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Raisa Tiilikainen

The effects of selective harvesting on life history traits of moose Alces alces

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ABSTRACT

Exploitation by humans has multifaceted consequences for wildlife. Selective harvesting regimes affect the demography of the remaining population, and increased mortality shortens life expectancy, affecting the optimal life history strategies. Moose populations are subject to intense harvesting, predominantly on juveniles and males, in order to maximise the annual harvesting yield. The aim of this thesis was to study the possible life history consequences of this selective harvesting. Along with major changes in hunting practices, Finnish male moose growth patterns in terms of both body weight and antler size have increased. The occurrence of the antler types most prominent in young males have also increased. Furthermore, the results indicate that the reproductive investment of young males has increased in Finland. This suggests that in female-biased populations with a young male age structure, hunting may increase the reproductive investment of males favouring current reproductive investment over reproduction in the future. In general, moose body condition seems to be relatively good in Finland. There is a positive relationship between the body weights of female calves and population productivity, as large calves often become large and more fecund adults, and more fecund females create a more productive population. As body mass is a key life history trait, the body weight of moose calves is important not only at an individual level but also at a population level. In populations of moose in poor condition, the variation in recruitment is more often due to varying environmental conditions than to varying body condition. Finnish moose population size and structure is regulated by harvesting. The results suggest that young males have become an increasingly important factor in the Finnish moose population. As in the long term, young male age structure has been associated in other moose populations with several demographic side effects, this underlines the importance of monitoring moose populations and of evolutionarily enlightened management.

*Universal Decimal Classification: 574.3, 591.134, 591.16, 599.735.31, 630*15, 639.111.1*

CAB Thesaurus: Alces alces; life history; populations; population structure; age structure; productivity; reproduction; growth rate; body condition; body weight; antlers; calves; selective harvesting; hunting; wildlife management; Finland

Preface

First of all, I would like to thank all Finnish moose hunters as well as the Finnish Game and Fisheries Research Institute, for providing the data for my studies. My thanks are also due to the FGFRI for providing the office facilities. I am also indebted to the Norwegian Institute for Nature Research (NINA), and Norwegian hunters for the Norwegian moose data. My warmest thanks go to Tuire and Kaarlo Nygrén, Mauri Pesonen, Riitta Tykkyläinen and Maija Wallén, who have played a key role in establishing and developing moose management and research in Finland over the years, and who have taught me a great deal. I am also grateful to University of Joensuu, Emil Aaltosen Säätiö and Suomen Riistanhoito-Säätiö for funding my research.

I wish to thank my team of supervisors, Jorma Tahvanainen at the very beginning and later Heikki Roininen. My warmest thanks go to Vesa Ruusila who guided me all the way during the years of my research, and to Jyrki Pusenius who became involved midway through my thesis work. All of you have always helped whenever needed, but also allowed me to work independently, which I believe is the best training for a researcher-to-be. I sincerely thank Esa Koskela and Jan Lindström who reviewed this thesis and gave helpful comments, and Rosemary Mackenzie who corrected my English.

I am also deeply indebted to Erling Johan Solberg for our collaboration and for teaching me a great deal about scientific thinking. My special thanks go to Erling Johan and also Håkan Sand for sharing their knowledge on everything concerning moose, but especially for welcoming me to take part in Scandinavian moose research.

I want to thank all of you at Joensuu Game and Fisheries Research for the company and the lively discussions during coffee breaks, and especially Hannu Pöysä, not only for your help and guidance in my studies but also for the shared lunch breaks as well as for the company during travel.

As writing a PhD is a learning process, I want to thank everyone at the Ecology and Evolutionary Biology division at the University of Jyväskylä, which I think of as my "scientific home". Without my studies there, surely the road I have travelled would have been a lot rockier. Even though I left Jyväskylä you never left me, and for that I am very grateful, especially my dear friends Carita and Santtu, Jenny, Heikki, Jonna, Panu, Ines, Miia and Miina.

I also want to thank the Joensuu University Choir and my friends there, especially the excellent first altos, for keeping music and Joy in my life, and providing an excellent counterbalance to the scientific work. Likewise, I wish to thank my family and relatives, and friends, especially the Saarinen family, Kaisa, Liinu, Sonja, Heidi and Ulla and my brother Tuomo. Without your friendship and support these past years would have been much harder.

I want to dedicate this thesis to my parents Esa and Jaana who have not only always supported me through my life when I have done things more or less my way, but who also, for example, often even fed me during the long office days. And finally my dearest thanks go to Jarkko for teaching me that nothing is impossible, and whose idea it was in the first place that I should study biology.

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by their chapter numbers in Roman numerals II-V.

II Nygrén T, Pusenius J, Tiilikainen R and Korpelainen J. Moose antler type polymorphism: age and weight dependent phenotypes and phenotype frequences in space and time. *Annales Zoologici Fennici 44: 445-461, 2007.*

III Tiilikainen R, Nygrén T, Pusenius J and Ruusila V. Variation in growth pattern of male moose after two contrasted periods of hunting. *Annales Zoologici Fennici 47: in press.*

IV Tiilikainen R, Nygrén T, Pusenius J and Ruusila V. Reproductive investment and sexual size dimorphism of moose (*Alces alces*) under variable population structure. Manuscript.

V Tiilikainen R, Solberg EJ, Nygrén T and Pusenius J. Spatio-temporal covariation in mean calf body mass and population productivity in Fennoscandian moose (*Alces alces*). Manuscript.

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In the first paper (Chapter II) I was responsible for a large part of the data handling and analysis, and writing, and in the other three papers (Chapters III-V) I was responsible for the majority of the planning, data analysis and writing, all in close collaboration with the co-authors.

Contents

1. General introduction

> "Why study life histories?
> Life histories lie at the heart of biology; no other field brings you closer to the understanding simplicities that unite and explain the diversity of living things and the complexities of their life cycles. Fascinating in themselves, life histories are also the keys to understanding related fields. Life history theory is needed to understand the action of natural selection, a central element of evolution. --- The evolution of life history traits and their plasticities determines the population dynamics of interacting species. Its explanatory power, barely tapped, could reach as far as communities. There is much to be done."
> Stephen C. Stearns, The Evolution of Life Histories (1992).

1.1 LIFE HISTORIES

Life history theory deals directly with natural selection, fitness, adaptation, and constraint. The most important life history traits are individual body size, age and size at maturity, number of reproductive events in life and offspring number and size. The allocation of limited resources between reproduction and survival involves costs, especially in young individuals (Stearns 1992). Body size affects the productivity and mortality of individuals as well as both their intra- and inter-specific relationships. Large body mass is also associated with high fecundity, and in many species large females produce large and/or more offspring (Gaillard et al. 1992; Sæther and Haagenrud 1985; Sand 1996b; but see Gaillard et al. 2000), and larger individuals tend also to mature earlier than smaller individuals (e.g. Sæther and Heim 1993; Garel et al. 2005). The selection pressures that shape the body sizes of individuals are therefore central issues in life history theory (Roff 1992). Age and size at reproduction are key elements shaping adult body size and thus influencing individual survival, reproductive investment and growth, offspring survival and hence the individual's lifetime reproductive success (Roff 1992; Stearns 1992), and therefore eventually also population dynamics.

Organisms differ enormously as to their life histories, and traits such as age at maturity, adult size, mortality rate and age-specific fecundity all show wide variation (Roff 2002). Population density and the structure of the adult population are important factors shaping the life history traits of a species (Stearns 1992). There are also two sources of mortality with which natural populations have evolved: intrinsic and extrinsic. Intrinsic sources of mortality are those that contribute to patterns of senescence and ageing, whereas extrinsic sources of mortality are associated with factors such as predation (Stearns 1992).

1.2 HARVESTING AND ITS EFFECTS ON HARVESTED POPULATIONS

There is an increasing interest in the effects of human activity on exploited species (Gordon et al. 2004; Milner et al. 2007; Coltman 2008; Fenberg and Roy 2008). Not only do human actions change the environment of the species, but they also target the populations themselves by selecting individuals with favourable traits, for example in the trophy harvesting of big-horned or -antlered bulls, and by regulating population structure and density. Size-selective harvesting is common practice in hunting and fishing, and can affect many aspects of the biology of an organism, from life history, demography, genetics and behaviour to the local abundance and biomass of populations, although the effects are multifaceted and often species-specific (Fenberg and Roy 2008).

When compared to natural predation, harvesting does not necessarily select prey according to availability or vulnerability (Ginsberg and Milner-Gulland 1994), but often according to restrictions set by laws and/or to hunter preferences (e.g. Nilsen

& Solberg 2006). Hunting effects can be particularly pronounced in license harvesting and/or if the population size and structure are regulated by hunting (Ericsson 1999; Milner et al. 2007). In harvested ungulate species, intense human exploitation may have particularly pronounced effects on population dynamics (Gaillard et al. 1997; Solberg et al. 1999), and hunters may affect population dynamics not only directly by increasing mortality, but also by generating delayed dynamic responses through changes in the age and sex distribution of a population (Sæther 1987; Solberg et al. 1999). Hunting also imposes directional selection on species, especially when the individuals targeted are selected on the basis of heritable morphological traits (Coltman et al. 2003; Milner-Gulland et al. 2003; Loehr et al. 2007).

Hunting regulations and harvest quotas are typically based on population goals (Festa-Bianchet 2003). Moose harvest, population management and research have long traditions in Scandinavia (Lavsund et al. 2003). The Finnish moose population size and structure have been controlled by licence-based harvesting since the 1970s (Nygrén 2009; Chapter III fig. 1a). A general goal of management actions has been to maintain a stable population size with a relatively high reproduction rate (Chapter V fig. 2), which in turn ensures high harvest rates (Nygrén and Pesonen 1993; Luoma 2002). When the population size is to be reduced, the annual harvest may exceed 50% of the estimated winter population size (Chapter III fig. 1). As a result hunting mortality is very high compared to other sources of mortality (Nygrén 2003; in Norway Stubsjøen et al. 2000). Hunting regulations often target harvesting at particular sex and/or age categories, depending on the harvest or population goals (Kokko et al. 2001). Moose harvesting in Finland is aimed at individuals of low reproduction value; males and young (calves and sub-adult) individuals (Chapter III fig. 1). With one hunting permit, hunters are allowed to shoot one adult or two calves, while females with a calf/calves are protected from harvesting by law. Hence the moose population sex ratio has become increasingly female-biased (Chapter III fig. 1), and the male age-structure towards younger ages.

1.3 THE STUDY SPECIES: MOOSE (ALCES ALCES)

The moose is the largest member of the deer family (Geist 1999) with a live weight of from 350-650 kg (Sand 1996a). The moose is a typical dimorphic species: adult males weigh approximately 24% more than adult females and have an approximately two years longer growth period than females (Garel et al. 2006; Chapter IV fig. 1). Moose body growth can be separated into a growth period and a more stable prime-age where the body weight and also the antler size of males (Chapter III fig. 2) fluctuates according to the environment and condition of an individual. Only males grow antlers that are cast and re-grown annually, hence providing an honest indicator of male condition and quality (e.g. Clutton-Brock & Albon 1982; Solberg and Sæther 1994). Antler size increases with age and body size (Sæther and Haagenrud 1985; Solberg and Sæther 1994; Chapter III fig. 2), and the type of antlers can be classified according to palm width into palmate, intermediate or cervina type (Chapter II fig. 1). Males at their prime have the largest, strongest and optimally designed antlers (e.g. Solberg and Sæther 1993; Geist 1999). The mating season (rut) takes place in September and early October (Geist 1999). The gestation period lasts for 230-240 days, and females normally give birth to one or two calves in late May or early June (Markgren 1969). Twinning frequency is highly variable among populations and may range from 20% to 70% (Franzman and Schwartz 1985; Chapter V). Triple births are rare (Nygrén 2003).

In Fennoscandia moose is a very important wildlife resource. The most efficient tools for increasing yield in managed ungulate species have been selective harvesting of males and young individuals (Sylvén 1995; Sæther et al. 2001). Moose populations began to increase rapidly in the 1960s and have since then been among the most productive and heavily harvested moose populations in the world (Lavsund et al. 2003; Chapter III fig. 1). As a result, a change in the sex and age composition of moose populations has occurred over large parts of Fennoscandia (Lavsund et al. 2003; Milner et al. 2007).

1.4 AIMS OF THE STUDY

The aim of this work was to study the effects of intensive harvesting and population management of moose on the factors that are of importance for the reproduction of the species. The main questions were:

1. Do harvest-induced demographic changes in population structure and selective harvesting of males and young individuals influence moose resource allocation between growth and reproduction?
2. How do the changes in adult population structure affect the sexual size dimorphism and the reproductive investment of the male moose?
3. What is the level of variation in the body weight of moose calves, and how does it translate to population productivity?

According to Finnish hunting legislation (Metsästyslaki 615/93), hunting must be sustainable without risking the populations of the game species, and the productivity of the species must be assured by appropriate management, while the levels of damage to forestry and traffic remain reasonable. Knowledge of the life history traits of the species harvested is important when planning the harvest, and in estimating and predicting its effects.

Despite the strong applied emphasis of this thesis, it also covers the basic issues in the ecology of life histories on growth rates, optimal reproductive investment and reproductive costs. The evolution and plasticity of these life history traits of and among species determines the dynamics of interacting species (Stearns 1992). The aim of the study was to gain a more profound knowledge of moose life histories and the factors that shape them. As the Finnish moose population has been managed and harvested fairly intensively over the past decades, the aim was also to find out whether these actions have influenced moose life histories and if so, what predictions can be made. The main research topics and the data descriptions are summarised in Table 1.

Table 1: *Summary of the main research questions, description of the data and the measured variables studied in the thesis. All data originates from moose observation and harvest data collected by hunters during the moose hunting period.*

Research topic	Description of the data	Measured variables
Chapter II: Spatio-temporal antler type polymorphism in relation to age and body weight	Adult (≥ 1.5 years) male moose in Finland in 1976-86 and 1991-99.	Antler type, tine numbers, antler spread (cm), carcass weight (kg), back fat thickness (cm), age (years).
Chapter III: Growth rates of body weight and antler size in two contrasted periods of hunting.	Adult (≥ 1.5 years) male moose in southern Finland in 1973-79 and 1997-99.	Antler tine number, antler spread (cm), carcass weight (kg), age (years).
Chapter IV: Reproductive investment of moose in two contrasted periods of hunting.	Adult (≥ 1.5 years) male and female moose in southern Finland in 1973-79 and 1997-99.	Carcass weight (kg), antler size relative to carcass weight, age (years).
Chapter V: Spatio-temporal covariation in mean calf body mass and population productivity.	Female and male calves, calving and twinning ratio in Finland and Norway in 1991-2006.	Carcass weight (kg), observed calves/female and % of twins of observed calves/female.

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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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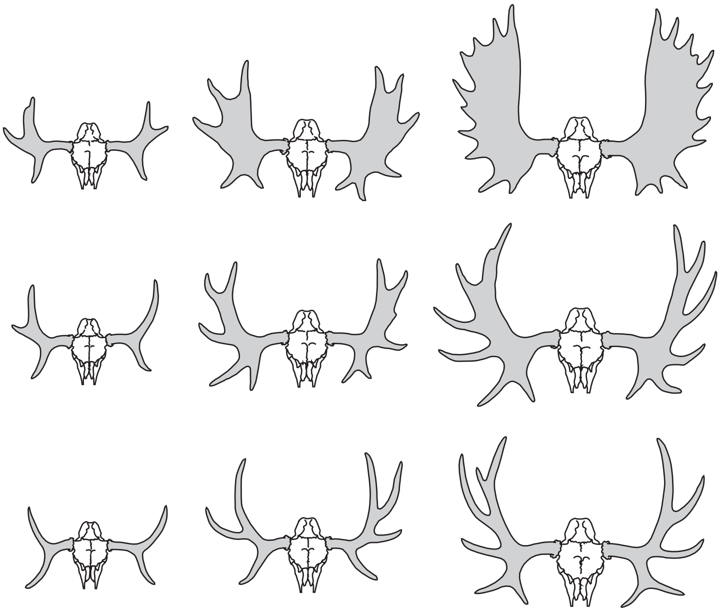

Fig. 1. Stylized drawing of typical palmate (top row), intermediate (centre), and cervina (bottom row) antlers on young (left) and middle-aged (centre) bulls, and on bulls at their prime breeding age (right). (Drawing by Maija Wallén).

