

## RAUNO VEEROJA

Effects of winter weather, population density and timing of reproduction on life-history traits and population dynamics of moose (*Alces alces*) in Estonia



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

**233**



## **RAUNO VEEROJA**

Effects of winter weather, population density and timing of reproduction on life-history traits and population dynamics of moose (*Alces alces*) in Estonia



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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in animal ecology at the University of Tartu on November 19, 2012 by the Scientific Council of the Institute of Ecology and Earth Sciences.

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Commencement: Room 301, 46 Vanemuise Street, Tartu, on 15 February 2013,  
at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu and by the Doctoral School of Earth Sciences and Ecology, created under the auspices of European Social Fund.



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ISSN 1024–6479

ISBN 978–9949–32–212–1 (print)

ISBN 978–9949–32–213–8 (pdf)

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University of Tartu Press

[www.tyk.ee](http://www.tyk.ee)

Order No. 640

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is a summary of the following papers, referred to in the text by the Roman numerals:

- I Veeroja, R., Tilgar, V., Kirk, A. Tõnisson, J. 2008. Climatic effects on life-history traits of moose in Estonia. *Oecologia* 154: 703–713.
- II Veeroja, R., Kirk, A., Tilgar, V. Tõnisson, J. Winter climate, age and population density affect the timing of conception in female moose (*Alces alces*). *Acta Theriologica* (in press). DOI 10.1007/s13364-012-0106-9
- III Veeroja, R., Kirk, A., Tilgar, V., Säde, S., Kreitsberg, M. Tõnisson, J. 2010. Conception date affects litter type and foetal sex ratio in female moose in Estonia. *Journal of Animal Ecology* 79: 169–175.
- IV Veeroja, R., Tõnisson, J. Tilgar, V. 2007. Effects of hunting, wolf-predation and winter climate on population dynamics of moose (*Alces alces*) in Estonia. In: The proceedings of the IVth International Symposium “Dynamics of game animal populations in Northern Europe”. September, 18–22, 2006. Petrozavodsk, Karelia, Russia, pp. 175–179.

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### Contributions

In all papers (**I**, **II**, **III** and **IV**) I initiated the study, participated in data collection and laboratory analysis. I was responsible for most of the data analyses in papers **II–IV** and was partly responsible for the data analysis in paper **I**. I wrote the first drafts of papers **II–IV** and partly wrote the first draft of paper **I**. I also contributed to the completion of all papers.

# I. INTRODUCTION

Climatic variation influences a number of life-history traits and population dynamics of large mammalian herbivores in a variety of ecosystems in temperate and arctic environments (Gaillard et al. 2000, Coulson et al. 2001). These results are often interpreted as unfavourable winter weather either directly impacting survival, growth or condition, or indirectly, through delayed effects, influencing maternal condition and offspring quality, which in turn influences individual performance (e.g. Solberg et al. 2004). For instance, winter severity have been found to effect body mass (Sæther & Gravem 1988, Hjeljord & Hystad 1999, Loison & Langvatn 1998), age at maturity (Sæther & Heim 1993) and fecundity (Sand 1996) in different ungulate species. There is also some evidence that winter weather may affect the timing of parturition in wild ungulates (Forchhammer et al. 2001). However, little is known about winter effects on the conception date, the trait that determines the timing of birth (Clements et al. 2011).

In parallel with the negative influence of severe winters, it has also been suggested that warmer than average winters may have negative impacts on ungulate populations. In Western Europe, warmer than average winters are often more stormy than average winters and lead to higher levels of precipitation (mainly as rainfall in the Baltic region) than normally occurs, which can directly impose greater energetic demands on thermoregulation (Milner et al. 1999). Hence, we can assume that changes in both the long-term mean of climatic indices and changes in the variability need to be considered when predicting the likely consequences of climate change on various life history traits of ungulates (Coulson et al. 2001). Additionally, considering that previous winters should have additive effects, it has been suggested that cumulative effects of winter weather over several years should have even stronger effects on ungulate populations than that of single years (Mech et al. 1987, Post & Stenseth 1999).

As well as considering the most suitable approach for capturing climatic effects, a second question is which weather parameter is most appropriate when describing local weather fluctuations? A range of parameters have been used for ungulates, including snow accumulation (Mech et al. 1987, Solberg et al. 2004), temperature (Langvatn et al. 1996) and summer rainfall (Langvatn et al. 1996). However, each of these parameters may capture a different aspect of weather and therefore none of them are likely to capture climatic effects in full (Hallett et al. 2004). In an attempt to capture the complexities of local weather in a simple index, vertebrate ecologists currently often use large-scale atmospheric phenomena, including the North Atlantic Oscillation (NAO) in Northern Europe (Post & Stenseth 1999, Weladji & Holand 2003). However, using large-scale climatic indices can also be problematic, because they are designed to capture climatic dynamics over very large areas, within which local weather varies markedly (Myrsetrud et al. 2003). Hence, although appealing at the level of integrating over multiple climatic events, large-scale indices are not expected to perform as well as appropriate measures of local weather. In this respect, an



alternative index to the NAO can be the maximal ice extent (MIE) of the Baltic Sea that has strong negative correlation with mean wintertime air temperature and a positive correlation with the duration of snow cover as well as snow depth (Jaagus 1999, Tooming 2003). Although this index has been recorded since 1720 and represents one of the best documented climate records in the region (Chen & Li 2004), this indicator has received little attention in terrestrial animal studies.

In addition to density-independent effects, dramatic changes in population densities can influence population dynamics as well as various life-history traits of northern ungulates (Clutton-Brock et al. 1987, Post & Stenseth 1999, Solberg et al. 1999, Forchhammer et al. 2001, Forchhammer et al. 2002, Stewart et al. 2005). For example, it has been shown that high population densities significantly reduced body size and fertility rates in several ungulate species such as the reindeer (*Rangifer tarandus*) (Skogland 1990), the moose (Sand et al. 1996), the red deer (*Cervus elaphus*) (Bonenfant et al. 2002) and the North American elk (*Cervus canadensis*) (Stewart et al. 2005). Moreover, increasing population densities have been found to significantly delay ovulation (Langvatn et al. 2004) and parturition dates (Clutton-Brock et al. 1987) in the red deer (*Cervus elaphus*), but on the contrary, advanced birth dates in the Soay sheep, *Ovis aries* (Forchhammer et al. 2001). Given that density-dependent effects are manifested principally through intraspecific competition, we can predict that the direction of such effects on life-history traits can be phase-specific, with negative effects near to ecological carrying capacity.

