) and logarithmically transformed tine number (df = 5513). Statistically significant combinations are set in boldface. The results are based on type III Sum of Squares.

		Weight			Antler spread			Tine number		
Source	df	MS	*F*	*p*	MS	*F*	*p*	MS	*F*	*p*
Period	1	0.18	0.44	0.511	0.89	2.04	0.153	6.81	14.78	< **0.001**
Region	1	3.53	8.30	**0.004**	2.12	4.85	**0.028**	0.37	0.81	0.369
Age	1	2903.95	6836.85	< **0.001**	1265.87	2898.91	< **0.001**	2288.64	4967.68	< **0.001**
Period × Age	1	23.51	55.34	< **0.001**	8.28	18.96	< **0.001**	9.35	20.29	< **0.001**
Region × Age	1	0.25	0.60	0.440	1.52	3.48	0.062	3.08	6.68	**0.010**
Period × Region	1	2.24	5.28	**0.022**	3.67	8.41	**0.004**	10.18	22.09	< **0.001**
Period × Region × Age	1	1.19	2.81	0.094	3.60	8.24	**0.004**	5.94	12.89	< **0.001**
Error		0.25			0.44			0.46		

was faster in 1997–1999 as compared with that in 1973–1979 (Fig. 2). There were also significant main effects of region and age. Body growth was greater inland than on the coast, and increased with age (Fig. 2). Growth was faster during the second period despite that the mean of the harvest-date adjusted carcass weight of male calves were smaller in both areas during 1997–1999 than during 1976–1979 (in 1976–1979: on the coast 83.1 ± 11.16 (SD) kg, $n = 619$; inland 84.4 ± 10.24 (SD) kg, $n = 645$; in 1997–1999: on the coast 81.6 ± 11.5 (SD) kg, $n = 7821$; inland 81.2 ± 10.72 (SD) kg, $n = 5413$).

Antler spread

The antler spread was affected by density of the year before the harvest ($F = 4.998$, df = 1, MS = 2330.437, $p = 0.025$) and the sex ratio during the year of harvest ($F = 13.171$, df = 1, MS = 6141.356, $p < 0.001$) of the population, as well as their interaction ($F = 5.197$, df = 1, MS = 2423.543, $p = 0.023$). There was also a significant interaction between the densities in the year of harvest and in the previous year ($F = 5.195$, df = 1, MS = 2422.218, $p = 0.023$) as well as a three-way interaction between both density measures and sex ratio in the harvest year ($F = 5.141$, df = 1, MS = 2397.418, $p = 0.023$).

The results of ANOVA with ‘repeated‘ contrasts for 1.5 year olds indicated that the increase of the antler spread levelled off at the age of 6.5 years in 1973–1979 and at 5.5 years in 1997–1999 on the coast (Fig. 2). Inland, the antlers mainly spread until the age of 5.5 years during both periods, but also between 6.5 and 7.5 years.

When the effects of density and sex ratio were removed, the residuals of the antler spread between 1.5 and 6.5 years revealed statistically significant interactions between period and age, period and region and between period, region and age (Table 3). These interactions indicated that, although the rate of increase in the antler spread was greater in 1997–1999 than in 1973–1979, the difference in the antler spread was smaller inland than on the coast, and that the antler spread relative to male age differed between regions and periods (Fig. 2). Regarding the effects of region and age, the antler spread differed regionally and increased with age.

Antler tine number

The antler tine number was affected only by sex ratio during the year of harvest ($F = 9.030$, df = 1, MS = 2.948, $p = 0.003$) of the population, and there were no significant effects of density (year of harvest: $F = 1.369$, df = 1, MS = 0.447, $p = 0.242$; previous year: $F = 0.383$, df = 1, MS = 0.125, $p = 0.536$) nor any significant interaction between sex ratio and density ($F = 1.575$, df = 1, MS = 0.514, $p = 0.210$).

The results of ANOVA with ‘repeated’ contrasts over 1.5 year olds indicated that the increase in antler tine number levelled off at the age of 6.5 years in 1973–1979 in both regions. During the second period (1997–1999), the tine numbers grew until the age of 5.5 in both regions, but also between 6.5 and 7.5 years inland (Fig. 2).