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.

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.

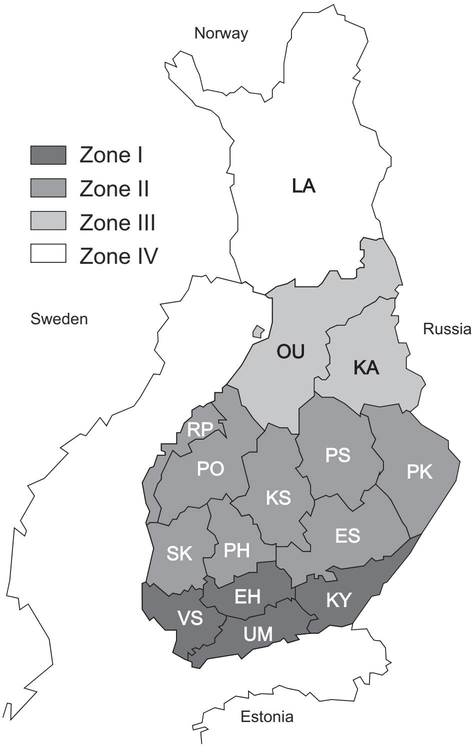

Fig. 2. The study area was divided into four geographic zones from south to north. Data and samples were collected from 15 game management districts (*see* Nygrén 2003).

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: $\chi^2 = 20.66$, df = 6, $P = 0.002$). Moreover, antler type frequencies depended on the age ($\chi^2 = 105.24$, df = 2, $P < 0.001$) and weight of

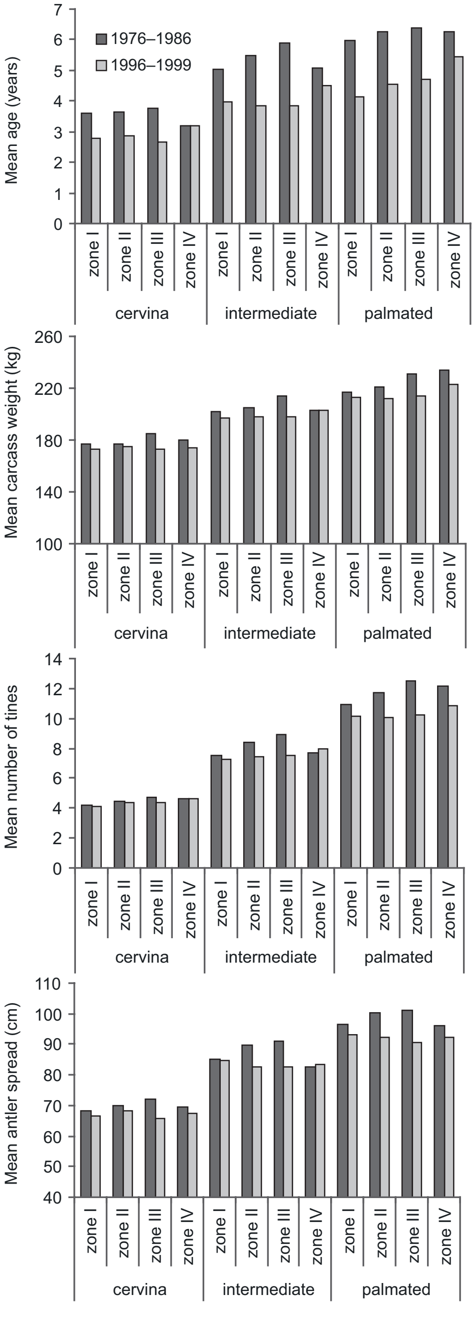

Fig 3. Average age (*N* = 8594), carcass weight (*N* = 42 334), number of tines (*N* = 46 258) and antler spread (*N* = 46 308) of the cervina, intermediate and palmated antlered bulls in four geographic zones in 1976–1986 and 1996–1999.

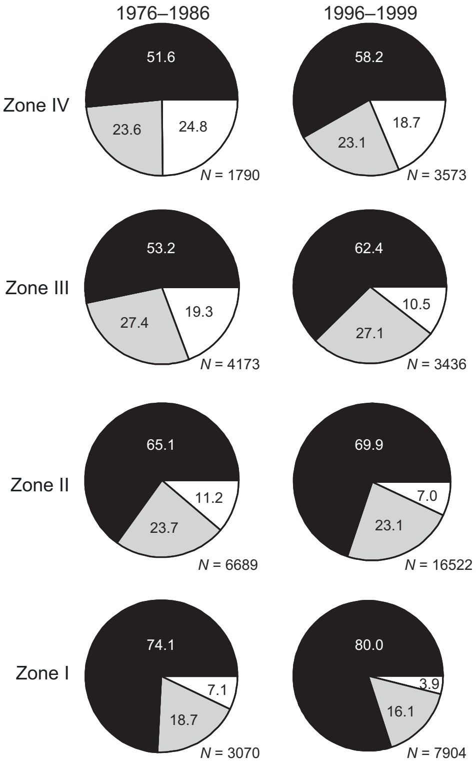

Fig. 4. The distribution of cervina (black), intermediate (grey), and palmated (white) antlers in four geographic zones in 1976–1986 and 1996–1999 (*N* = 47 157).

the bulls. The relationship between weight and antler type frequency changed from period I to II as indicated by the significant weight × period interaction ($\chi^2 = 19.43$, 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

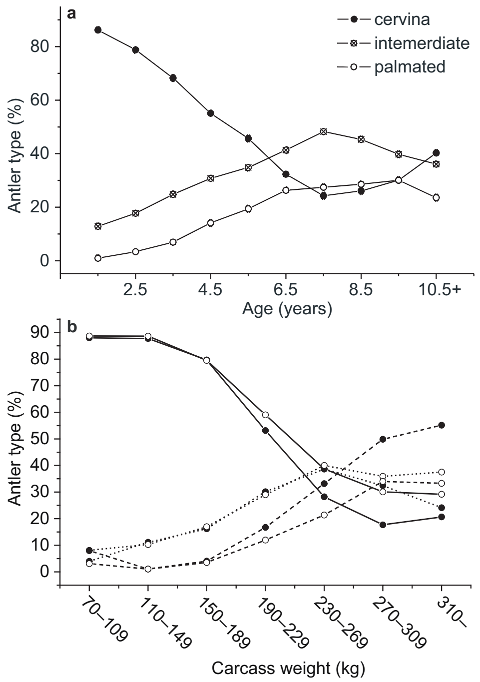

Fig. 5. (**a**) Change in the percentage of cervina, intermediate and palmated antlers with age in 1976–1999 (N = 8362). (**b**) Change in the percentage of cervina (solid line), intermediate (dotted line), and palmated (dashed line) antlers (N = 78 051) with weight in 1976–1986 (black dots) and 1996–1999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

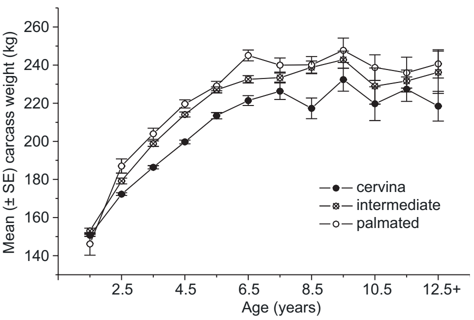

Fig. 6. Mean age-dependence of carcass weight in cervina, intermediate, and palmated antlered bulls in 1976–1999 (N = 7485).

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).

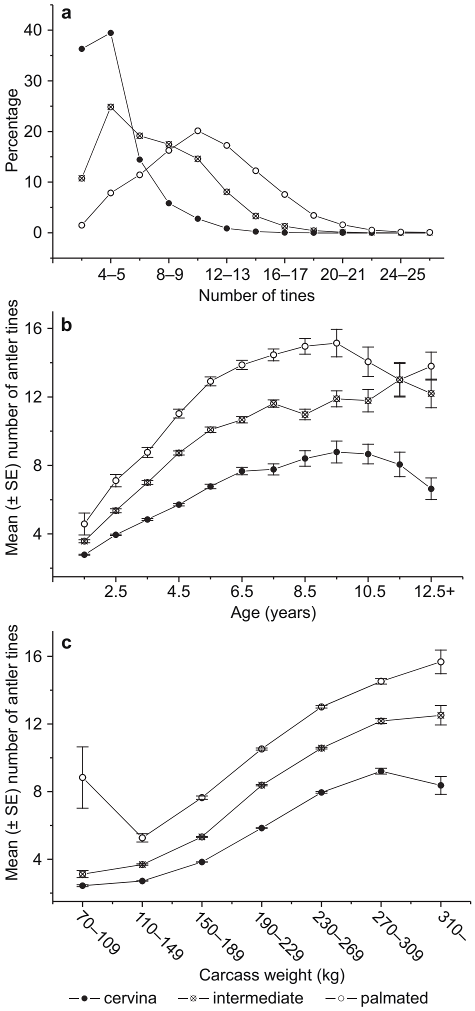

Fig. 7. (**a**) Percentage distribution of the number of tines on cervina, intermediate and palmated antlered bulls in 1976–1999 (N = 76 987). Right and left antler tines and successive even and odd tines are summed up. (**b**) The relationship between mean number of antler tines and age in cervina,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

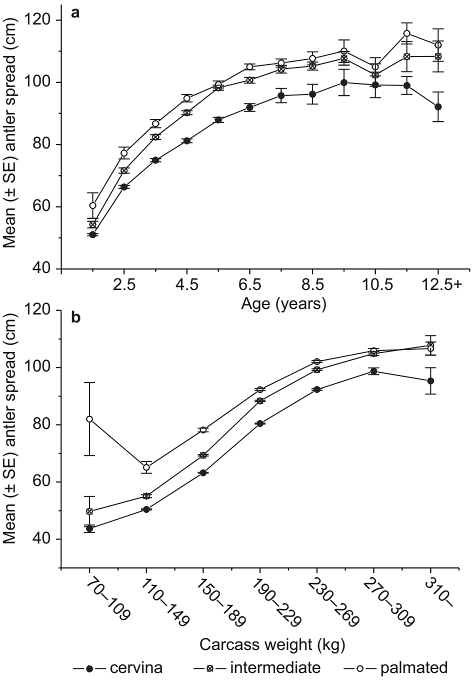

Fig. 8. (**a**) The relationship between antler spread and age in cervina, intermediate and palmated bulls in 1976–1999 (N = 6523). (**b**) The relationship between antler spread and carcass weight in cervina, intermediate and palmated antlered moose in 1976–1999 (N = 49 973).

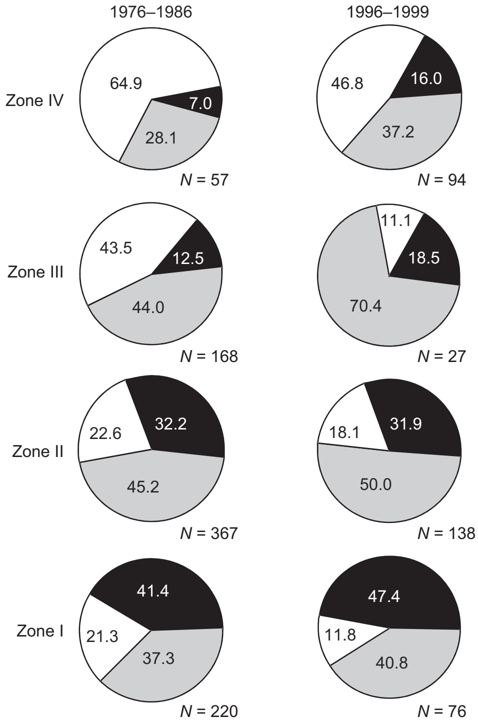

Fig. 9. The distribution of cervina (black), intermediate (grey) and palmated (white) type antlers of 6.5–10.5 year old prime bulls in four geographic zones in 1976–1986 and 1996–1999.

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, Prieditis 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

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

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

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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-

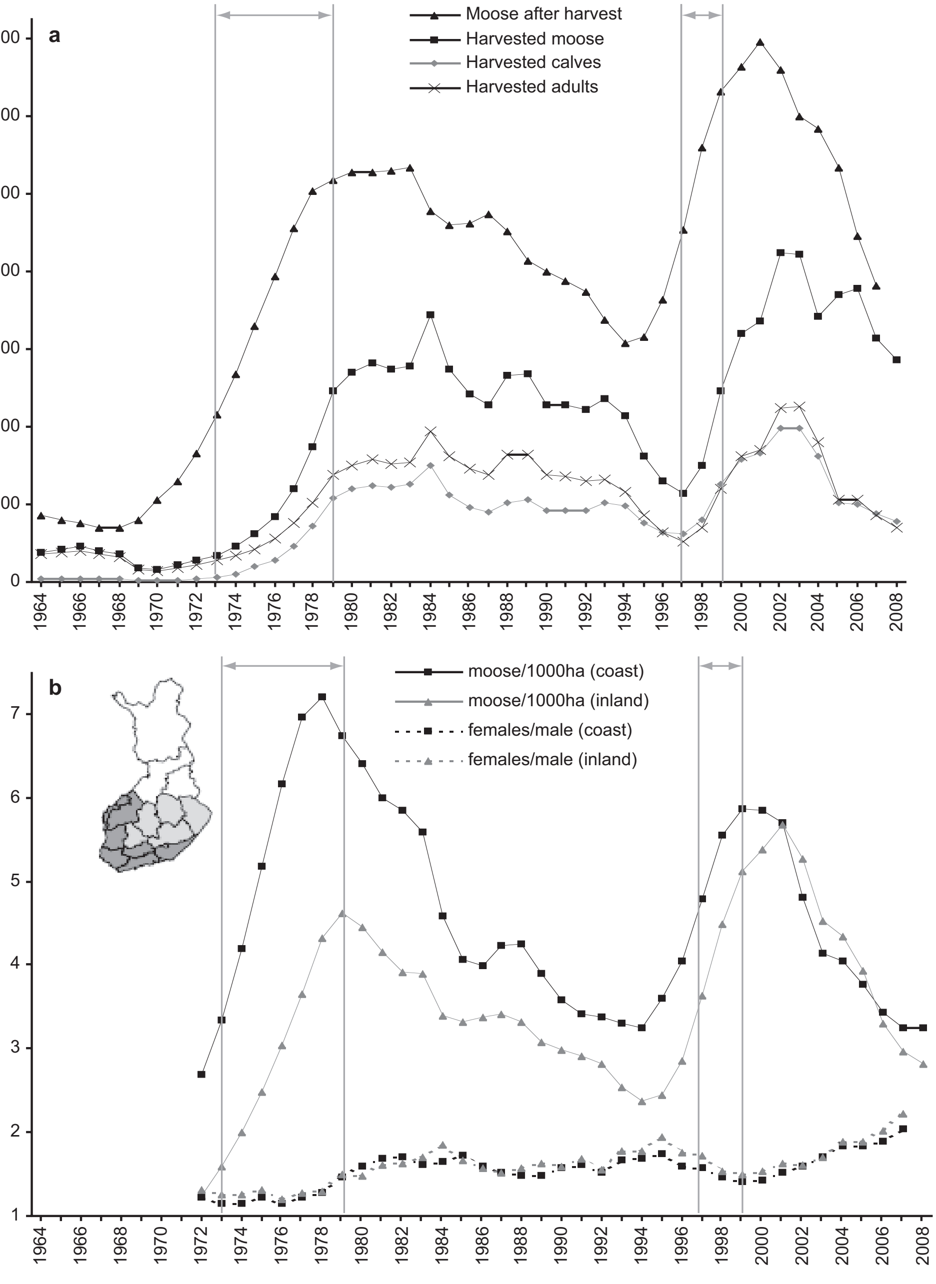

Fig. 1. — **a**: Total harvest numbers and moose numbers after harvest during 1964–2008 in Finland. — **b**: Moose density (moose/1000ha) and sex ratio (females/males) during 1973–2008. The study periods are indicated with grey vertical lines and arrows. The study area (map in the lower panel) was divided 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