In strongly seasonal environments, the timing of reproductive events like conception and parturition can also have profound impact on several key life-history traits that are directly related to individual fitness. For instance, early conception and birth date may be associated with higher fitness returns for mothers, owing to improved condition (Festa-Bianchet 1988, Holand et al. 2006, Solberg et al. 2007) and future reproductive performance of the offspring (Albon et al. 1987, Kruuk et al. 1999; Lindström 1999, Langvatn et al. 2004). Hence, an intriguing idea arises to look for associations between the timing of conception and various components of maternal fitness such as fecundity and foetal sex ratio. It is noteworthy that the positive effect of birth size on future survival (Loison et al. 1999) and reproductive success (Clutton-Brock et al. 1988, Kruuk et al. 1999) in ungulates is usually greater in males than in females. Consequently, mothers in good condition should produce an offspring sex ratio biased towards males (Trivers & Willard 1973). Accordingly, it might be predicted that in highly dimorphic and polygynous mammals such as northern ungulates, females that conceive earlier during the rut should produce a higher proportion of male offspring than those that conceive later (Kruuk et al. 1999). This hypothesis has gained support from an experimental study with female reindeer in Kaamanen Experimental Reindeer Station in Finland (Holand et al. 2006). However, this topic is poorly studied in other ungulate species, including the moose.

The general aim of this thesis is to explore the effects of winter weather and population density on body size, fecundity (**I**), the timing of conception (**II**) and on the moose population-growth rate (**IV**) in a wild moose population in Estonia. My central objective was to test the correlation between a composite index of regional winter weather – the maximal ice extent (MIE) of the Baltic Sea – and the phenotypic variability of moose life-history traits as well as moose population dynamics, and to compare the magnitude of these relationships with NAO effects (**I**, **II**, and **IV**). Assuming that organisms have adapted to both the local mean and variance of environmental variables, it was predicted that both winter severity and variability depress moose body size and fecundity parameters (**I**). Additionally, I tested the effects of mean air temperatures in April (the beginning of the period of active vegetation), May (main time of parturition in moose), August (the beginning of mating season) and September (the main period of mating season) on the key life-history trait, the timing of conception (**II**).

Given that an earlier conception date can be beneficial in terms of offspring fitness, the effect of conception date on the type of litters produced by female moose in Estonia was also explored (**III**). Specifically, we predicted that females conceiving earlier are expected to produce a relatively higher proportion of expensive litters (male-biased litters with a higher twinning rate), compared with females that conceive later.

## 2. MATERIAL AND METHODS

### 2.1. Study area

Estonia experiences a climate that is midway between a maritime and continental climate, with characteristically warm summers and fairly mild winters. During the period 1966 to 2010, the average annual rainfall within the territory of Estonia has varied from 550 to 750 mm, and the average yearly air temperatures have varied from 4.6°C to 6.8°C in different weather stations. During the same period, the mean wintertime (DJFM) air temperature has varied from -4.7°C to -0.9°C and the sum of wintertime precipitation from 119 to 209 mm in different weather stations. Snow cover forms in mid-December and lasts until April, being the thickest at the end of February (about 30–40 cm). In very mild winters, there is no permanent snow cover. Vegetation period (with air-temperature over 5°C) lasts 165–185 days and the period of active vegetation (over 10°C) 110–135 days. Approximately 50% of Estonia is covered with forests (approximately 26 000 km<sup>2</sup>).

Given that there are slight climatic, floristic and topographic differences between different geographic regions in Estonia, the data gathered by wildlife boards were categorized as originating from either the northern, western or south-eastern area, primarily based on the borders of administrative units.

### 2.2. Data collection

This study is mainly based on data analysis of reproductive tracts and lower jawbones of female moose harvested from across Estonia during regular hunting seasons. Reproductive tracts of female moose were collected during seventeen successive years from 1993–2009. Lower jawbones were collected during the period 1987–2009 (with the exception of 1989, when data were not collected). For each moose shot, hunters recorded date, locality and collected the lower jaw for determination of age and body size. In order to study the effects of climate and population density on moose life-history traits, we used data on the lower jawbone length of 3614 individuals hunted in 1987–2002 (**I**), data on fecundity of 937 individuals hunted between 1993–2002 (**I**), and data on conception dates of 918 female moose shot between 1993–2009 (**II**). The effects of conception date on litter type and foetal sex ratio were studied for 289 individuals hunted between 1999–2004 with developing embryos at least four weeks old (**III**). Population dynamics of Estonian moose population (**IV**) was monitored in relation to winter weather over a forty year time series (1965–2005).

## 2.3. Measurements

The age of females was determined as a function of tooth development and the degree of wear of molars and premolars (Knorre & Shubin 1959). Age was determined throughout the study period by the same person. Females were divided into six age groups: juveniles (0.5 years old – age-group used only in the study **I**), yearlings (1.5 years old), sub-adults (2.5-years old), sub-adults (3.5-years old), prime-aged (4.5–7.5 years old) and older ( $\geq 8.5$  years old) individuals. (For more details see **I**, **II** and **III**).

As there is a strong correlation between body mass and jawbone length (e.g. see Toïgo et al. (2006) for a study on roe deer), lower jawbone length was used as a measure of body size (**I**).

Analysis of reproductive tracts consisted of determination of the number of *corpora lutea* in the ovaries (**I**) and number, age and sex (if possible) of embryos in the uterus.