When the effects of density and sex ratio were removed, the residuals of antler tine number between 1.5 and 6.5 years revealed statistically significant main effects of period and age (Table 3), which indicated that antler tine number increased with age and differed between the study periods. There were also statistically significant interactions between period and age, region and age, period and region, and also between period, region and age (Table 3). These interactions show that the increase in tine number was higher in 1997–1999 than in 1973–1979, but the difference was greater on the coast than inland. The growth patterns in relation to age also differed between regions (Fig. 2).

Discussion

Our results show that there were major changes in Finnish male moose growth patterns during the past decades. Along with major changes in hunting practices, both body weight and antler growth increased in young males during the second study period (1997–1999). The increase was affected by population density and sex ratio, but even when those effects were removed, growth of body weight and antler size were still faster during the second period. On the other hand, it could also be that our population variables for density and sex ratio were only rough measures, although the hunters' observations have been proven to reflect the variation in e.g. population sex ratio reasonably well (e.g. Solberg *et al*. 2002). Depending on the region and measured character, this faster growth may have led to male moose reaching the prime-age at younger age. Our results are contradict the size-selection theory that mortality among small individuals is predicted to induce delayed maturation at larger sizes (female red deer: Proaktor *et al*. 2007). The results are, however, consistent with theories that predict high mortality rates in all age classes increasing the optimal reproductive effort early in life and decreasing the optimal age of maturity (Gasser *et al*. 2000, Fenberg & Roy 2008). When resources are not scarce, the principle benefit of early maturation is demographic as early maturing individuals have better possibilities to survive at least until first reproduction, and their offspring can start reproducing earlier which results shorter generation times, and thus higher fitness (Stearns 1994).

When harvest focuses on young individuals and/or males, the age distribution of males shifts towards younger individuals and sex ratios shift towards females (Ginsberg & Milner-Gulland 1994, Solberg *et al*. 1999, Mysterud *et al*. 2002, Lavsund *et al*. 2003, Nygrén *et al*. 2007). This alteration accentuates the need to be able to compete with other (mainly young) individuals of the same sex and the need to breed at a younger age. The average body and antler size of harvested male moose in general decreased in Finland between 1976–1999 (Nygrén *et al*. 2007: fig. 3), which implies the younger age structure in the male-moose population. Also the antler type frequencies changed towards cervina and intermediate types which are most common in young males (Nygrén *et al*. 2007). Yet, according to our results, the growth rates of Finnish male moose increased as indicated by the increase in body and antler sizes relative to age. When survival and thereby future reproductive success is decreased by increasing extrinsic mortality, the investment in current reproduction should increase. With a high harvest pressure on a moose population consisting of relatively young individuals, a strong selection among males from yearling to prime age might lead to a population where sexual maturity is gained early in life, since males reproducing before others will be positively selected (Festa-Bianchet 2003).

During our study, Finnish moose population became more female biased (Fig. 1) and the age structure of males biased towards young individuals (Nygrén *et al*. 2007). In hunted ungulate populations, sub-adult males are more likely to reproduce at a younger age because of the reduced number of competitive older males during the rutting season (Milner *et al*. 2007, Laurian *et al*. 2000). Reproduction involves costs, especially in young males, because until the somatic growth is completed, there is a negative trade-off between survival and reproduction (Mysterud *et al*. 2003, Garel *et al*. 2006). Therefore, in polygynous ungulates, males often use an income breeding strategy when young and shift to capital breeding tactic at prime age (Mysterud *et al*. 2005, Mysterud *et al*. 2008). However, in an intensively harvested moose population where male mortality is high, a high growth rate could also increase fitness more than a long period of slow growth. Accordingly, we detected larger size and faster growth rates in antlers after mixed age class harvest. Antlers are secondarily selected reproductive ornaments grown every year, which reflect males' present reproductive effort and physical condition (Clutton-Brock 1982, Solberg & Sæther 1993). Consequently, antler growth pattern is very flexible and subject to various effects including environmental ones (Solberg & Sæther 1993, 1994). These and relatively low sample sizes may partly explain the fluctuating antler sizes in prime-age males in our study. The age- and sex-specific harvesting may also influence the reproductive effort of the species (e.g. Festa-Bianchet 2003, Gordon *et al*. 2004), especially in a population where the age structure of males is biased towards young individuals and population density is relatively low.