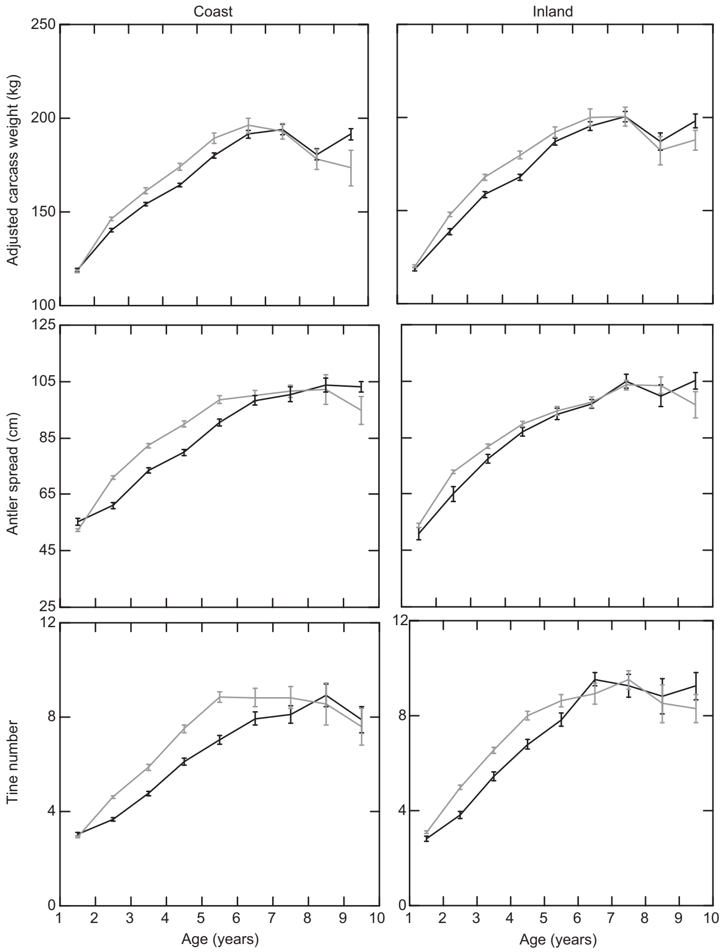

Fig. 2. The mean ± SE killing date adjusted carcass weight (kg), antler spread (cm), and antler tine number in relation to male age from actual data sets of the adult-biased harvest structure in 1973–1979 (black) and of mixed age harvest structure in 1997–1999 (grey) on the coast and in the inland. The ≥ 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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4. Reproductive investment and sexual size dimorphism of moose (Alces alces) under variable population structure.

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Manuscript.

4. Reproductive investment and sexual size dimorphism of moose (*Alces alces*) under variable population structure

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ABSTRACT

Many ungulate populations are subject to intense harvesting, predominantly of juveniles and adult males in order to maximize the annual harvesting yield. An indirect effect of such a strategy is that the proportion of adult males in the population decreases, causing several potential life history consequences. In polygynous mammals such as moose, sexual size dimorphism (SSD) results from the different selection pressures affecting male and female growth tactics in relation to reproduction. Such tactics reflect the sexual selection on males for access to females and the competitive selection on females for access to food. Along with major changes in hunting practices, Finnish male moose growth patterns, in terms of both body weight and sexually selected antler size, have increased. Thus we also

hypothesized an increased reproductive investment of young males (larger antlers relative to body size) due to the reduced competition from older males, and hence increased SSD in the Finnish moose population. Our results indicate that, as well as the SSD, the reproductive investment of young males has also increased in moose populations. The results concur with the earlier results showing increased growth rates in males, hence we suggest that with the increased extrinsic mortality of males, hunting may increase the reproductive investment of males, favoring current reproductive investment over reproduction in the future in a population with a female-biased sex ratio and a young male age structure.

4.1 INTRODUCTION

The most prominent life-history trade-off involves the cost of reproduction, and has two major components, costs paid in survival and costs paid in future reproduction (Stearns 1989). Especially long-lived iteroparous animals balance between allocating their limited resources to current reproduction or to survival and future reproduction (Stearns 1992). The investment in reproductive activity can reduce growth and thereby future reproductive success, and as a result the costs of reproduction are believed to be higher for younger animals than for older ones (Clutton-Brock 1991; Stearns 1992). The allocation of energy to reproduction increases with age (Mysterud et al. 2004), and in size-dependent reproduction, any factor that affects variation in growth rates and thus body size, will indirectly affect the age at maturity and adult fecundity rates of individuals (Sand 1996).

Life-history trade-offs are predicted to evolve in response to differences in extrinsic mortality rates (Gasser et al. 2000). Furthermore, the elevated mortality induced by harvesting is expected to lead to a situation where a very small number of individuals survive to old age and large size, leaving relatively young individuals to dominate the population (Proaktor et al. 2007; Fenberg and Roy 2008). As extrinsic mortality rates increase, reproduction at older age contributes less to fitness since fewer individuals survive to a given age (Gasser et al. 2000). The principle benefit of early maturation is demographic: early maturing individuals have a higher probability of surviving until maturity, and their offspring start reproducing earlier, which leads to shorter generation spans, and thus higher fitness (Stearns 1992). Harvesting of ungulate populations often focuses on young individuals and/or males, skewing the sex-ratios towards females and the age distribution of males towards younger animals (Nygrén and Pesonen 1993; Ginsberg and Milner-Culland 1994; Mysterud et al. 2002; Lavsund et al. 2003), which may ultimately have many demographic side effects (Milner et al. 2007). In intensively managed ungulate populations selection pressure for earlier maturation may arise for two different reasons: Firstly, 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), and secondly, with a high harvest pressure on a population consisting of relatively young individuals, higher mortality among males from yearling to prime-age might lead to a population where sexual maturity is gained early in life, since individuals reproducing before others will be positively selected (Festa-Bianchet 2003).

The body mass of large ungulates varies according to density-dependent food limitation and stochastic environmental variation (Sæther et al. 1996; Sæther 1997), and indirectly according to hunting as a response to changes in the density or structural composition of the population (Ginsberg and Milner-Gulland 1994; Solberg and Sæther 1994; Langvatn and Loison 1999; Solberg et al. 1999, 2000; Laurian et al. 2000; Coltman et al. 2003; Sæther et al. 2003). In polygynous mammals such as moose, sexual size dimorphism (SSD) results from the different selection pressure on male and female growth tactics in relation to reproduction (Clutton-Brock et al. 1988; Andersson 1994; Post et al. 1999). These tactics reflect sexual selection on males for access to females and competitive selection on females for access to food. Consequently, sexual selection favours large male size achieved through rapid early growth to large adult body size and delayed maturation, whereas females are selected to invest in improved body condition and early sexual maturity at the expense of structural size (Clutton-Brock et al. 1988; Andersson 1994). In moose, SSD seems to result from a combination of sexual selection and sex-specific responses to variation in environmental conditions (Garel et al. 2006). Sex differences in body growth strategies due to sexual selection thus promote divergent responses to ecological factors, which in turn ultimately affect SSD (Sæther and Haagenrud 1985; Sand et al. 1995; Loison et al. 1999; Post et al. 1999; Leblanc et al. 2001).

The reproductive investment of male moose consists of primary growth of body size and weight and sexually selected secondary growth of the antlers. Both body weight and antler size increase with age (Nygrén et al. 2007; Tiilikainen et al. 2010), and are closely related to fighting ability and mating success, and consequently to fitness (Solberg and Sæther 1993; Van Ballenberghe and Miquelle 1993; Solberg and Sæther 1994; Bartos and Losos 1997; Stewart et al. 2000; Ditchkoff et al. 2001; Kruuk et al. 2002; Mysterud et al. 2004). Because male reproductive success in ungulates typically depends on male-male combat, it is suggested that males adopt a riskier strategy than females to achieve the greatest possible development of antlers and horns (Festa-Bianchet et al. 2004). An investment in antlers at the expense of body development in younger age classes may result in decreased reproductive success overall, because those individuals ultimately may not be able to obtain the body or the antler size needed in intra-specific competition among males and/or for compatibility with females (Clutton-Brock 1982; Clutton-Brock et al. 1985; Stewart et al. 2000, but see also Sæther et al. 2003). In moose, large prime-aged males stop eating during the rut, in contrast to smaller and younger individuals (Miquelle 1990), and thus rely on accumulated body reserves to satisfy the energy needs of reproduction and survival (Mysterud et al. 2005). Nevertheless, young males participate more actively in reproduction when competition from older males is reduced

(Solberg & Saether 1994; Laurian et al. 2000; Mysterud et al. 2004, but see Sæther et al. 2003).

In the Finnish moose population, hunting is mainly targeted at males and young individuals. This sex-selective harvesting has increased the proportion and average age of females, decreased the proportion and age of males and resulted in an overall increase of population productivity (Nygrén et al. 2000, 2007; Nygrén 2009). Accordingly, there have been major changes in Finnish male moose growth patterns during the past few decades (Tiilikainen et al. 2010). Along with the major changes in hunting practices and population structure, both body weight and antler growth in young males have increased. Hence, in this study, we examine the harvest-induced demographic effects on the male reproductive investment, i.e. antler size relative to body weight. We also examine the variation in sexual size dimorphism (SSD) in the Finnish moose population. By decreasing the proportion of adult males in the population, as a result of which rutting starts earlier in life, hunting may reduce SSD by increasing the reproductive cost for young males. On the other hand, through the increased extrinsic mortality of males, hunting may increase SSD by increasing the reproductive effort of males, favouring current reproductive investment over reproduction in the future.

4.2 MATERIAL AND METHODS

4.2.1 Study area and population variables

Our study area consisted of 12 game management districts in southern Finland (see Tiilikainen et al. 2010). The size of the study area was ca 152 960 km^2 (land area). The game management districts were further combined into two regions according to the length of the median growing season in 1964-1999: ≥ 165 days on the coast and ≤ 165 days inland.

The estimates for population size were calculated retrospectively yearly for each game management district as the number of moose after harvest. We used the simple model (Eq. 1) of population growth of a harvested population

$$N(t+1) = (1+R(t)) \times N(t) - H(t+1) \quad (1),$$

where N(t) was the minimum number of moose present after harvest in year t, H(t+1) was harvest in year t+1, and R(t) was 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 the hunting season. The yearly values of N(t) were solved from equation 1, starting from the year 2007 and using the number of moose remaining after hunting, as given by hunters in the year 2008, as a proxy for Nt+1. The value of N(t) obtained for year 2007 was then used as the value of N(t+1) when solving N(t) for the year 2006 etc. As an estimate for the population sex ratio, we used the ratio of the number of adult females to the number of adult males observed during the hunting season.

During both the study periods 1973-79 and 1997-99, the moose population was in a growth phase. However, the first period came after several years of relatively low density (Nygrén 1987), while the latter period followed a period of higher, although declining population density (Lavsund et al. 2003; Nygrén 2009; Tiilikainen et al. 2010 fig. 1). In addition, the moose densities were higher in coastal Finland, where the higher densities were found during the first study period 1973-79. Inland, the densities were higher during the latter period 1997-99, and in both areas the sex ratio (females/male) and the productivity of the moose population were higher during the latter period (Lavsund et al. 2003; Nygrén 2009; Tiilikainen et al. 2010 fig. 1; Table 1).

4.2.2 Moose data

The data was collected from adult (≥ 1.5 year old) moose (females n = 3901, males n = 7547) during the hunting seasons of 1973-79 (October 15th-December 15th) and 1997-99 (the last Saturday of September-December 15th) (Tiilikainen et al. 2010). Hunters carried out all measurements of carcass weight (kg), number of antler tines and antler spread (cm). During the latter study period, hunters reported carcass weight as measured (n = 1961) or estimated (n = 1448) weights in kilograms (Nygrén et al. 2007). Where both were available (n = 156), both estimated and measured weights were strongly correlated (r = 0.905) and measured weights tended to be slightly higher than estimated weights (measured mean = 187.19, sd = 39.869; estimated mean = 184.58, sd = 34.337; t = 1.914, df = 155, P = 0.057). Antler spread is the maximal width of the antlers measured vertically from tine to tine. The total tine numbers were summed for both antlers. 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, age was determined by the Finnish Game and Fisheries Research Institute, and from 1997 to 1999 by Matson's Lab in Montana, USA. The ≥ 9.5-year-old males were pooled on account of the small sample sizes in the older age classes.

4.2.3 Data analysis

The male moose has a distinct growth period and relatively stable prime-age phase while 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; Nygrén et al. 2007; Tiilikainen et al. 2010). According to our earlier studies, Finnish male moose achieve prime age at approximately 6.5 years (Nygrén et al. 2007; Tiilikainen et al. 2010). As our earlier studies have also indicated increased growth of body weight and antler size, i.e. antler spread and tine number, in young males, we wanted to investigate whether there has also been a corresponding change in the reproductive investment of young male moose. We therefore analysed the reproductive investment of 1.5 to 6.5 year-old males using age as a continuous covariate. As the killing date varied in the harvest data, and moose weight is known to change during the course of the harvest period (e.g. Solberg et al. 2004), we first adjusted the carcass weight to the 15th of October, the first killing date available in both study periods. We calculated the adjusted body weight by regressing carcass mass against killing date after splitting the data on sex and age. To study the relationship between moose antler size and body weight, we used principal component analysis to combine the two antler measures used, antler spread and tine number. As a measure for the actual reproductive investment we used standardised residuals from the regression of antler size (obtained from the principal component analysis) against adjusted carcass weight of the same individual.

As both population density and sex ratio have been found to influence male moose growth and reproductive effort (e.g. Solberg and Sæther 1994), we aimed to control their possible effects on male moose reproductive investment by using a univariate analysis of variance (ANOVA) as follows. First we performed ANOVA with the dependent variable 'reproductive investment' and the independent variables density and sex ratio on year t, and their interaction. The standardised residuals of this analysis were retained and aggregated, and then used in an ANOVA analysis where period, region and the covariate age and their interaction were the explanatory variables. A significant interaction between age and period would indicate differential reproductive investment between the periods studied.

Sexual size dimorphism (SSD) was assessed using the standardised residuals from the regression of male carcass weight against female carcass weight (Ranta et al. 1994; Garel et al. 2006). As the changes in male moose body growth have mostly affected young age classes (Tiilikainen et al. 2010), we analysed the SSD of male and female moose under 6.5 years old. As the examination of the residuals against predicted values did not indicate heteroscedasticity, we used the residuals without any further transformations in our analyses. In order to study SSD between the regions and study periods we used the residuals as the dependent variable in an ANOVA test, where the independent variables were period, region and age, and their interaction. All the statistical tests were performed using SPSS 16.0 for Windows.