Age of embryos was determined to an accuracy of 1 week using methods described by Markgren (1969) and Kurnosov (1973). Using the age of embryos and culling date, a conception date was calculated to an accuracy of 1 week (expressed as the number of weeks since the beginning of August; first week, Aug. 1–7, **II** and **III**). In moose the developing embryos become visible at the age of three weeks, so conception dates were calculated only in cases of females with developing embryos at least three weeks old and with known date of harvest. In the study of the effects of climate and population density on conception date (**III**), only females harvested after 30 October were included (see **III** for details).

The sexing of embryos older than 6 weeks was based on visual inspection of secondary sexual characteristics (Markgren 1969). In the case of younger embryos (4–5 weeks old), an embryonic tissue sample was taken and cells were fixed and stained on a slide with 0.005% methyl-blue. The samples were then examined using a microscope and scored for the presence or absence of a Barr body (see study **III** for additional information). The latter method was applied up until 2004.

## 2.4. Moose density

Moose abundance and hunting rates were reported by wildlife boards across the full geographical range of moose in Estonia. The density estimates of moose were based on counts of moose (based on tracks) carried out throughout Estonia at the end of winter before parturition (official counts). Density was calculated as the number of individuals per km<sup>2</sup> of suitable moose habitat (approximately 24 000 km<sup>2</sup>). These estimates were closely correlated to the number of moose seen during hunting in each study plot (R Spearman = 0.8, P < 0.01, N = 11 years). During the period 1993–2009, this density estimate has been highly correlated with the number of moose hunted in the following autumn (Spearman correlation coefficients in different regions vary from 0.91 in the south-eastern

to 0.98 in the northern region). In 1987–2009, the density of moose in the wintering population in Estonia varied between 0.24 to 0.61 individuals (mean 0.41 individuals) per km<sup>2</sup>.

In the study of winter effects and predation on moose population dynamics (IV), this abundance estimate is used to calculate the moose population growth rate ( $R_t$ ), by a formula ( $R_t = \ln(N_t/N_{t-1})$ ); where  $N_t$  is the number of moose in the wintering population in the year  $t$ .

## 2.5. Weather data

In the studies I, II and IV, two different indices of winter weather were used: 1) the annual values of maximum ice extent (MIE), defined as the area of sea cover with ice per 1000 km<sup>2</sup>, for the Baltic Sea (Seinä and Palosuo 1993) and 2) the widely used NAO index (station-based NAO index averaged over December, January, February, and March), data provided by the Climate Analysis Section, NCAR, Boulder, USA (Hurrell 1995). Data of sea ice were obtained from the Finnish Institute of Marine Research. The maximum extent of sea ice (MIE) in the Baltic Sea has a strong negative correlation with mean wintertime air temperature (averaged over November, December, January, February, and March,  $r = -0.88$ ), a positive correlation with the duration of snow cover ( $r = 0.68$ , Jaagus 1999) and maximum snow depth (correlation coefficients range from 0.53 in inland to 0.86 in coastal weather stations, Tooming 2003) in Estonia. During the study period, the MIE was negatively correlated with the NAO index ( $r = -0.57$ ). To assess the effect of annual and inter-annual variability of winter weather on moose body size and fecundity (I), absolute values of the standardized deviates (VMIE) from the long-term average of the MIE were used in addition to the MIE and the NAO index.

In the study II, we also used data on air temperatures in April, May, August and September as potential predictors of the timing of conception. Weather conditions in spring, late summer and early autumn are also expected to have profound impact on the timing of reproduction of the moose because i) April is the period for the onset of vegetation growth as well as for the beginning of parturition, ii) May is the main period of parturition, iii) August is the beginning of the rut and iv) September is the main period of the rut, when approximately 70% of female moose in Estonia conceive. The data of air temperatures observed in three different weather stations located in Tallinn, Pärnu and Tartu was obtained from Estonian Meteorological and Hydrological Institute.

## 2.6. Data analysis

Statistical analysis was performed using Statistica 7 and 8 (Statsoft, Tulsa, OK, USA) and SAS 9 (GLMM, SAS Institute, Inc., Cary, NC, USA). The parsimony of full models with parameters of interest was assessed with Akaike's Infor-

mation Criterion (AIC) and  $\Delta$ AIC (Burnham & Anderson 1998) using generalized linear/nonlinear models (**I**, **II**, **IV**). After selection of the most parsimonious subsets of models using the AIC, the magnitude and direction of relationships between independent variables and response traits was analyzed by using general linear mixed models for body size, conception date and moose population-growth rate, and generalized linear mixed models for ovulation data (see **I**, **II** and **IV** for specific details). The effect of conception date on embryonic sex ratios and litter characteristics was studied using ordinal multinomial logistic regression for the type of litter and embryonic sex ratio, and binomial logistic regression for litter size (**III**). Due to the nonlinear relationship between embryonic sex ratio and conception date, an alternative approach was used by dividing the conception period into three stages based on the peaks (median) in conception date for each year separately. Thereafter, chi-squared tests were applied separately within each stage (**III**). See original papers for more details.

## 3. RESULTS

### 3.1. Weather effects

Both direct, delayed and cumulative effects of climatic indices including the NAO and two measures of regional weather – the maximal extent of ice on the Baltic Sea (MIE) and absolute values of its annual deviations from the multi-year mean (VMIE) – were assessed on the moose life-history traits. Lower jawbone length, as a relative measure of body size, was negatively related to direct and delayed effects of winter severity (large values of MIE at time lag –1 and –3) and winter variability (large values of VMIE at time lag –1 and –2) (I). Cumulative effects of the first and second previous winter using MIE and VMIE had also a negative relationship with moose jawbone length. The NAO had no significant effect on the jawbone length (I). The magnitude of direct, delayed as well as cumulative effects of winter weather on jawbone length varied among age classes. None of direct effects of the preceding winter predicted the jawbone length of calves (I).

The proportion of fertilized females (presence or absence of *corpora lutea*) was examined only in 1.5 year-old individuals because in older age classes the proportion of unfertilized individuals was very low (I). The proportion of fertilized yearlings was negatively related to delayed effects of VMIE at time lag –2 and cumulative effects of VMIE at time lag –1 and –2 (I). In contrast, no direct, delayed or cumulative effects of the MIE and the NAO were revealed (I).