Higher somatic growth before prime age is expected to detract from reproductive resources (Yoccoz *et al*. 2002, Mysterud *et al*. 2004, Garel *et al*. 2006). In our study, the growth rates of both body weight and antler size were higher after mixed age class harvest, but contrary to our predictions, on the coast also the maturation size (when reaching prime age) was higher (Fig. 2). On the other hand, the costs might be paid later in life in the form of, for example, earlier senescence but these implications could not be studied using our transversal data consisting of mainly young individuals. It is also possible that the trade-offs between current reproduction and survival will only appear under food stress (Strearns 1994). The fairly moderate moose densities in Finland probably insure enough forage to moose. Although the age structure of Finnish forests has become younger due to commercial forestry practices (Finnish Forest Research Institute 2001), the proportions of the forest development classes important to moose, i.e. young and advanced seedling stands (Heikkilä & Mikkonen 1992, Heikkilä & Härkönen 1998), have in fact slightly decreased (Finnish Forest Research Institute, national forest inventory data). Nevertheless, the effect of managed forests on moose growth patterns needs more research in the future.

Strength of the changes in the growth rates differed regionally, although the general patterns were similar. The differences between the regions are probably due to differences in the environmental conditions: inland, the growing season is shorter and cooler which has been found to affect positively male moose growth and body size (Garel *et al*. 2006, Herfindal *et al*. 2006a, Herfindal *et al*. 2006b, Nygrén *et al*. 2007). Both study periods represent a phase of increasing population size (Fig. 1). Before the first period (1973–1979), moose population had relatively low density (Fig. 1), and most older males harvested would have lived at a low population density during early development, and many yearlings would have experienced conditions of growing population density. In the second period, harvest followed several years of relative stability of higher density, albeit it was slightly declining (Fig. 1). Density and climate that occur early in life have been found to influence male adult body mass (Solberg *et al*. 2004), and therefore there might be cohort effects (Solberg *et al*. 2004, Solberg *et al*. 2007), which require further research. Increased density is expected to decrease male body size (Solberg & Sæther 1994). However, density is not only a matter of population size but a complex interaction between population size and habitat quality (Garel *et al*. 2006). Also in our study, the period effect remained even after removing the effects of density and sex ratio on male moose growth. In the Finnish moose population, the effects of harvesting seem to override other sources of population fluctuation (Luoma 2002), and the Finnish moose population dynamics appears to reflect the harvesting policy and its structural properties.

Generally in moose harvest, hunters have been shown to select larger/older males, but the selectivity decreases as the hunting pressure on the moose population increases (e.g. Solberg *et al*. 2000). Although we cannot fully rule out possible effects of hunters' selectivity on our data, moose hunting in Finland is not focused on trophy or management hunting (*see* Mártinez *et al*. 2005 on red deer ranch hunting), which can give rise to differences in age–size relationships depending on the hunting method. Selectivity in Finnish moose harvest is mainly aimed at calves and young adult males, females with calf/calves being protected from the hunt by law to ensure high reproduction. Larger males are, to some extent, shot at the beginning of the harvest period but as the hunting season proceeds and there are still quotas left, smaller males become harvested as well. When population needs to be cut down, the harvest targets to also adult females. Furthermore, hunting with a dog has become more popular (Ruusila & Pesonen 2004), which may increase hunting pressure on females (Ball *et al*. 1999).

A major difficulty in addressing these issues is the lack of detailed data on harvested populations that span a sufficiently long time for evolutionary changes to occur (Proaktor *et al*. 2007). Whether in Finnish moose population these implications on growth rates caused by harvesting are adaptive or due to phenotypic plasticity or simply caused by demographic changes (female biased sex ratio and young male age structure) cannot be fully argued using our data. Our results show that growth of both primary and secondary characters in young males have increased, which may have also brought on prime age at a younger age.

As the period effect still remains in the growth of young male moose after removing the effects of density and sex ratio, we suggest that the change in male moose growth patterns might be caused by harvest-induced demographic changes in population structure and higher harvest pressure towards young, sub-adult male moose. Increased role of young males in reproduction has been connected to several demographic side effects (Milner *et al*. 2007). In future, we need to study more in detail the effects of a different harvest structure as well as harvest pressure on moose body weight and antler size, and find out their influence on moose life histories. Age and size at maturation affect the population reproductive potential, and therefore any change in these traits might have a strong impact on population dynamics and sustainable harvesting (Milner *et al*. 2007, Proaktor *et al*. 2007). Our results highlight the need for taking evolutionary effects into account in the responsible long-term management of exploited populations.

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