4.3 RESULTS

4.3.1 The antler size relative to body weight

The reproductive investment of male moose (antler size relative to carcass weight adjusted for killing date) was affected by both the population sex ratio (females/male) and population density (moose/1000ha) in the game management district in question during the harvest year (Table 2). After eliminating these effects, analysis of the reproductive investment of males between 1.5 and 6.5 years revealed statistically significant interaction between period and region, and also between period, region and age (Table 2). The results indicated that the reproductive investment was higher in 1997-99 compared to 1973-79, and that the change differed between the regions (Fig. 2). The growth pattern was similar in both areas but the change between study periods was greater in coastal Finland than inland. There was also a significant main effect of age, indicating that the antler size relative to body weight increased with age (Fig. 2).

4.3.2 Sexual size dimorphism

In general males grew faster and for a longer time, and were heavier than females (Fig. 1). The sexual size dimorphism (SSD) increased with age (Fig. 1): the mean body weight of yearling males was only 1% higher than that of females (males' mean = 152 kg, n = 1639, sd = 18.7 ; females' mean = 151 kg, n = 982, sd = 19.3), whereas 6.5 year old males' mean body weight was 17.2% (39 kg) higher than the mean body weight of females (males' mean = 227 kg, n = 374, sd = 27.9; females' mean = 188 kg, n = 198, sd = 21.8). The analysis of the SSD of moose between 1.5 and 6.5 years of age revealed statistically significant main effects of period, region and age (Table 3), indicating that SSD increased with age and depended on the period and the region. There was also a statistically significant interaction between period, region and age, indicating that the periodic change of SSD was most obvious among those sub-adult age classes where the body weight of males increased most (from 2.5 to 5.5. years old). The change in SSD differed slightly between the study regions: on the coast the change occurred between 2.5-5.5 years of age and inland mostly between 3.5 to 6.5 years of age (Fig. 3).

4.4 DISCUSSION

Our results suggest that there have been changes in the reproductive investment of young male moose in Finland. These results correspond to our previous results (Tiilikainen et al. 2010) indicating increased growth rates of body and antler size in young males following major changes in hunting practices. The results also suggest that the increased mortality and demographic changes among males induced by harvesting may have contributed to the changes in both male reproductive investment and the sexual size dimorphism (SSD) found in the Finnish moose population. The reproductive investment of male moose is affected by population density and sex ratio, which in Finland are regulated by harvesting. Intensive moose harvesting in Finland has produced female-biased populations with a young male age structure (Lavsund et al. 2003; Nygrén et al. 2007; Nygrén 2009; Tiilikainen et al. 2010). In an intensively managed moose population where male mortality is high, a high growth rate and also an increased reproductive investment probably contribute more to increased fitness than does a long growth period. When body condition is better and/or somatic growth is completed younger (Tiilikainen et al. 2010), it is also possible to invest more to the reproduction at a younger age.

Our study supports the earlier results that differences in the body size of male and female moose result from both sexual selection and sex-specific responses to environmental conditions (Sæther and Haagenrud 1985; Schwartz et al. 1987; Sand et al. 1995; Garel et al. 2006). The increased SSD may reflect divergent growth tactics in relation to reproduction corresponding to changes in ecological factors, males allocating abundant resources to body growth and ornaments and females to increased reproduction. Indeed, the growth rates of male moose as well as the productivity of females have increased at the population level (Lavsund et al. 2003; Nygrén 2009; Tiilikainen et al. 2010; Table 1). Nevertheless, the environmental conditions during our study periods, which should favour SSD, a shorter growing season length and an even or more male-biased sex-ratio (Garel et al. 2006), have developed in the opposite direction (Table 1). The higher population productivity during the study periods may simply be a factor of female-biased sex ratio and/or possibly also of the older average age structure of females. It has also been suggested that high selective harvesting of calves may reduce the cost of reproduction in female moose (Ericsson 2001), which would in turn favour higher SSD in a moose population. We would need individual-level data on female reproduction to fully investigate this.

For young male moose, the somatic growth of body size and weight, as well as the conservation of fat reserves, are highly important for both survival and fitness. At the same time, it is also important to gather experience of rutting events, and young males therefore have to invest an adequate amount of energy in antler growth. A male moose is already able to reproduce at an age of one year, but depending on population demography, it usually takes up to 6 years to achieve the prime age for reproduction (e.g. Mysterud et al. 2005; Nygrén et al. 2007; Tiilikainen et al. 2010), as during the rut, the sub adult ungulate males often lose to older and larger males, and/or are rejected by females (Clutton-Brock et al. 1992; Noyes et al. 1996; Schwartz 1998; Komers et al. 1999). Until somatic growth is completed, there is a negative trade-off between survival and reproduction, and the investment in antler growth must be made with regard to future fitness. Therefore in polygynous ungulates, males often use an income breeding strategy when young and shift to a capital breeding tactic at prime age (Mysterud et al. 2005; Mysterud et al. 2008).

The antlers and horns of ungulates represent one of the most spectacular examples of male secondary sexual traits in vertebrates (Vanpé et al. 2007), and antlers are regarded as an honest advertisement of the male condition (e.g. moose Kokko 1997; red deer Malo et al. 2005; roe deer Vanpé et al. 2007).

Because antlers are cast and re-grown annually and are costly to produce, there should be a strong relationship between energy allocation to antler growth and current environmental conditions (Andersson 1994). On the other hand, selection favours isometry between a trait and body size (Bonduriansky and Day 2003), because even though larger traits are always favoured, larger-bodied individuals have more energy at their disposal and are therefore better able to produce a larger trait size. Accordingly, changes in age and body mass have been found to be more influential than changes in environmental factors in shaping the variation observed in roe deer antler size (Vanpé et al. 2007).

However, sexual advertisement is a reproductive effort of a special kind: what matters is the relative performance when compared to other members of the population, making the problem a game rather than a simple optimisation routine (Kokko 1997). Antlers signal male quality (red deer Vanpé et al. 2007; moose Solberg and Sæther 1993), and therefore investing in antler size may be important for male moose in order to attract females (Clutton-Brock 1982; Solberg and Sæther 1993). A female-biased sex-ratio in harvested moose populations should reduce intra-specific competition among the males (Garel et al. 2006; Nygrén 2009). On the other hand, young male moose are known to increase their reproductive investment when prime-aged males are lacking in the population (Laurian et al. 2000). This raises a question of the role of female choice in the reproductive tactics of moose. The young males that have been able to invest in antler growth would, when larger prime-aged males are lacking, be selected by females (Nygrén 2009). In fish, individuals with a low prospect of survival may invest relatively more in present reproduction when they have less to lose from signalling at a high level than do males in a good condition, especially under conditions of lower competition among males (Candolin 1999, 2000). Also, all males increase their risk-taking when future reproductive opportunities are affected by a high predation risk (Candolin 1998).

The reproductive investment measured as antler size relative to body weight increased with age in our data. This implies that younger males invested less in reproduction relative to body weight than did prime-aged males, but as extrinsic mortality rates increased, also the young males invested more in antler growth and thus in reproduction. For a long-lived iteroparous animal such as the moose, changes in growth rates during the early years of life are vital and can even be critical. When intensive hunting increases the extrinsic mortality of males, however, it is much crucial to be able to reproduce at all, even at a younger age and even when this involves gambling with the chances of survival and/or future reproduction. This may have many demographic side effects over the long term in harvested populations (Milner et al. 2007).

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Figure legends

Figure 1. Adjusted carcass weight (kg, mean ± standard error) of male (—) and female (---) moose during the study periods 1973-79 (black) and 1997-99 (grey) in Finland.

Figure 2. Reproductive investment (standardised residuals from the regression of antler size on adjusted carcass weight) of male moose ≤ 6.5 years of age in coastal (—) and inland (---) Finland between 1973-79 (black) and 1997-99 (grey).

Figure 3. Temporal (study period 1973-79 in black, 1997-99 in grey) and spatial (region 1 = coastal, region 2 = inland Finland) differences in the standardised residuals showing the sexual size dimorphism of adult moose carcass mass between 1.5 and 6.5 years of age. Error bars show 95% of mean.

Table 1: *The differences in growing season length, productivity (calf-cow %, twin %, calves/100 adults, and calves/100 cows), sex ratio (females/male) and density (moose/1000ha) of the populations in the study regions coastal (1) and inland (2) Finland between the study periods 1973-79 and 1997-99. The standard deviations (±SD) are also given.*

	growing season length		**calf-cow %**	
Region	**1973-79**	**1997-99**	**1973-79**	**1997-99**
1	165±21.1	175±15.4	62.2±4.9	67.9±2.0
2	147±10.1	163±14.3	60.5±7.0	68.4±4.5
	twin %		**calves/100 adults**	
Region	**1973-79**	**1997-99**	**1973-79**	**1997-99**
1	47.1±9.4	48.9±4.5	51.4±9.3	59.7±3.0
2	41.3±11.7	46.7±4.3	50.1±12.8	61.5±6.3
	calves/100 cows		**sex ratio (females/male)**	
Region	**1973-79**	**1997-99**	**1973-79**	**1997-99**
1	91.7±7.9	101.0±3.4	1.23±0.16	1.47±0.11
2	86.1±14.7	100.4±7.7	1.31±0.16	1.54±0.15
	density (moose/1000ha)			
Region	**1973-79**	**1997-99**		
1	6.56±2.30	5.03±1.18		
2	3.49±1.34	4.28±0.78		

Table 2: *The results of the ANOVAs analysing firstly the effects of sex ratio (females/male) and density (moose/1000ha) on the male moose reproductive investment (3846), and secondly the effects of period, region, age and all their interactions on the retained residuals of reproductive investment (1354). The significant terms are highlighted in bold. The error degree of freedom is given in parentheses.*

Source	**df**	**MS**	**F**	**Sig.**
Sex ratio	**1**	**14.819**	**16.210**	**<0.001**
Density	**1**	**16.092**	**17.602**	**<0.001**
Period (p)	1	1.954	2.151	0.143
Region (r)	1	0.082	0.090	0.764
Age (a)	**1**	**21.922**	**24.140**	**<0.001**
p x r	**1**	**7.468**	**8.224**	**0.004**
p x a	1	0.873	0.922	0.337
r x a	1	0.065	0.072	0.789
p x r x a	**1**	**6.043**	**6.655**	**0.010**

***Table 3:** The results of an ANOVA analysing the effects of period, region, age and all their interactions on the SSD of moose (935). The significant terms are highlighted in bold. The error degree of freedom is given in parentheses.*

Source	**df**	**MS**	**F**	**Sig.**
Period (p)	**1**	**10.223**	**15.607**	**<0.001**
Region (r)	**1**	**3.219**	**4.602**	**0.032**
Age (a)	**5**	**48.854**	**69.839**	**<0.001**
p x r	1	0.425	0.608	0.436
p x a	5	0.633	0.905	0.477
r x a	5	1.321	1.889	0.094
p x r x a	**5**	**1.775**	**2.538**	**0.027**

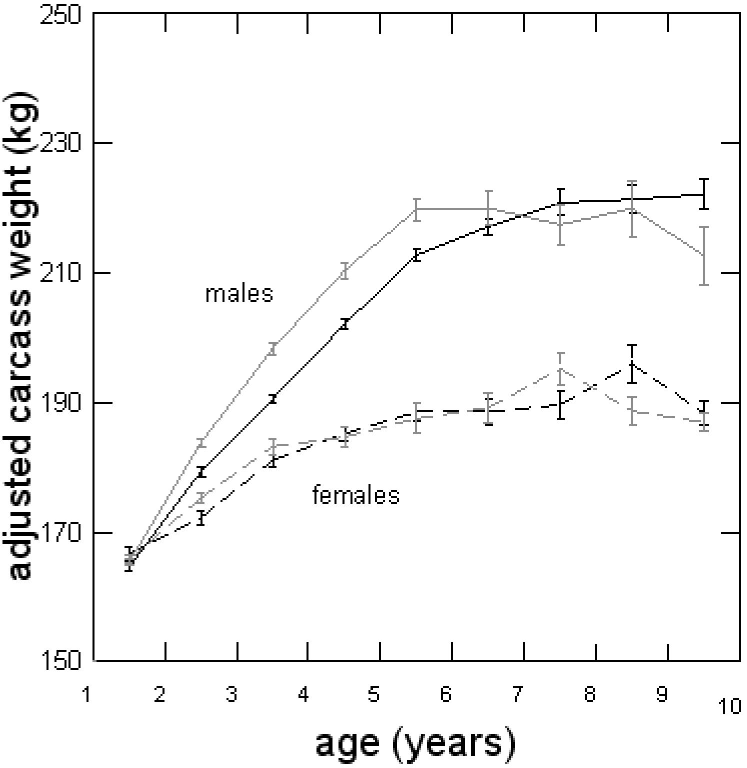
250
230
210
190
170
150
1
2
3
4
5
6
7
8
9
10
adjusted carcass weight (kg)
age (years)
males
females

Figure 1.

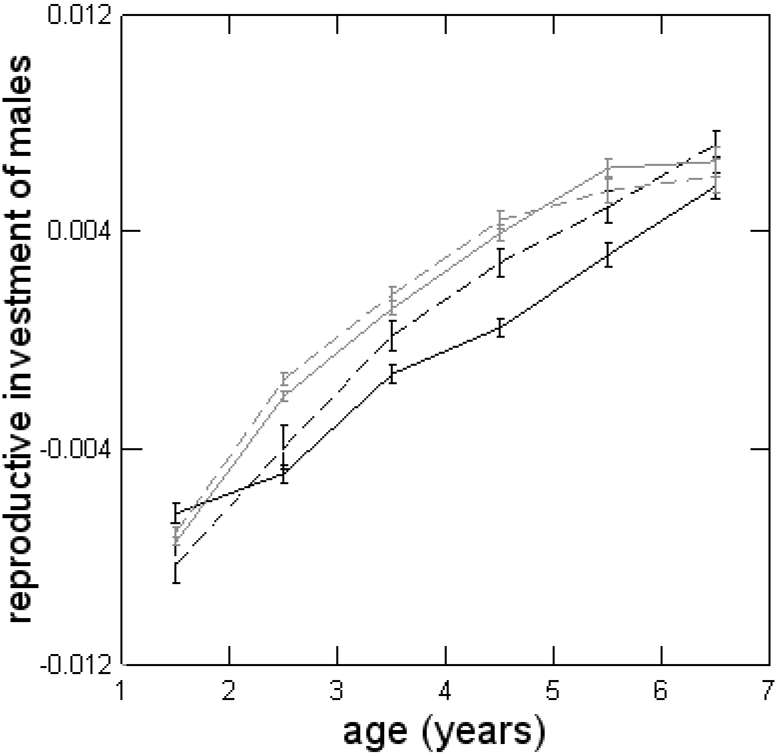
reproductive investment of males
0.012
0.004
-0.004
-0.012
1
2
3
4
5
6
7
age (years)

Figure 2.