The probability of multiple ovulation was negatively influenced by direct effects of winter variability (VMIE) and delayed effects of winter severity as reflected by the MIE (at time lag –2) and the NAO (at time lag –3). Cumulative climatic effects did not influence the probability of multiple ovulation (I).

The conception date was related non-linearly to the MIE effects, indicating a significant delay in the season following severe winters (II). The timing of conception was also postponed in warm autumns as reflected by high mean air temperatures in September (II).

The MIE and NAO effects on population dynamics were also examined. The moose population growth rate ( $R_t$ ) was positively influenced by delayed effects of the MIE and negatively by delayed effects of the NAO-index (at time lag –2; IV).

In most cases, the studied life-history traits as well as population growth rate were remarkably better related to the MIE than the NAO-index (I, II and IV).

### 3.2. The effects of population density

In addition to climatic effects, density-dependent effects partly accounted for variation in moose body size and fecundity (I). Population density had a significant negative effect on the jawbone length in models with delayed effects

of the MIE and cumulative effects of the VMIE. Significant effects of population density on the probability of multiple ovulation was evident in the models with delayed effect of the MIE and the NAO (I).

The conception date of moose cows was negatively related to population density, indicating that increased population density was related to the advancement of conception (II).

No significant effect of population density on litter type and foetal sex ratio was revealed (III).

### 3.3. The effects of conception date

The conception date significantly affected the type of litter conceived (III). In agreement with Williams's (1979) model, females that conceived earlier had a higher probability of producing more expensive litters than those conceived later in the season. Conception date also predicted the twinning rate. Earlier conceived females had more twins (III).

Foetal sex ratio varied nonlinearly with the progress of the conception period, with the proportion of male embryos highest in the first stage (III). Moreover, a nearly significant age by conception date interaction emerged. In yearlings and subadults (1.5–3.5 years old), the best-fit model included the third degree polynomial relationship between the sex ratio and conception date, whereas no relationship was found in adults (III).

Owing to the nonlinear relationship between sex ratio and conception date, an alternative analysis was conducted in which the conception period was divided into three consecutive stages and sex ratio was examined separately within each (see III for details). The foetal sex ratio of yearlings and subadults differed considerably between the different conception stages. In the first stage, the embryonic sex ratio did not differ significantly from the balanced (1:1) sex ratio. The embryonic sex ratio was most strongly female-biased in the second stage of conception (3.2 female per 1 male), and still moderately female-biased (2.5 female per 1 male) in the third stage. In adults (4.5 years old and older), no significant differences from the balanced (1:1) foetal ratio were found during any of the conception stages (III).



## 4. DISCUSSION

### 4.1. Weather effects

Variation in winter weather influenced moose life-history traits (**I**, **II**) as well as population growth rate (**IV**) significantly. It is noteworthy that the magnitude of these effects varied considerably between different climatic indices, demonstrating the complexity of the relationships between different aspects of environmental fluctuation and individual as well as population level responses.

Winter severity as reflected by the MIE had a direct negative effect on moose body size (**I**), a nonlinear effect on the conception date (**II**), and no effect on different measures of fertility (**I**). Consistent with our findings, winter severity (i.e. thick snow cover, low temperatures) has been found to have a direct negative effect on the body mass of moose (Hjeljord & Histol 1999, but see Solberg et al 1999), red deer (in yearlings – Loison & Langvatn 1998) and reindeer (Skogland 1983). In severe winters extreme cold can lead to increased cost of thermoregulation (Parker & Robbins 1985), while thick snow cover can restrict forage intake or increase the costs of locomotion (Parker et al. 1984) and cratering (Fancy & White 1985). The nonlinear effect of winter weather on the conception date may indicate that this trait was relatively unaffected by moderately cold winters, but strongly delayed after severe winters. For instance, after cold winters, the delay in plant growth may lead to the postponement of parturition. To compensate for the negative effects of late parturition, mothers may try to increase their offspring quality by prolonging the lactation period (Gaillard et al. 2000), which can lead to delayed onset of the next reproductive cycle (Hogg et al. 1992). The effect of winter weather on conception date may also be mediated through its effect on female body condition given that decreased body mass has been found to be related to delay in ovulation (Garel et al. 2009). It was also found that climate variability (VMIE) of the previous winter significantly depressed moose body size and the probability of multiple ovulation (**I**). These findings support previous prediction that average winters provide the best living conditions for local populations of ungulates and both severe and mild winters may have negative additive effects on the moose life-history traits. However, although unfavorable effects of harsh winters are widely known, it is difficult to understand why warm winters should have such effects. Studies of Soay sheep (Milner et al. 1999) and of Northern Yellowstone elk (Coughenour & Singer 1996) have shown that warm, rainy and windy winters can be bad for herbivores, which suggests an increase in energy expenditure on thermoregulation. It has also been proposed that rain on snow, or alternating periods of warm and freezing temperatures, could produce a crust that may increase energy expenditure for locomotion (Coughenour & Singer 1996). Moreover, warm winters may have indirect negative effects on summer foraging conditions (Post et al. 1997, but see Pettorelli et al. 2005). One mechanism may be that late development of snowpacks in mild winters could result in increased soil freezing, damaging the fine roots of plants and soil

microbial populations and potentially having long-term effects on forest ecosystems (Groffman et al. 2001).