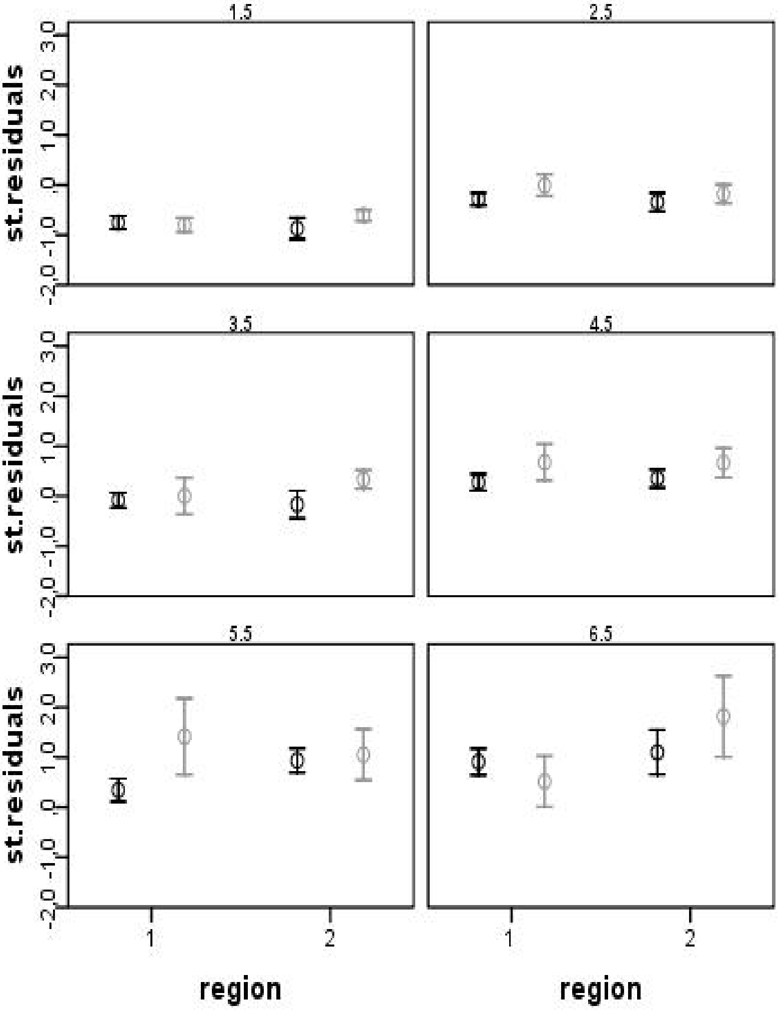

Figure 3.

5. Spatio-temporal covariation in mean calf body mass and population productivity in Fennoscandian moose (Alces alces).

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5. Spatio-temporal covariation in mean calf body mass and population productivity in Fennoscandian moose (*Alces alces*)

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ABSTRACT

Body mass is an important life history trait related to survival, mating success and fecundity. Large body mass is associated with high fecundity, and in many species large females produce more or larger offspring. Accordingly, there should be a relationship between the average size of calves and population productivity. However, several factors may modify this relationship, e.g. different trade-offs between maturity and body growth, adult age structure, sex ratio and density among populations. Here, we studied within and between populations in Norway and in Finland the relationship between body growth and fecundity at the population level. We also examined the use of moose observations during harvest by contrasting the annual variation in mean calf body mass with the variation in calving

ratio and twin ratio. According to our results, twin/calving ratio co-varies positively with the regional mean and annual body masses of female calves of the previous year. The patterns for twin ratio and calving ratio were similar, showing that the population recruitment rate increases more with annual mean body weight in Finland (high mean body weight) than in Norway (low mean body weight). This could indicate that in populations with poor moose condition, the variation in recruitment is due to varying winter conditions rather than to varying body condition. Also, in Finland annual twin ratio can be used as a good proxy for the annual variation in mean population condition.

5.1 INTRODUCTION

Body mass is an important life history trait in many organisms, being related to survival, mating success and fecundity (Stearns 1992; Bérubé et al. 1999; Gaillard et al. 2000a). Large body mass is also associated with high fecundity, and in many species large females produce larger and/or more offspring (Gaillard et al. 1992; Sæther and Haagenrud 1985; Sand 1996, but see Gaillard et al. 2000b), and larger individuals tend to mature earlier than smaller individuals (e.g. Sæther and Heim 1993; Garel et al. 2005). Variation in juvenile body mass is usually explained by both spatio-temporal variation in the environment (Sæther 1997) and/or by parental characteristics (Skogland 1984; Coté and Festa-Bianchet 2001; Don Bowen et al. 2001). In ungulates, body mass as a calf is important for body mass as an adult (Albon et al. 1987; Festa-Bianchet et al. 2000; Beckerman et al. 2002; Solberg et al. 2004, 2007), although some compensatory growth may occur (e.g. Toïgo et al. 1999).

The positive relationship between early growth and adult fecundity suggests that body mass variation should also influence population dynamics (e.g. Gaillard et al. 2000a; Hewison and Gaillard 2001). Accordingly, on the population level, there should be a relationship between the average size of calves within and between populations, and population productivity. However, several factors may modify this relationship. First, trade-offs between maturity and body growth differ among populations, e.g. following different mortality patterns (Proaktor et al. 2007). In some populations, females may also mature earlier than in others, leading to a halt in body growth and subsequent increase in fecundity (Garel et al. 2008). Secondly, high productivity can mediate offspring size in species that produce multiple young, such as moose (Nygrén 2003). Hence, if the increasing number of offspring is at the expense of their size (Stearns 1992), populations with high productivity may be associated with small offspring.

A third factor that can influence the relationship between juvenile size and population productivity is population age structure. Maternal effects transmit individual life-history responses from generation to generation and may have strong effects on the distribution of phenotypes in a population (Wolf et al. 1998; Beckerman et al. 2002; Solberg et al. 2007). Consequently, variation in the age, body condition and social status of mothers may affect the size and quality of their offspring (Skogland 1984; Coté and Festa-Bianchet 2001; Keech et al. 2000; Landete-Castillejos et al. 2005; Garel et al. 2009), as well as offspring fitness (e.g. Beckerman et al. 2002). Similarly, variation in the population age structure of males have been found to influence population productivity (Solberg et al. 2002; Sæther et al. 2004). Thus, high productivity may also be due to high average age of reproductive males and females in a population, and not necessarily to the fact that they were on average larger as calves.

Moreover, variation in population sex ratio has also been suggested as a factor affecting population productivity whenever the number and/or age of males become inappropriate to ensure the impregnation of all the females (Solberg et al. 2002; Sæther et al. 2004). The adult age structure and sex ratio of a population may therefore be particularly relevant factors in the population productivity of harvested species, since biased harvesting of sex and age groups can create biased population structures (e.g. Nygrén and Pesonen 1993, Ginsberg and Milner-Gulland 1994, Nygrén 2009). Besides having an effect on the covariation of offspring size and population productivity between populations, these factors may also affect the level of covariance within populations. If fecundity mainly depends on the resources available in the year of reproduction, recruitment rates can be expected to correlate positively with current offspring size (income breeders, Jönsson 1997). However, if fecundity is mainly a product of accumulated reserves (as in capital breeders, Jönsson 1997), there may still be a positive relationship, but with a certain amount of time delay.

In Fennoscandia, moose (*Alces alces*) have become the most important wildlife resource by far during the past 40 years. One important factor behind this development has been the introduction of selective harvesting of males and young animals in the early 1970s (Caughley 1977; Nygrén 1987; Nygrén and Pesonen 1993; Sylvén 1995; Sæther et al. 2001; Lavsund et al. 2003), leading to a change in the population sex and age composition and an increase in productivity and densities over large parts of Fennoscandia (Lavsund et al. 2003; Milner et al. 2007). Recently, there has been increasing concern that these changes may affect life history traits and other demographic variables not directly affected by hunting, such as the sex ratio and body weight of calves recruited to the populations (Sæther et al. 2004; Mysterud et al. 2005; Milner et al. 2007; Nygrén 2009). Moreover, in areas of high population densities, there is also a growing concern about the potential impact of food competition on average body condition. For the same reasons there is a need for improved parameters for management in order to monitor the variation in population size and structure. Since the 1970s, population structure and condition is mainly monitored by using moose observations and sampling of body mass from harvested moose (e.g. Lavsund et al. 2003).

Here, we want to utilise moose observations and the body mass information of harvested moose to learn more about the relationship between body growth and fecundity at the population level. We will do this by contrasting the annual variation in mean calf body mass with the variation in calving ratio and twin ratio (both recruitment indices, see Methods) within and between populations in Norway and in Finland. In general, we predict a positive relationship between mean calf body mass and recruitment indices within and between populations. However, as indicated above, several factors may modify this relationship, and we therefore also predict that: 1) lower observed recruitment rates are expected in years and populations with a high calf to female ratio in the harvest, i.e. because more calves than females are removed during the observation period. 2) Relatively lower calving ratios in populations and years periods with a low proportion of males in the population, because not all mature females will be impregnated (Noyes et al 1996; Komers et al. 1999). As the moose is generally believed to adopt a mixture of capital and income breeding tactics (Carranza 1996; Jönsson 1997; Mysterud et al. 2005), we 3) expect stronger relationships between annual recruitment rates and mean calf body mass 1-3 years earlier than by using calf body mass in the current year. A similar delayed relationship may occur if variation in the adult female age structure is the main reason for the variation in recruitment rate. However, as we do not have good measurements of the adult female age structure, we cannot test this prediction directly.

5.2 METHODS

5.2.1 Study areas in Finland and Norway

The study area covers populations from most of the distributional range of moose in Norway and all of Finland (Fig. 1). In Norway, the study areas are part of the national monitoring program for cervids (Solberg et al. 2006), whereas the study areas in Finland constitute the 15 game management districts (Nygrén and Pesonen 1993).

Finland and Norway are found at the same latitudes (Fig. 1), and are covered mainly by the same vegetation types. Both countries are dominated by coniferous forests, mostly spruce. However, Norway has a more oceanic climate than Finland, and the moose areas are generally found at higher altitudes. For more details on the study areas in Norway, see Solberg et al. (2002) and Garel et al. (2009), and in Finland Nygrén et al. (2007).

5.2.2 Moose population density, management and monitoring in Finland and Norway

In both Norway and Finland, moose populations began to increase in the 1960s, and reached a peak in Norway in the 1990s. In Finland the moose population has peaked twice: first in the late 1970s and early 1980s and again in the late 1990s and early 2000s (Lavsund et al. 2003; Nygrén 2009). Currently, the density of moose in Norway is almost twice the density in Finland, mainly because of the official enforcement of relatively moderate density thresholds in Finland (Nygrén and Pesonen 1993; Lavsund et al. 2003; Nygrén 2009). Otherwise, moose management is very similar in these countries (Lavsund et al. 2003). Moose hunting occurs in autumn at much the same period (September-December), but the hunting season is shorter in Norway and has varied somewhat over time (Nygrén et al. 2007; Garel et al. 2009). Hunting is mainly carried out by a group of hunters hunting as a team (Koskela and Nygrén 2002), with the use of dogs and/or beaters to flush out the moose from cover (Ruusila and Pesonen 2004).

Moose harvesting is based on a quota system, and the number of harvested moose is obligatorily recorded and reported according to age (calf, yearling and adult in Norway, calf and adult in Finland) and sex, and moose observations (see below) are collected by hunters as a standard routine during ordinary hunting (Lavsund et al. 2003). Also, the body mass of harvested moose is recorded on a more or less regular basis (Nygrén et al. 2007; Solberg et al. 2006; Fig. 1). In order to harmonise the study period between Norway and Finland, we here only used data from 1991-2006. Similarly, we used only the first four weeks of Finnish moose observation data in order to adapt them to the four-week hunting season in Norway.

5.2.3 Observation data

Moose observation monitoring in both Norway and Finland is a systematic recording and collecting of the sex and age (calf or adult) of moose observed by moose hunters during the hunting season (Lavsund et al. 2003). Hunting effort is measured as number of hunting days. The observations are classified in both countries into six categories: calves, adult (≥ 1 year old) males, adult females without calf, females with one calf, females with twins, and individuals of unknown sex and/or age (e.g. Solberg et al. 2006). In Finland observations are recorded on a daily basis, whereas in Norway only the sum of values for the entire hunting season is reported. In Finland currently more than 5000 hunting clubs with about 100,000 hunters annually record 200,000-300,000 moose observations, whereas about 60,000 Norwegian hunters record and report approximately 200,000 observations each year (Lavsund et al. 2003; Rolandsen et al. 2004).

Several indices of population structure are calculated from the observation monitoring data (e.g. Nygrén and Nygrén 1976; Nygrén and Pesonen 1993; Solberg and Heim 2002, 2006; Lavsund et al. 2003; Nygrén 2009). The most important are the indices of population productivity; “calves/adult” (calves/100 adults in Finland), “calves/cow” (calves/100 cows in Finland), proportion of cows with calves and proportion of calving cows with twins as well as the population sex ratio “cows/bull”. In addition, population density is indexed by the number of observations per unit hunting effort, i.e. in Norway as “moose seen per hunter day” and in Finland as “moose seen per team-hunting day”. In Finland population density is also indexed by the numbers of moose that the hunters estimate to be living in their hunting grounds after the hunting season. Despite the rather crude sampling procedure and the high number of probable confounding variables (variation in weather, hunting skills, number of hunters, hunting methods etc.), the observation data are found to provide precise information on the temporal changes in recruitment rate, population density and adult sex ratio within ungulate populations (Ericsson and Wallin 1994, 1999; Sylvén 1995; Solberg and Sæther 1999; Solberg et al. 2002;

Mysterud et al. 2007; Rönnegård et al. 2008; Bjørneraas et al. 2009), provided that the number of observations is relatively high (Ericsson and Wallin 1994; Sylvén 2000).

5.2.4 Body mass

As a measure of variation in calf body mass, we used the carcass mass of harvested calves from 1991-2006. The carcass mass of calves constitutes from about 50% of their live body mass (Wallin et al. 1996). Because carcass mass may vary during the harvest period (e.g. Solberg et al. 2004), and there are slight differences between countries as regards harvest periods, during which the kill dates vary, we adjusted all masses to the 15th of October by using a regression of carcass mass on kill date within country. In total we had body mass data from 16,841 calves (8742 males, 8099 females) in Norway and from 152,034 calves (80,059 males, 71,975 females) in Finland. The number of calves within a year and a population ranged between 10 and 1834, ensuring that the mean carcass masses constitute relatively precise reflections of the mean calf body mass in the population. In the forthcoming text carcass mass is referred to as body mass.

5.2.5 Calf production

Calf recruitment was measured as calving ratio and twin ratio. Calving ratio is the proportion of females that are observed with calves during the hunting season, whereas twin ratio is the proportion of calf-rearing females that are observed with twins. Because moose are harvested while observations are recorded it is likely that variation in harvest pressure and structure may affect the estimated recruitment rates. For instance, in populations with a high harvest of calves per harvested female, both recruitment rate indices are likely to decrease during the hunting season. This is regularly controlled in Finland, where harvest and observation data are recorded on a daily basis, i.e. the pre-harvest recruitment rates can be estimated (Nygrén and Pesonen 1993; Nygrén 2009). On the based of the Finnish data the effect of variation in the harvesting of calves was found to have only minor effects on the variation in twin ratio, but it may have substantial effects on the variation in calving ratio. Particularly pronounced effects on the calving ratio were found in populations where the number of harvested calves per harvested female deviates greatly from the observed calves per female, and vice versa.

Since the Norwegian data were aggregated over the entire hunting season, we were not able to adjust these observations similarly for variations in harvesting of calves within and between populations. We therefore decided to use unadjusted indices from both countries and then control for varying calf harvesting by including a calf harvest index as a covariate in the statistical analyses. This index was calculated as the number of calves per female in the harvest divided by the number of calves per female in the observations. High values would mean that hunters shoot more calves per females than the ratio found in the population, indicating that the observed proportion of calves (calving/twin ratio) is most likely lower than was present in the pre-harvested population.

5.2.6 Statistical analyses

We first examined the variation in mean body mass of calves and recruitment rates within and between populations in Norway and in Finland. We expected lower body masses and recruitment rates in Norway than in Finland due to the overall higher population density. We then examined to what extent males and females showed the same variation in body mass over time among populations, and whether the ratio of mean male to mean female body mass differed between populations. In general we expected higher body mass in males than in females, but very close annual covariation between males and females within populations.