Besides direct effects of the previous winter, we revealed negative time-lagged effects of winter weather on moose body size and fecundity (**I**), and on population growth rate (**IV**). Given that in the study **I** the models using the MIE and the NAO of the year of birth had the most pronounced effect, we can assume that these long-lasting effects operated mainly through maternal condition. Consistently, such delayed winter effects prevailing during the year of birth have been shown to affect subsequent body mass and fecundity in several cervid species (reviewed in Post & Stenseth 1999, Solberg et al. 2004). It is noteworthy that winter climate as reflected by the MIE and the NAO values showed the strongest influence on moose population growth rate for the time lag of two years, indicating the negative effect of warm winters (**IV**). It is likely that this indirect effect can be regarded as two-stage process. Initially, mild winter conditions may have positive effects on population density via increased survival and fecundity of lower-quality individuals that, in turn, produce higher than average proportion of low-quality offspring. Later, increased competition for resources and the reduction of average quality of breeding individuals may diminish population size through negative effects on survival and *per capita* fertility rates. Hence, it seems that delayed climatic effects may influence population dynamics also through density-dependent effects.

Considering that previous winters should have additive effects, it has been hypothesized that cumulative effects of environmental fluctuation should have an even stronger impact on ungulate populations than that of single years (Post & Stenseth 1999). However, study **I**, in which the cumulative effects of winter weather were studied, provides weak support for this assumption because only one out of three weather indices (VMIE) had a strong cumulative influence on moose body size, while no cumulative effects were observed in the case of fecundity.

In this study, the magnitude of winter effects on body size and fecundity also varied between age classes (**I**). The direct effects of MIE and VMIE on the body size were highly significant for subadults (2.5 and 3.5 years old), marginally significant for yearlings (1.5 years old), and nonsignificant in the case of calves (0.5 years old). Consistently, Solberg et al. (1999) found that direct winter effects had strong impact on yearlings and subadults, but not on calves. Although I cannot provide an exact mechanism to explain these age-specific differences in responses, I can speculate that the immediate effect of environment, operating through access to food, mobility, and thermoregulation (Schwartz 1998), can be buffered by maternal condition during the foetal period. Moreover, given that subadults usually move very long distances (Saether & Heim 1993), they may be highly susceptible to climate harshness during the first years of independence due to their lower competitive abilities in interactions with older individuals, or due to poorer quality food than in their mother's home-range (see references in Sæther & Heim 1993).

In contrast to most previous studies (e.g., Post & Stenseth 1999), the results of my thesis (**I**, **II**, **IV**) show that winter effects based on the MIE index were consistently stronger than those based on the NAO index. Therefore I cannot regard the NAO as the most suitable composite climatic index for predicting moose life history traits or population dynamics in Estonia. However, given that both compared climatic measures capture slightly different aspects of winter weather, I suggest that these indices – the maximal extent of ice on the Baltic Sea (MIE) and the NAO – can be used in parallel as determinants of growth and fecundity of northern ungulates in coastal regions of the Baltic Sea.

Although this study was mainly focused on capturing weather effects prevailing during the wintertime, the effects of mean air temperatures in April, May, August and September on the key life-history trait, the timing of conception, were also studied (**II**).

Among these climatic predictors, only increasing air temperatures in September (during the rut) were related to the delay in conception dates (**II**). As a large herbivore species living in high northern latitudes, the moose is well adapted to extremely cold temperatures in winter, but has difficulties with warm temperatures in summer (Renecker & Hudson 1986). Hence, it is likely that high temperatures in September, when male moose have reached their yearly peak in body mass (Schwartz 1998), can cause significant heat stress and result in reduced activity and delay in the rut.

## **4.2. The effects of population density**

Population density had only a marginal effect on moose body size and fertility parameters (**I**). The weak negative effect of increased density may be explained by increased food competition, as previously reported in several ungulates in different geographical regions (Weladji & Holand 2003). However, it is important to note that according to our data, density-independent effects on moose body growth were markedly stronger than density-dependent effects. Nevertheless, the effect of population density on the timing of conception was much stronger than its effect on other life-history traits (**II**). The results showed that increased population abundance was related to the advancement of conception date among females (**II**). This finding is in accordance with earlier findings on the Soay sheep, which demonstrated that increased population density consistently resulted in earlier born lambs (Clutton-Brock et al. 1992, Robertson et al. 1992, Forchhammer et al. 2001), but contrasts to several previous studies on the red deer reporting negative relationships with ovulation time (Langvatn et al. 2004), conception date (Clutton-Brock et al. 1997) and parturition date (Clutton-Brock et al. 1987). Given that density-dependent effects are manifested principally through intraspecific competition that increases near to ecological carrying capacity, we can predict that body size, fertility rates and recruitment of yearlings into the population would be lower in the high density population than for the population at low density (Bowyer et al. 1999, Langvatn et al. 2004,

Stewart et al. 2005). In our case, the weak relationship between population density and body size as well as different measures of fertility (I), suggest that during the study period the population density of moose has been remarkably below the carrying capacity. An explanation can be that intensified forestry during recent decades has significantly improved the feeding conditions for moose due to increased availability of younger forest stands, and therefore presumably increased the level of carrying capacity in Estonia. Hence, it is likely that increasing population abundance does not appear to increase density relative to carrying capacity of the environment and therefore the results regarding the Estonian moose population (I, II) are more related to increasing habitat quality concurrent with increasing density.

### 4.3. The effects of conception date

Phenological events such as conception or parturition dates may have profound impact on several key life-history traits at the individual as well as the population level (Langvatn et al. 2004, Holand et al. 2006, Solberg et al. 2007, Feder et al. 2008). Correspondingly, the current study showed that earlier-conceived females more frequently produced expensive litters (male-biased litters with high twinning rate) in comparison with later-conceived females (III). However, it remains to be established whether the mechanism of sex allocation is directly related to conception date *per se*, or whether the effect of conception date is mediated by maternal condition. Why should females that conceive early bias their foetal sex ratio in favour of males? It has been shown that an early start in life can be beneficial in terms of offspring fitness – higher body mass at birth and in the first autumn (Holand et al. 2006), a higher probability of survival (Festa-Bianchet 1988, Langvatn et al. 2004) and a higher lifetime reproductive success (Kruuk et al. 1999). Given that the effect of birth size on future survival (Loison et al. 1999) and reproductive success (Clutton-Brock et al. 1988, Kruuk et al. 1999) is more pronounced in males (due to sexual selection) than in females, sons that are born earlier are relatively more successful than earlier-born daughters. The negative effects of delayed calving might be reduced to some extent if extra resources could be allocated to offspring during the lactation period or if the period of maternal care could be prolonged (review in Gaillard et al. 2000). However, an increase in investment during lactation, which is considered to be the most energy demanding period in the reproductive cycle (Clutton-Brock 1991), would probably further reduce the fertility and probability of survival of the mother (review in Myrsterud et al. 2002). Hence, fitness returns to mothers can be increased not only by adjusting the foetal sex ratio, but also by advancing conception as a strategy to minimize the postpartum costs of reproduction.

It is noteworthy that the effect of conception date on embryonic sex ratio was dependent on female age. Foetal sex ratio varied nonlinearly with conception date in yearlings and subadults (more male embryos in the first stage

of conception), while no relationship was found among older age classes. This finding is somewhat contrary to my initial predictions. However, the costs of reproduction are indeed considered to be the highest among younger individuals (Clutton-Brock 1991) because young animals are more constrained by a trade-off between reproduction and future body growth (Sand 1996, Landete-Castillejos et al. 2004) in comparison with fully grown individuals. Accordingly, preweaning maternal care has been found to increase as the age of the mother increases (Weladji et al. 2003). This suggests that prime-aged and older females may be able to compensate for giving birth to their offspring late in the season by increasing their maternal care with relatively little cost, compared with younger individuals. Hence, it is likely that the effect of advancement of conception (and hence birth) is more important among younger age groups. Secondly, we cannot exclude the possibility that foetal sex ratio and the type of litter produced by prime-aged and older females remained relatively constant throughout the conception period because such females mated with higher-than-average quality males.

#### **4.4. Conclusions**

This thesis reveals significant direct as well as time-lagged effects of winter weather on several life history traits and population dynamics of free-living moose in Estonia. The relationships between climate and life-history traits are not always linear, suggesting that both greater or lower than the long-term mean of weather conditions can have significant impact on ungulate performance. Weak negative effects of population density were established on moose body size and fecundity, and a strong negative effect on the conception date. The latter effect is opposite to what was expected. An explanation may be that density-dependent effects might be mediated by increasing ecological carrying capacity concurrent with increasing population density. Intensified forestry during recent decades has improved the feeding conditions for moose due to increased availability of younger forest stands, thereby increasing moose habitat quality in Estonia.

The findings of this thesis also emphasize that the timing of conception can have profound impact on several fitness-related traits. Earlier-conceived females produced larger litters with higher proportion of male embryos than those conceived late. These adjustments are in accordance with the Trivers-Willard hypothesis, that females that conceive earlier are in better condition. However, given that conception date affected foetal sex ratio only in yearlings and subadults, it is likely that prime-aged and older females adopt more flexible reproductive strategies by being more selective in their choice of mates and by investing more into postnatal maternal care.

## SUMMARY

Life-histories and population dynamics of large mammalian herbivores living in a variety of ecosystems have been found to be closely related to density-independent as well density-dependent processes. In ungulates, living in temperate and arctic environments in the northern hemisphere, the effects of climate are often interpreted as harsh winter weather directly impacting survival, growth or condition, or indirectly influencing maternal condition and offspring quality, which in turn influences individual performance. However, in parallel with the negative influence of severe winters, negative effects of warmer than average winters on ungulate populations have also been described. Hence, when predicting the likely consequences of climate change on various life history traits of ungulates, the changes in both the long-term mean of climatic indices and changes in the variability need to be considered.

In this thesis, long-term data were used to explore the effects of weather and population density on body size, fecundity parameters (**I**), the timing of conception (**II**) and on the population-growth rate (**IV**) in a wild moose (*Alces alces*) population in Estonia. In parallel, two different composite indices of winter weather were used – the maximal ice extent (MIE) of the Baltic Sea and the NAO (North Atlantic Oscillation). As a novel approach, it was assumed that individuals have adapted to both the local mean and variance of environmental variables, the effects of winter variability on moose body size and fecundity were studied using absolute values of the standardized deviates (VMIE) from the long-term average of the MIE (**I**). The results showed that winter weather had significant direct as well as time-lagged effects on several life history traits and population dynamics of free-living moose in Estonia. The lower jawbone length, reflecting body size, was negatively related to direct, delayed as well cumulative effects of winter severity (MIE) and winter variability (VMIE), the size of the effect varying between respective climatic indices (**I**). In contrast, the NAO index had no significant effect on jawbone length. The proportion of fertilized yearlings was negatively related only to delayed and cumulative effects of the VMIE, while the probability of multiple ovulation was negatively influenced by direct effects of the VMIE and delayed effects of the MIE and the NAO (**I**). The conception date was non-linearly related to MIE effects, indicating a significant delay in the season following severe winters (**II**). This is the first study documenting winter effects on the conception date of the moose, suggesting that previous winter conditions have direct or indirect carry-over effects on the timing of conception in the following autumn. Direct negative effects of severe winters (large values of MIE) on moose traits are probably related to increase in energy expenditure because of large snow depth or low temperature, while the warmer than average winters may impose greater energetic demands on thermoregulation due to wet and windy weather, or may have indirect negative effects on summer foraging conditions. Prevailing winter climate during the year of birth can influence maternal condition and thereby subsequent body size of offspring and fecundity in the adulthood.

Besides significant direct and delayed effects of winter weather on several moose life history traits, the delayed negative effect of warm winters on moose population growth rate was revealed in this thesis (IV).

The results of this thesis also demonstrate that winter effects based on the MIE index were consistently stronger than those based on the NAO index, and the effects of winter variability (VMIE) were generally stronger as compared to the effects of winter severity (MIE and NAO). Therefore, I can draw two important conclusions. First, I suggest that the MIE index can be regarded as the more suitable composite weather index for predicting moose life history traits in Estonia when compared with the NAO index. Second, MIE and VMIE capture different aspects of the local climate, and these indices can be used in parallel as predictors of growth and fecundity of northern ungulates in coastal areas of the Baltic Sea.