We also examined the annual relationship between calving ratio and twin ratio within and between populations (country and region). We expected a positive relationship, given the fact that both ratios are strongly affected by female body condition (Sand 1996). However, because of the stronger impact of calf harvesting on the variation in calving ratio than on the variation in twin ratio, we expected that controlling for variation in the calf harvest index would improve the fit. We then tested to what extent the variation in annual calving or twin ratio was related to variation in mean calf body mass. In these analyses we used only the body mass of female calves. Moreover, because the calving ratio (p) and twin ratio (p) are proportions, we normalised them by arcsine transformation (arcsine($\sqrt{p}$) (Sokal and Rholf 1995), and used these transformed ratios in all the analyses.

We also split the annual mean body weights of female calves into mean and annual values within regions. This was done by first subtracting the grand mean body mass from the annual mean body masses within populations. Based on these values, we calculated population mean body masses by averaging over the study period (1991-2006) within the region, and centred the annual values by subtracting the population mean body mass from the within-population annual values. By splitting the body mass into mean and centred annual values, we were able to specifically test to what extent the relationship between recruitment rates and body mass was due to between-population variation or within-population variation over years. Moreover, rather than indicating some abstract value related to x-values equal 0, intercept estimates would indicate mean differences between populations (e.g. countries).

We analysed the variation in recruitment rates using linear mixed effect models with annual recruitment rate (twin or calving ratio) as a dependent variable and region-specific centred mean and annual body mass of female calves as covariates. Population (region) was included as a random factor. We tested the variation in recruitment rate (calving and twin ratio) against body mass in the current year (year t) as well as in the three previous years (years t-1, t-2 and t-3). We also included country as a fixed factor in the models, in addition observed sex ratio (females per male) and the calf harvest index as additional covariates. We expected lower recruitment rates in years and populations with a female-biased sex ratio and a high calf harvest index (more calves removed during hunting), all else being equal.

To provide a baseline model against which we could compare the more complex models, we estimated the variance components in a model with only region included as a random factor. Two variance components were extracted from this model, representing the variances in twin/calving ratio that are attributed to variation within (residual variance) and between regions. Based on this model we could then 1) determine to what extent the annual twin/calving ratio varied between regions, and 2) estimate the fraction of explainable variation accounted for by the fixed effects in the more complex models. Following Singer (1998), we computed the proportion of explainable variation as

(VC1-VC2)/VC1,

where VC1 and VC2 are the variance components in the baseline and the more complex model, respectively (see also e.g. Solberg et al. 2007 for the use of the method).

We considered the models with the lowest Akaike information criterion (AIC) score to be the most parsimonious and thus the 'best' model applied to the data (Burnham & Anderson 2002). We used AICc (corrected AIC) to account for the relatively high number of covariates compared to the number of years and regions. Models that differed in AICc by two or less (ΔAICc ≤ 2) were considered to be equally well supported by the data (Burnham & Anderson 2002). Since we were comparing models with different fixed effect structure, we used Maximum-Likelihood (ML) for model selection (Singer 1998; Crawley 2002) and Restricted Maximum-Likelihood (REML) for parameter estimation. All the statistical analyses were performed using SPSS 16.0 for Windows.

5.3 RESULTS

5.3.1 Variation on calf body mass

The body mass (Fig. 2) of male calves ranged from 25 kg to 120 kg in Finland (mean = 81 kg, SD = 7, n = 4264) and from 44 kg to 96 kg in Norway (mean = 67 kg, SD = 7, n = 489). The corresponding figures for female calves (Fig. 2) were from 40 kg to 107 kg (mean = 77 kg, SD = 7, n = 4245) and from 28 kg to 91 kg (mean = 63 kg, SD = 7, n = 488), respectively.

Generally calves were heavier in Finland than in Norway (Fig. 1 and 2). The smallest calves in Finland were found in Lappi (males mean = 72 kg, SD = 7, n = 267; females mean = 69 kg, SD = 8, n = 249) and in Norway in Vest-Agder (males mean = 59 kg, SD = 5, n = 34; females mean = 56 kg, SD = 6, n = 32). The largest calves were found in Varsinais-Suomi, Finland (males mean = 85 kg, SD = 6, n = 290; females mean = 81 kg, SD = 6, n = 287) and in Hedmark, Norway (males mean = 74 kg, SD = 5, n = 33, females mean = 70 kg, SD = 4, n = 33), respectively.

As expected, we found a strong positive relationship between annual mean body mass of male and female calves in both countries (Finland r = 0.618, SE = 0.013, t = 48.348, P < 0.001; Norway r = 0.677, SE = 0.039, t = 17.514, P < 0.001). Male calves were approximately 5% heavier than female calves (in Finland the difference was 4.2 kg and in Norway 3.5 kg). The size difference was also affected by year (df = 15, MS = 1.788, F = 2.029, P = 0.011) and region (df = 22, MS = 17.674, F = 21.204, P < 0.001). There was an overall negative trend in body mass (Fig. 2) in both Finland (r = -0.223, SE = 0.017, t = -13.088, p < 0.001) and Norway (r = -0.277, SE = 0.053, t = -5.243, p < 0.001) during the study period.

5.3.2 Variation in calving ratio and twin ratio

Calf recruitment was generally higher in Finland than in Norway (Fig. 1 and 2). The calving ratio varied between 0.22-0.90 in Finland (mean = 0.59, SD = 0.07, n = 8502), and between 0.07-0.86 in Norway (mean = 0.51, SD = 0.82, n = 936), and the twin ratio varied between 0.04-0.88 in Finland (mean = 0.38, SD = 0.09, n = 8504), and between 0.00-0.63 in Norway (mean = 0.28, SD = 0.14, n = 936). In Finland, population productivity was highest in 1998 (Fig. 2) and in Norway in 1991. The lowest population productivity (Fig. 2) was in 2006 in Finland. In Norway the lowest calving ratio was found in 1995 (mean = 0.48, SD = 0.11, n = 59) and the lowest twin ratio in 2000 (mean = 0.25, SD = 0.12, n = 62). The spatial distribution of population productivity can be seen in Fig. 1. The annual twin ratio and calving ratio co-varied within both countries (Finland $R^2 = 0.204$, $r = 0.750$, $SE = 0.096$, $t = 7.803$, $P < 0.001$; Norway $R^2 = 0.129$, $r = 0.937$, $SE = 0.221$, $t = 4.234$, $P < 0.001$).

5.3.3 Spatio-temporal covariation between calf recruitment and female calf body mass

The best linear mixed effect model explaining the variation in twin ratio and calving ratio included country, population mean body mass, centred annual mean body mass, the calf harvest index and the observed adult sex ratio. In addition, region was included as a random factor (Table 1). On average, calf recruitment was higher in Finland than in Norway, and, as expected, we found a positive effect of both mean regional and centred annual body mass on calving and twin ratio. The recruitment rates are thus higher in years and regions that provide good conditions for calf body growth. However, the strongest effect of centred annual mean body mass was found with a time lag of one year (year *t*-1), indicating that the growth conditions during the previous summer were the most important factors. In addition, we found the effect of centred annual body mass to be stronger in populations (regions) with high mean body mass (positive mean body mass x annual body mass interaction), and stronger in Finland than in Norway (Table 2). Conversely, we found the effect of population mean body mass on recruitment rates to be stronger in Norway than in Finland (Table 2).

The effects of adult sex ratio and calf harvest index were also in accordance with expectations. We found a negative effect of sex ratio, indicating that higher recruitment rates for a given mean calf body mass occur in years and populations with a higher proportion of males. Similarly, higher recruitment rates were recorded in years and populations with a low off-take of calves relative to calves per female in the population. However, this effect seems primarily to be present in Norway (significant country x calf harvest interaction) (Tables 1 and 2; Figs. 3 and 4).

For both calving and twin ratio, we found three alternative models for twin ratio and one for calving ratio within ΔAIC = 2 (Table 1). Alternative good models for twin ratio included the interaction country x annual mean body mass in year t-1 or excluded the interaction country x regional mean body mass, or both (Table 1). The alternative good model for calving ratio had no additional factors compared to the best model but it was simpler, as it excluded the interaction country x annual mean body mass in year t-1 (Table 1). This suggests that the general patterns regarding body mass of calves and population recruitment rates were relatively similar between countries.

The best model for twin ratio accounted for about 31% of the variation within regions and about 59% of the variation between regions. The second best model accounted for about 32% and 58% of the within- and between-region variation, respectively (Table 1). The best model for calving ratio accounted for about 42% and 82% of the within- and between-region variation, respectively. Hence, apparently a larger proportion of the explainable variation was accounted for between than within populations, possibly due to the stronger influence of stochastic processes (female age structure and/or winter climate) on the annual variation.

5.4 DISCUSSION

Our results show that there is wide variation of both calf body mass and recruitment rates between Finnish and Norwegian moose populations and also to some extent over time (Figs. 1 and 2), and that the recruitment rates co-vary positively with the regional and annual mean body weights of female calves on the previous year (Figs. 3 and 4). This is to be expected if the body weight of calves reflects the body growth conditions for adult females during the summer (e.g. Solberg et al. 2007), and if females respond by varying their ovulation rate in autumn and hence the calving/twinning ratio in the subsequent spring (Garel et al. 2009).

The body mass of calves differed greatly between countries, and as expected, the average body mass of calves and also the population recruitment rates were generally higher in Finland than in Norway (Figs. 1 and 2). The results indicate that these differences are particularly pronounced between Finland and Norway, providing a good opportunity to test our main hypothesis on the relationship between body growth and fecundity at the population level. In Finland the highest productivity (twin ratio) was found in populations with the highest mean body mass of calves, and vice versa. In agreement with this result, we found a positive relationship between calf body mass and both recruitment rates, but as expected, the relationship with calving ratio was weaker than the relationship with twin ratio. However, there was great variation in the strength of the relationship among populations, pointing to the importance of environmental factors. The twin ratio seemed to increase more with the annual body weight of calves in Finland (high mean body weight) than in Norway (low mean body weight). This may be due to the poorer body mass data for Norway (i.e. they do not reflect body weight in the population very well), the smaller samples, greater variation in female age structure or some other biological factor. Regarding the latter, it could be that in populations with poor condition (e.g. Norway), the variation in twin ratio is more due to varying winter conditions than to varying body condition in the previous autumn, as there is quite a difference between the ovulation rate and the calving ratio in many Norwegian populations, indicating that a fair number of calves are aborted or die during the summer (e.g. Garel et al. 2009; Bjørneraas et al. 2009).

Our results show that body condition at an early stage is important for the productivity of the population and also for individual fitness. The strong relationship between the body mass of female calves and recruitment rates was expected on the basis of previous studies on maternal effects in moose. Large size is often correlated with high phenotypic quality (Gaillard et al. 2000b; Hewison and Gaillard 2001), and large mothers therefore are able to allocate more resources to offspring than are smaller mothers (e.g. Loison and Strand 2005). Both mothers and offspring are dependent on high-quality food and hence, the effects of resources and habitat are of vital importance. As in temperate ungulates the feeding conditions during summer are important for early growth (Sæther 1997), whether a young animal is raised in a good or a poor habitat is of crucial importance for body growth (Pettorelli et al. 2001; Sæther and Heim 1993). Also, temporal variation in population density and climate may affect food quality and per-capita quantity of food (Sæther 1997). Such annual effects can have a strong impact on the variation in body mass in ungulates (e.g. Post et al. 1997; Coltman et al. 1999; Pettorelli et al. 2002) and have the potential to generate cohort effects that may have long-lasting fitness consequences (Albon et al. 1987; Rose et al. 1998; Gaillard et al. 2003; Solberg et al. 2004, 2007). There is also evidence that cohort effects in fitness-related traits derive from the parents (Clutton-Brock and Albon 1989; Beckerman et al. 2002; Solberg et al. 2007).

Capital breeding (Stearns 1992; Jönsson 1997) is a resource use tactic common in many ungulates (e.g. Mysterud et al. 2005), although females rely at least partly on ingested food during reproduction and hence adopt a mix of capital and income breeding, while young males may adopt alternative tactics. In capital breeders, large individuals may reproduce more successfully and at a lower fitness cost than small individuals, especially in species with little or no variability in litter size, such as many ungulates (Carranza 1996). As there was a positive relationship between the average body mass and the productivity of the population, our results could indicate that the moose female is a capital breeder. However, as the recruitment rates of the population were mainly affected by the body mass of female calves in the previous year (*t*-1), the results suggest that the reproductive tactic of a female moose is more flexible and could therefore be categorized as income breeding with a fairly stable age-size maturation relationship. Falling trends in population condition increase the covariance between body mass and twin ratio over time.

In many Norwegian moose populations, the proportion of male calves in the harvest (Sæther et al. 2004) and also body condition and fecundity (Solberg et al. 2002) have decreased. Simultaneously, population densities have increased in most areas in combination with a fall in the mean age of adult males (Solberg et al. 1999, 2002; Mysterud et al. 2005). Although the Finnish moose population has experienced dramatic changes in numbers and structures (Lavsund et al. 2003; Nygrén 2009) compared to the Norwegian population, moose densities in Finland are kept relatively low, and the general condition of harvested moose is high, which also reflects the high productivity of the moose population (Nygrén 2009; Fig. 1). By focusing the moose harvest on calves, yearlings and adult males, the proportion of productive females and annual population growth have been increased in both countries. By contrast in Norway, female body mass, fecundity and recruitment rates have decreased (Solberg et al. 2002, 2006; Lavsund et al. 2003), and recently there has been a decline in population twin ratios also in Finland. The deterioration of maternal condition and lower reproduction rates of Norwegian moose are probably related to the large increase in population density during recent decades (Lavsund et al. 2003; Solberg et al. 2006), which is reflected in the very low general body mass of calves compared to that in Finland.

If maternal condition is negatively influenced by density-dependent or density-independent food limitation (Sæther 1997; Gaidet and Gaillard 2008), females may be less capable of weaning calves during periods of abundant resources when population density increases and environmental conditions deteriorate (Monard et al. 1997; Kruuk et al. 1999; Mysterud et al. 2000). The general high population productivity may be a consequence of the relatively old female age structure, i.e. a higher proportion of prime-aged females in the population. Maternal body condition is often found to be positively related to age in ungulates (e.g. roe deer: Hewison and Gaillard 2001; moose: Sæther et al. 2001; Solberg et al. 2004), and accordingly older mothers are assumed to have more body reserves available for calf production than younger mothers. However, the very recent declining trend in calf body mass and population recruitment rates observed in both countries may be an effect of over-ageing females. Also in Finland, in order to achieve the density goals, the size of the moose population was radically reduced in the early 2000s (Nygrén et al. 2000; Ruusila et al. 2001, 2002, 2003), which may eventually have reduced the number of reproductive females correspondingly, hence decreasing the recruitment rates during subsequent years (Ruusila et al. 2003; Pusenius et al. 2008).

Our results also confirm that both calf body mass and twin ratio are good indices for monitoring moose population conditions. In Finland the annual twinning ratio can be used as a good proxy for annual variation in moose population condition, whereas in Norway more research is required in order to determine whether it is the twin ratio or calf body mass (or even the body mass of yearlings) that best describes the variation in body condition of moose. As moose observations are easier to collect during the harvest period, we strongly encourage moose population managers and hunters to continue collecting this data. The results also highlight the importance of long time scales and continuity in the observation data, as the longer the time scale, the better their usability for population level studies. In addition to the importance of the temporal scale, the great variation among populations found in our results also highlights the need for wide spatial coverage of such a data. The time and effort put into collecting the data is well rewarded, not only in terms of the short-term managerial implications but also in terms of usefulness for long-term population level studies.