Besides winter effects, high mean air temperatures in September were also related to delayed conception date in autumns (II). It is likely that high temperatures in September, when male moose have reached the yearly peak in body mass, can cause significant heat stress and result in reduced activity and delay in the rut.

Increase in population density had only a marginal negative effect on moose body size and fertility parameters (I), while it was significantly related to advancement of conception date of female moose. The latter finding (II) is opposite to the expected and may indicate that the effect of population density on conception date is mediated by the increase in habitat quality concurrent with increasing population abundance.

Given that in the strongly seasonal environments, the timing of reproductive events like conception can also have profound impact on several key life-history traits that are directly related to individual fitness, I also looked for associations between the timing of conception and various components of maternal fitness such as litter size and foetal sex ratio (III). There was a clear relationship between conception date and litter characteristics (III). Overall, litters conceived earlier were more likely than those conceived late to contain multiple embryos and a high proportion of males. However, while foetal sex ratio varied nonlinearly with conception date in yearlings and subadults (1.5–3.5 years old), no relationship was found in adults. These results show that female moose adjust foetal sex ratio and litter size depending on their age and the date of conception, and that these adjustments are in accordance with the Trivers-Willard hypothesis if females which conceive earlier are in better condition.

## SUMMARY IN ESTONIAN

### Talvise ilmastiku, populatsiooni asustustiheduse ja sigimisaja mõju põdra (*Alces alces*) elukäigutunnuste ning populatsioonidünaamikale Eestis

Suurte taimtoiduliste maismaaimetajate elukäigutunnuseid ja populatsioonidünaamikat mõjutavad suurel määral nii populatsiooni asustustihedusest sõltumatud ilmastikutingimused kui ka asustustihedusest sõltuvad protsessid. Ilmastikutingimuste olulist mõju arktilises ja parasvöötme ökosüsteemides elavatele sõralistele on kirjeldatud paljudes töödes. Laialdaselt on teada karmide talvede otsesed negatiivsed mõjud isendite ellujäämusele ja konditsioonile. Peale selle on näidatud talvetingimuste hilinemisega avalduvaid kaudsemaid mõjusid. Näiteks on leitud, et ontogeneesi varases staadiumis – looteas, mil emaslooma organism on puhvriks oma järglase ja otseste keskkonnamõjude vahel – kandub osa keskkonnamõjudest ema konditsiooni vahendusel järglasele edasi ning võib seeläbi mõjutada nii järglase kui ka ema enese kohasust. Paralleelselt karmide talvede negatiivse mõjuga on mitmetes uuringus kirjeldatud ka tavapärasest soojemate talvede negatiivseid mõjusid sõraliste elukäigutunnustele. Seoses globaalse kliimasoojenemisega on vastavate uuringute osakaal viimase viieteistkümne aasta jooksul märgatavalt kasvanud. Seega, püüdes ennustada kliimamuutuste võimalikku mõju isendite erinevate elukäigutunnuste kujunemisele, on vajalik lisaks muutustele ilmastikunäitajates arvestada ka nende näitajate varieeruvust pikaajalise keskväärtuse suhtes.

Käesolevas doktoritöös vaadeldakse talviste ilmastikutingimuste ja populatsiooni asustustiheduse mõju põdralehmade kehakasvule, viljakusnäitajatele (I), viljastamisajale (II) ja põdrapopulatsiooni kasvukiirusele (IV). Paralleelselt kasutatakse kahte talvist ilmastikku iseloomustavat näitajat – Läänemere talvise jäätumise maksimaalset ulatust (MIE) ja Põhja-Atlandi ostsillatsiooni indeksit (NAO indeks). Tuginedes eeldusele, et organismid on kohastunud kohalike kliimaatiliste tingimuste pikaajalise keskmise ning ilmastikutingimuste muutlikkuse suhtes, uurisin ka talvetingimuste varieeruvuse seoseid põdralehmade kehasuuruse ja viljakusnäitajatega. Selleks kasutasin MIE pikaajalise keskmise suhtes arvatud iga-aastaste standardiseeritud hälvete absoluutväärtusi (VMIE) (I). Töö tulemusena selgus, et põdralehmade erinevad elukäigutunnused olid tihedalt seotud nii vahetute kui ka hilinemisega avalduvate talvemõjudega. Kehasuurust peegeldav alalõualuu pikkus oli negatiivselt seotud karmide talvede (MIE) ja talvede muutlikkusega (VMIE) ning seejuures ilmsid mõlema näitaja puhul nii vahetud, hilinemisega avalduvad kui ka kumulatiivsed mõjud. Samas NAO indeksi ja alalõualuu pikkuse vahel oluline seos puudus. Viljastatud mullikate (1,5-aastaste) osakaal oli negatiivselt seotud talvede varieeruvusega (VMIE) nii hilinemisega avalduvate kui ka kumulatiivsete mõjude kaudu. Põdralehmade mitmikviljastamise tõenäosus oli negatiivselt seotud talvede muutlikkuse otseste, ning karmide talvede (MIE ja NAO) hilinemisega avalduvate mõjudega (I). Põdralehmade viljastamisaja ja karme talvi iseloo-



mustava Läänemere maksimaalse jäätumise vahel oli mittelineaarne seos, mis osutab viljastamisaja märkimisväärsele hilinemisele pärast külmi ja lumerohkeid talvi (**II**). Käesoleva doktoritöö autorile teadaolevalt on see esimene uuring, mille tulemused näitavad, et eelneva talve ilmastikutingimuste ja sügise põdralehmade viljastamisaja vahel on otsene ja/või isendite konditsiooni vahendusel toimiv seos.

Töös tuvastatud karmide talvede otsesed negatiivsed mõjud on tõenäoliselt tingitud suurenenud energeetilistest kulutustest külmadel ja lumerohketel talvedel. Talvede muutlikkuse (VMIE) tugevad mõjud põdralehmade kehasuurusele ja erinevatele viljakusnäitajatele (**I**) annavad kinnitust oletusele, et ka tavapärasest soojematel talvedel on isendite elukäigule tuntav negatiivne mõju. Ühelt poolt võivad tavapärasest soojemad talved oma erinevate omadustega, nagu tuulisus, sagedased vihasajud ja jääkoorik lumel, suurendada isendite energeetilisi kulutusi, kuid teisalt võivad sellised talved mõjutada suurel määral ka sõraliste suviseid toitumistingimusi.