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Figure legends

Figure 1. The study areas in Norway (Vest-Agder, Aust-Agder, Vestfold/Telemark, Hedmark, Nord-Trøndelag, Nordland, Beiarn, and Troms) and Finland (EH = Etelä-Häme, ES = Etelä-Savo, KA = Kainuu, KS = Keski-Suomi, KY = Kymi, LA = Lappi, PH = Pohjois-Häme, PK = Pohjois-Karjala, PO = Pohjanmaa, PS = Pohjois-Savo, RP = Ruotsinkielinen Pohjanmaa, SK = Satakunta, VS = Varsinais-Suomi, and UM= Uusimaa). The numerals I-V indicate the category of mean body mass of female calves and the twin ratio respectively in the region, category I being the lowest and V the highest population body mass of female calves/twin ratio, respectively.

Figure 2. Annual variation in the carcass mass of calves (males black, females grey), the twin ratio and calving ratio in the moose populations in Finland (black) and Norway (grey) during 1991-2006.

Figure 3. Centred female calf body weight in year t-1 within regions in relation to the arcsine transformed twin ratio in Finland (black, R2 linear = 0.177) and Norway (grey, R2 linear = 1.492E-4) and calving ratio (R2 linear = 0.087 and 0.034, respectively). The corresponding total (black solid lines) R2 linear were 0.012 and 0.031, respectively.

Figure 4. Centred regional mean body weight of female calves in relation to arcsine transformed twin ratio in Finland (black, R2 linear = 0.16) and Norway (grey, R2 linear = 0.372) and calving ratio (R2 linear = 0.034 and 0.051, respectively). The total (black solid line) R2 linear were 0.424 and 0.33, respectively.

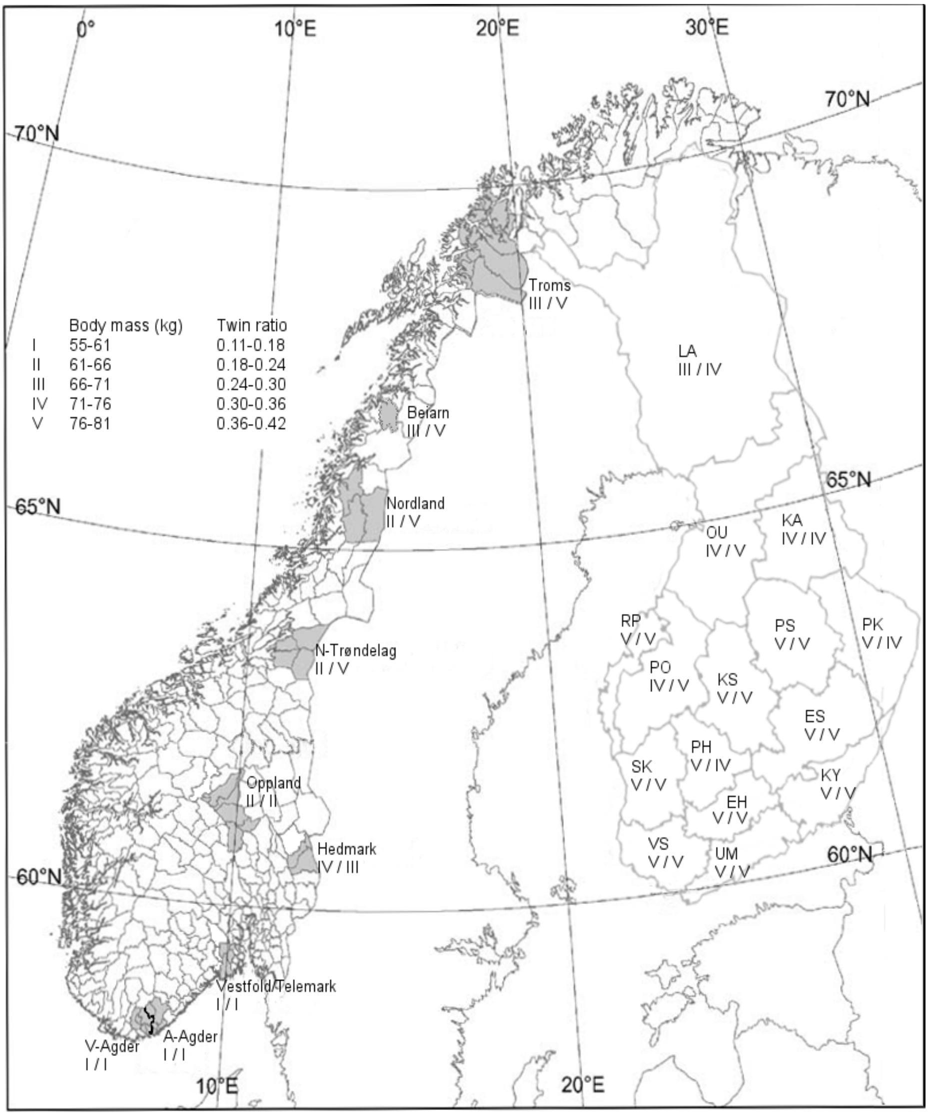
Table 1: The best candidate models explaining the spatio-temporal covariation between female calf body mass and arcsine transformed twin ratio and calving ratio in Fennoscandian moose (Alces alces) using linear mixed effect models with region as the random intercept. ΔAICc refers to the difference in AICc between the best model and the candidate model. All candidate models with ΔAICc ≤ 2 are presented in the table. The best model (model 1) explained 31% of the within-region and 59% of the between-region variance compared to the baseline model (BM) for twin ratio. The corresponding numbers for calving ratio were 42% and 82%, respectively.

Model	**Country (c)**	**Region**	**Regional body weight (rbw)**	**Body weight (bw) year t-1**	**rbw x bw year t-1**	**calf harvest**	**sex ratio**	**c x bw year t-1**	**c x rbw**	**c x calf harvest**	**within regions variance**	**between regions variance**	**ΔAICc**
Twin ratio													
BM		x									0.001862	0.010505	116.43
1	x	x	x	x	x	x	x		x	x	0.001277	0.004346	0.00
2	x	x	x	x	x	x	x	x	x	x	0.001268	0.004381	0.16
3	x	x	x	x	x	x	x			x	0.001277	0.005112	1.49
4	x	x	x	x	x	x	x	x		x	0.001268	0.005145	1.61
Calving ratio													
BM		x									0.001325	0.001437	180.03
1	x	x	x	x	x	x	x	x	x	x	0.000770	0.000260	0.00
2	x	x	x	x	x	x	x		x	x	0.000768	0.000254	1.78

x indicates the variable included in the model. BM is the baseline model with only region as the random factor (intercept) and arcsine transformed twin/calving ratio as the fixed factor (AICc for twin ratio = -1007.57 and for calving ratio = -1154.21). ΔAICc indicates the difference in AICc between the selected best model (model 1, for twin ratio: AICc = -1124.0; for calving ratio: AICc = -1334.24) and the alternative good models.

Table 2: Parameter estimates and test statistics for analysis of the centred regional body weight of female calves and arcsine transformed twin/calving ratio based on the model with the lowest AICc values (AICc twin ratio: -1124.0; calving ratio: -1334.24; Table 1).

Parameter	**Estimate**	**SE**	**T**	***P***
Twin ratio				
Intercept	0.871	0.059	14.773	<0.001
Country	-0.338	0.078	-4.356	<0.001
Regional body weight (rbw)	0.021	0.005	4.429	<0.001
Body weight (bw) year t-1	0.006	0.001	7.705	0.001
Calf harvest	-0.077	0.023	-3.431	0.001
sex ratio	-0.017	0.005	-3.430	<0.001
rbw x bw year t-1	0.001	0.000	5.850	<0.001
Country x rbw	-0.015	0.007	-1.985	0.059
Country x calf harvest	0.160	0.034	4.640	<0.001
Calving ratio				
Intercept	0.999	0.025	40.460	<0.001
Country	-0.149	0.039	-3.829	<0.001
rbw	0.004	0.001	3.024	0.006
bw year t-1	0.000	0.001	0.290	0.772
calf harvest	-0.064	0.014	-4.486	<0.001
sex ratio	-0.033	0.004	-9.146	<0.001
rbw x bw year t-1	0.000	0.000	-1.827	0.069
country x bw year t-1	0.004	0.002	1.993	0.047
country x rbw	-0.005	0.002	-2.455	0.022
country x calf harvest	0.124	0.024	5.165	<0.001


0°
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20°E
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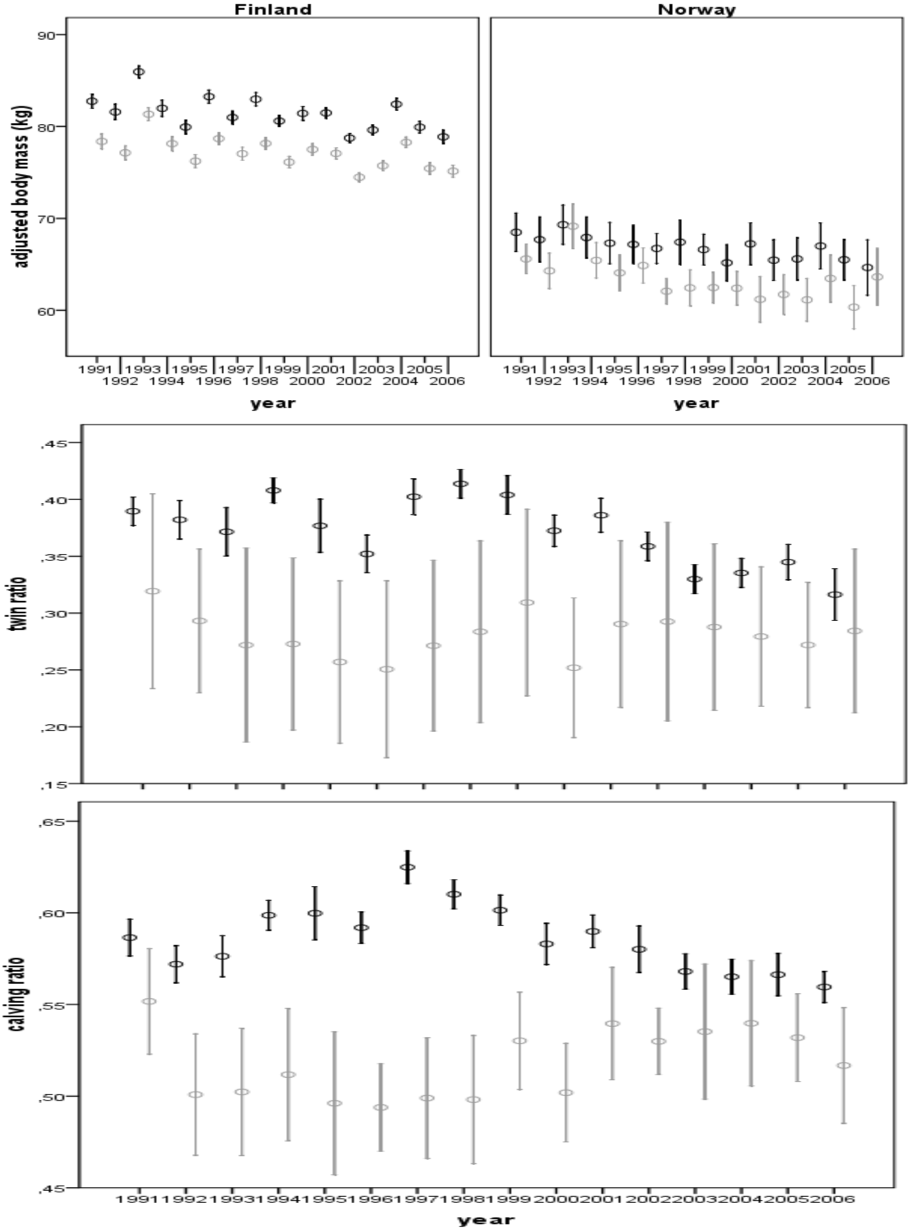
Body mass (kg) Twin ratio
I 55-61 0.11-0.18
II 61-66 0.18-0.24
III 66-71 0.24-0.30
IV 71-76 0.30-0.36
V 76-81 0.36-0.42
Troms III / V
LA III / IV
Beiarn III / V
Nordland II / V
OU IV / V
KA IV / IV
RP V / V
PS V / V
PK V / IV
N-Trøndelag II / V
PO IV / V
KS V / V
ES V / V
PH V / IV
SK V / V
Oppland II / II
KY V / V
EH V / V
Hedmark IV / III
VS V / V
UM V / V
Vestfold/Telemark I / I
V-Agder I / I
A-Agder I / I

Figure 1.


Finland
Norway
adjusted body mass (kg)
90
80
70
60
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
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2002
2003
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2005
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year
twin ratio
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calving ratio
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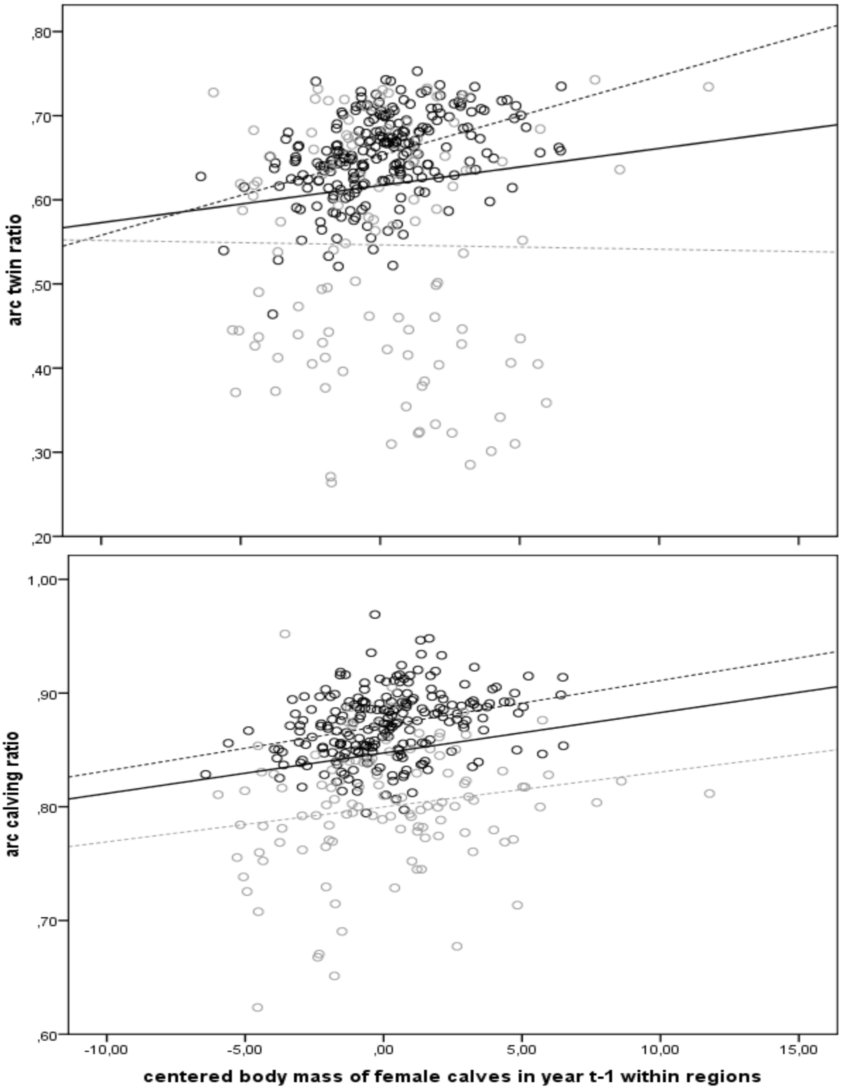
19911992199319941995199619971998199920002001200220032004 20052006
year

Figure 2.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arc calving ratio
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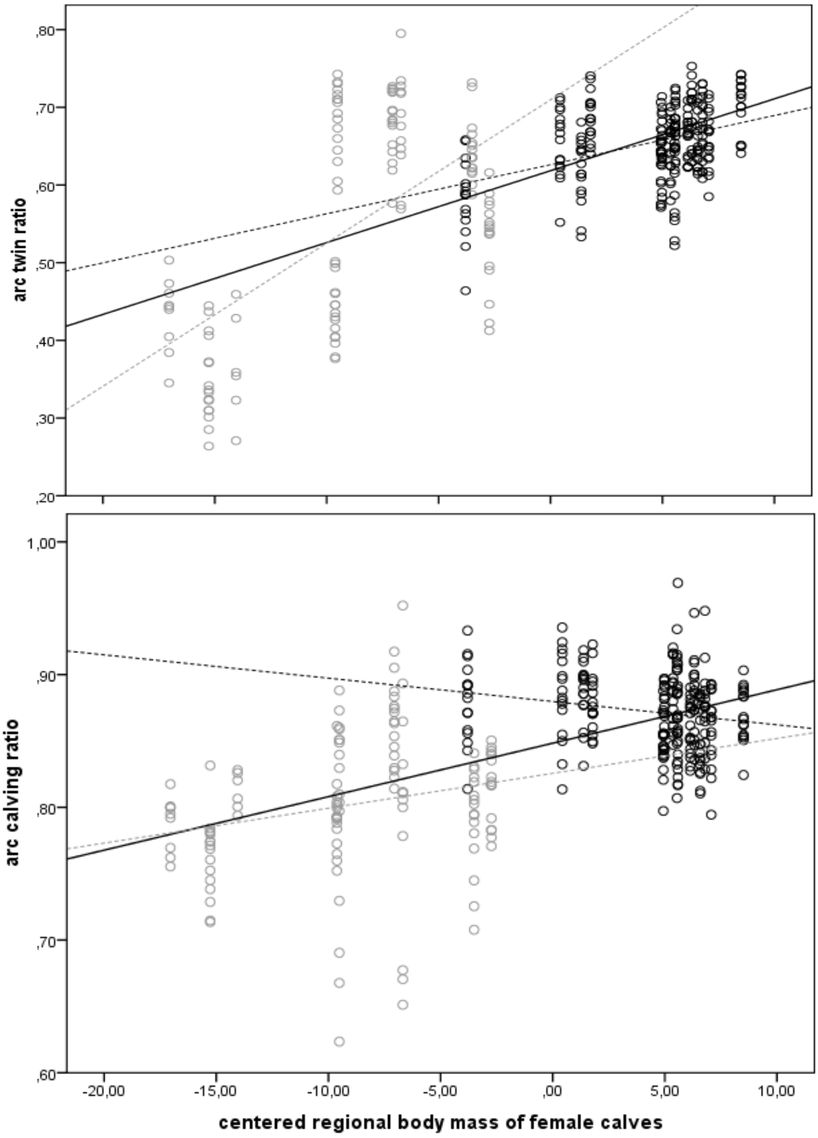
centered body mass of female calves in year t-1 within regions

Figure 3.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centered regional body mass of female calves

Figure 4.

6. General discussion

6.1 INDIVIDUAL BODY SIZE AND GROWTH

Following major changes in moose hunting practices (Nygrén 2009), I found that the body growth of young male moose in Finland has increased (Chapter III). The general condition of Finnish moose seems to be relatively good, i.e. compared to moose in Norway, although there seems to be a slightly decreasing trend in the body weights of moose calves and population productivity (Chapter V). These results are concurrent with earlier findings that, in addition to environmental conditions, the body mass of large ungulates also vary indirectly, depending on hunting, as a response to changes in the density or structural composition of the population (Ginsberg and Milner-Gulland 1994; Solberg and Sæther 1994; Langvatn and Loison 1999; Solberg et al. 1999, 2000; Laurian et al. 2000; Coltman et al. 2003; Sæther et al. 2003; Chapters III and IV).

Body size is a key life history trait that reflects existing trade-offs between energy allocation and age of maturity, current and future reproduction, and growth of parent and offspring (e.g. Roff 1992; Stearns 1992; Sand et al. 1995; Sand 1996b; Ericsson et al. 2001; Ericsson et al. 2002). Large body mass is associated with high fecundity, and often large females produce larger and/or more offspring (Gaillard et al. 1992; Sæther and Haagenrud 1985; Sand 1996b, but see Gaillard et al. 2000; Chapter V). Moose is a dimorphic species (e.g. Loison et al. 1999) that grows during several years (e.g. Solberg and Sæther 1994; Sand 1996a; Solberg et al. 2004; Chapter IV fig. 1), and as shown here, large part of the variability in moose body mass is thus explained by sex and age (Chapter IV fig. 1). In addition to this, body mass in adult moose of both sexes is influenced by environmental conditions such as climate and population density, and especially in males, conditions during the birth year have long-lasting effects on body size (Solberg et al. 2004). Environmental seasonality has often been found to affect moose growth (Garel et al. 2006; Herfindal et al. 2006a; Herfindal et al. 2006b), and especially the conditions during early summer have been found to be important for moose body mass (Sæther 1985; Solberg and Sæther 1994; Sand 1996b; Solberg et al. 1999).

In Finland, moose population densities have been kept relatively low compared to environmental carrying capacity by licence-based harvesting, which has continued during several decades, probably providing better conditions for moose growth. However, my results show that this does not appear from the body weight and growth of female moose (Chapter IV), as there is no similar increase in the growth pattern of female moose to that of males (Chapter III). This might be because females allocate abundant resources to reproduction, which at the population level has in fact increased in Finland. On the other hand, the higher population productivity might simply be a factor of the female-biased sex ratio, as reproductive females are protected from harvesting. The increased sexual size dimorphism found in the Finnish moose population (Chapter IV) could thus be caused by higher reproductive investment (i.e. increased body and also antler size) of male moose.

6.2 REPRODUCTIVE INVESTMENT

6.2.1 Moose antler type polymorphism

I studied the antler type (palmated, cervina and intermediate type, Chapter II fig. 1) frequencies in Finnish male moose and found that they vary regionally and temporally in the harvested moose population (Chapter II). Also, antler type frequencies depend on the age and weight of the males: the antlers of young and light males are predominantly of the cervina type, whereas heavier prime-aged males have intermediate and palmate type antlers. Even when antler characteristics are influenced by genetic and environmental factors (Harmel 1983; Hundertmark et al. 1998; Schmidt et al. 2001; Kruuk et al. 2002) I could show that they also express phenotypic plasticity according to male age and condition (Chapters III and IV).

Moose antler type frequencies change as males grow older and larger. The antler type of a male is closely related to its reproductive maturity and physical condition (Chapter II). As the palmated antlers are larger, they are most likely more expensive to produce, and therefore more frequent only among large prime-aged males. If the cervina antler was a construction form to other antler types as previously suggested by Bubenik (1973), any male would be able to produce cervina type antlers regardless of the male's age and condition. The decrease in the number of palmated antlers between the study periods could therefore indicate a general decrease in the male age structure of the Finnish moose population. As the full size of the cervina type is reached at a smaller size and younger age than that of the palmated type, it might also be that cervina type antlers provide a fitness benefit over the palmated type in a population consisting mainly of young males. However, this remains to be studied in the future.

6.2.2 The reproductive investment of males

Along with the increased growth rates of both body and antler size (III), the reproductive investment of male moose, i.e. the antler size relative to body size, has also increased (IV) in Finnish male moose. The reproductive investment of male moose increases with age (e.g. Mysterud et al. 2005), and with a higher growth rate of body and antler size, the reproductive investment of male moose also increases (Chapter IV). The sex ratio of the Finnish moose population has become female-biased (Chapter III fig. 2) through intensive harvesting of male moose (Nygrén et al. 2000), and the age structure of males now tends towards young individuals. This should decrease the competition among males, and therefore decrease the body and antler size (Loison et al. 1999). On the other hand, the high harvest pressure on males, both young and adult, may have led to a decrease in the costs of current reproduction through increased mortality.

Male reproductive success in most ungulates appears to be determined mainly by an individual’s ability to beat other males in male-male competition for receptive females (Festa-Bianchet 2003). Antler or horn size is, presumably, only one component of fighting ability: body size and condition can also play a role, especially if very large weapons suffer risk of breakage (Alvarez 1994). Also in polygynous mammals, where the males' fighting ability largely determines their access to receptive females, male breeding success depends more strongly than that of females on early growth rates (Clutton-Brock and Albon 1982; Clutton-Brock et al. 1984; Meikle et al. 1984). Hence the increased growth rates of male moose body and antler size found in my studies could indicate the increased reproductive investment of males, yet e.g. the role of maternal effects on these early growth rates remain to be studied in the future.

The relationship between current and future reproduction is one of the most important trade-off situations in life history theories, and it is shaped through changes in extrinsic mortality rates (Stearns 1989). Especially in long-lived iteroparous species, such as moose, the allocation of limited resources between current and future reproduction and survival is highly important (Stearns 1992). This involves costs, especially in young individuals, as the young are struggling with issues of body growth and condition, while at the same time they should gather experience in reproductive events (Clutton-Brock 1991; Stearns 1992). When survival, and hence the opportunities for reproduction in the future decrease, the investment in current reproduction should increase correspondingly because of the lower costs (Festa-Bianchet 2003; Proaktor et al. 2007; Fenberg and Roy 2008). It can thus be concluded that the changes in male moose growth rates reported in Chapter III and in the reproductive investment of young males (Chapter IV) may be related to contemporary changes in harvest structure and moose population management. When mortality is high, individuals that are capable of reproducing young, even at small sizes, benefit (Fenberg and Roy 2008). If most mature males are removed by hunters, younger males may take over the role of breeders, and hence over the short term, there may be a demographic effect without the evolution of novel mating strategies. Over the long term, selection could favour males with high reproductive effort over their first few years of life, possibly including faster growth, lower fat reserves, and riskier behaviour during the rut (Festa-Bianchet 2003).

6.3 COVARIATION IN MEAN CALF BODY MASS AND POPULATION PRODUCTIVITY

I found a positive relationship between the body weights of female calves and population productivity, as large calves often become large and more fecund adults, and more fecund females create a more productive population (Chapter V). As body mass is a key life history trait (e.g. Roff 1992; Stearns 1992; Sand et al. 1995; Sand 1996a; Ericsson et al. 2001; Ericsson et al. 2002), the body weight of moose calves is important not only at an individual level but also at a population level. Small calves are more likely to become small adults, and therefore cohort effects are important in the population dynamics of cervids (Albon et al. 1987; Solberg et al. 2004, 2007, 2008). On average, calf recruitment was higher in areas where calves had higher body masses (Chapter V), suggesting that recruitment rates are higher when the annual and regional conditions for calf body growth are good. As the moose is generally believed to adopt a mixture of capital and income breeding tactics (Carranza 1996; Jönsson 1997; Mysterud et al. 2005), the growing conditions of calves during the previous summer seemed to be the most important factor for population recruitment rates.

Recently, the body weights of moose calves as well as the productivity of Fennoscandian moose populations have been decreasing (Chapter V fig. 2). By focusing the moose harvest on calves, yearlings and adult males, the proportion of productive females and annual population growth have increased. By contrast, female body mass, fecundity and recruitment rates have decreased (Lavsund et al. 2003; Solberg et al. 2002, 2006). The decrease in the maternal condition and reproduction rates of Norwegian moose is probably related to the large increase in population density (Lavsund et al. 2003; Solberg et al. 2002). At the same time in Finland, moose population densities have been relatively low compared to Norway, and accordingly, the body weights of calves, and hence the population reproduction rates, are generally much higher in Finland, although very recently they have been decreasing (Chapter V fig. 2). This is most likely an effect of the very intensive culling of the Finnish moose population in the early 2000s, when, in order to achieve the density goals, adult females were also harvested (Nygrén et al. 2000; Ruusila et al. 2001, 2002, 2003; Pusenius et al. 2008).

Interestingly, I found that higher recruitment rates occurred in the years and populations with a higher proportion of males (Chapter V). In populations where the number and/or age of males has decreased, the productivity of females deteriorates (Mysterud et al. 2002; Solberg et al. 2002; Sæther et al. 2003; Milner et al. 2007), mainly as a consequence of the delayed rutting period of moose. An additional factor is that the primiparous females become oestrous later than do older females and therefore also give birth later (Sæther et al. 2003). Thus, the optimal scenario for moose parturition would be that fertilisation occurs during early autumn. If the parturition period is prolonged, the calves (and mothers) may not have the time needed to prepare for the winter (Geist 1999; Milner et al. 2007), and thus they become small adults and their survival rate decreases. As moose populations in Fennoscandia have become increasingly female-biased, this may eventually affect recruitment rates in the long term.

6.4 MAIN FINDINGS AND CONCLUSIONS

The results of my dissertation show that with changes in moose hunting practices, there have been major changes in moose growth patterns (Chapter III) and reproductive investment (Chapter IV) as well as in the productivity of the populations (Chapter V). The antler types most prominent in young males have also increased (Chapter II). For sustainable moose harvesting and population management, it is essential to study in more detail the factors and mechanisms behind the higher growth rates of both body weight and sexually selected antlers (Chapter III), the higher reproductive investment of males (Chapter IV), and hence the role of young males in the population dynamics of moose. With the relatively low density of the Finnish moose population, it is difficult to separate the ultimate reason for the higher growth rates of males from environmental causes, e.g. intensive forestry practices and hence the forage conditions. The productivity of the moose population has increased simultaneously (Chapter V) with the higher growth rate of males. It could be, that good forage conditions also influence the male moose reproductive investment positively. As the antlers are sexually selected, the role of sexual selection and female choice needs to be studied further in the future. Provided that females prefer larger and older males raises the question of female choice in a population where the sex ratio is biased towards females and the male age structure towards younger (and thus smaller) individuals. There is an increasing awareness that heavy harvesting can lead to a rapid evolution towards earlier sexual maturation (Mysterud et al. 2009). The Fennoscandian moose population has become increasingly female-biased, with a young male age structure. The role of young males in reproduction is therefore crucial to population dynamics. Selective harvesting has been associated with several demographic side effects that may eventually affect population dynamics and lower population productivity (e.g. Milner et al. 2007).

The Fennoscandian moose populations have been intensively managed and harvested in a relatively similar manner since the 1970s (e.g. Lavsund et al. 2003). The thousands of hunters in three countries provide huge data sets voluntarily as a by-product of the moose harvest. These data sets, very rare in their scale, not only temporally and spatially, but also numerically, provide researchers material for a wide range of topics, from the management level to highly theoretical questions, all levels being equally important for the management and understanding of the species, ecologically, economically and socially. This thesis highlights the need to take evolutionary effects into account when managing and harvesting moose populations. At the individual level, the age and size at reproduction are important determinants of the individual's lifetime reproductive success, which at population level strongly influences population growth rates. In addition, changes in life history traits can affect the level of sustainable yield of a moose population, and they are therefore highly important when planning sustainable harvesting and population management. As the twin ratio seem to reflect relatively well the condition of the moose population in Finland, it could be used, together with other observation and harvest data, as a tool for annual variation in moose population condition.

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RAISA TIILIKAINEN

The effects of selective harvesting on life history traits of moose Alces alces

Moose populations are subject to intense harvesting, predominantly on juveniles and males, in order to maximise the annual harvesting yield. Along with changes in moose hunting practices, there have been changes in moose growth patterns and reproductive investment as well as in the productivity of the populations. Changes in life history traits can affect the level of sustainable yield of a moose population, and they are therefore highly important when planning sustainable harvesting and population management.

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