Doktoritöö tulemused kinnitavad ka sünniaegsete ilmastikumõjude olulisust ning näitavad, et ilmastikutingimuste otsesed mõjud ema konditsioonile kanduvad edasi nende järglastele ning avaldavad suurt mõju järglaste kehasuurusele ja viljakusele hilisemas elus (**I**).

Peale talvetingimuste ja eri elukäigutunnuste vaheliste seoste leiti käesolevas töös ka kaheaastase hilinemisega avalduv soojade talvede oluline negatiivne mõju põdraasurkonna juurdekasvule (**IV**).

Erinevate talvist ilmastikku iseloomustavate näitajate võrdluses oli maksimaalse jäätumise ulatus (MIE) võrreldes NAO indeksiga valdavalt tunduvalt tugevamini seotud vaadeldud elukäiguparameetrite (**I**, **II**) ja populatsiooni juurdekasvuga (**IV**). Lisaks olid üldjuhul seosed talve muutlikkuse (VMIE) ning põdralehmade kehasuuruse ja viljakusnäitajate vahel tugevamad kui nende samade tunnuste seosed talvekarmust iseloomustavate MIE ja NAO indeksiga (**I**). Seega näitavad töö tulemused, et Läänemere iga-aastane maksimaalse jäätumise ulatus (MIE) on võrreldes NAO indeksiga märksa sobivam talvise ilmastiku ja põdra elukäigutunnuste vaheliste seoste indikaator. Kuna MIE ja VMIE kirjeldavad kohaliku ilmastiku erinevaid aspekte, võib ilmastikutingimuste muutuste ja Läänemere piirkonnas elavate sõraliste elukäigutunnuste vaheliste seoste ennustamisel kasutada neid näitajaid paralleelselt.

Peale talvemõjude olid ka kõrged keskmised septembrikuu õhutemperatuurid seotud põdralehmade viljastamisaja hilinemisega (**II**). Suurte kehamõõtmetega ja Arktikasse ulatava levikuga põder on liigina üsna hästi kohastunud karmide talvetingimustega, kuid talub halvasti kõrgeid suviseid õhutemperatuure. Kuna põdrapullid saavutavad oma iga-aastase kehamassi maksimumi vahetult jooksuaja hakul, siis on üsna tõenäoline, et kõrged õhutemperatuurid põtrade jooksuaja alguses ja kulminatsiooniperioodil septembris võivad põhjustada põtradele märkimisväärset kuumastressi ning isasloomade vähenenud aktiivsuse tõttu tuua kaasa jooksuaja hilinemise.

Põdrapopulatsiooni asustustihedus avaldas põdralehmade kehasuurusele ja viljakusele kõigest marginaalset negatiivset mõju (**I**). Populatsiooni asustus-

tiheduse tõus oli aga vastupidiselt meie eeldustele olulisel määral seotud emasloomade varasema viljastamisega (II). Töös käsitletava uurimisperioodi jooksul on Eestis samaaegselt põdraasurkonna arvukuse kasvuga oluliselt suurenenud metsanoorendike osakaal, mis on märkimisväärselt parandanud põtrade toitumistingimusi ja tõstnud põdra jaoks sobilike elupaikade kvaliteeti. Seega on töös leitud mõneti üllatav seos populatsiooni asustustiheduse ja põdralehmade viljastamisaja vahel tõenäoliselt tingitud keskkonna kandevõime suurenemisest asustustiheduse tõusu perioodil.

Eelnevate uuringute tulemused viitavad sellele, et selgelt eristuva aastaajalisusega kliimas on paljud isendite kohasusega seotud elukäigutunnused suurel määral mõjutatud viljastamise või sünni ajastamisest. Sellest tulenevalt analüüsisin viljastamisaja seoseid põdralehmade erinevate kohasusekomponentidega, nagu pesakonna suurus ja loodete sooline jaotus (III). Töös leiti selge seos viljastamisaja ja pesakonnatüübi vahel. Jooksuaja alguses viljastatud põdralehmade pesakonnad koosnesid oluliselt sagedamini mitmikloodetest kui hiljem viljastatute omad, ning samuti oli nendes pesakondades palju kõrgem isasloodete osakaal. Kui varem viljastatud isendid on ka paremas konditsioonis, on antud töö tulemused vastavuses Trivers-Willardi hüpoteesiga. Samas, kuna viljastamisaja ja soolise jaotumuse vaheline oluline seos oli tuvastatav ainult nooremate (1,5–3,5-aastaste) isendite puhul, on võimalik, et varane viljastamine jooksuajal on oluline eeskätt nooremate loomade kohasuse jaoks. Vanemad isendid saavad kasutada aga märksa paindlikumat sigimisstrateegiat, näiteks olles valivamad oma sigimispartnerite suhtes ning investeerides rohkem sünnijärgsesse vanemlikku hoolde.

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## ACKNOWLEDGEMENTS

First of all, I am exceptionally grateful to Vallo Tilgar for his hard work and patience in supervising my PhD studies during ten years long period.

My greatest respect and gratitude belongs also to Anne Kirk who was my supervisor during my BSc and MSc studies and to my good colleague Jüri Tõnisson with whom I have spent countless hours and days discussing about moose. Anne has been also the initiator of moose life history studies in Estonia and Jüri is the key person responsible for the extensive long-lasting moose monitoring program that also plays essential part in my studies.

My special thanks belong to Professor Raivo Mänd for his optimism and persistence in motivating me to go on with the studies when I had already lost hope.

Great thanks to Professor Jaak Jaagus for his consultations and help in obtaining climatic data and literature, and also to Robert Davis and John Davison for their help in improving the language of the manuscripts and the thesis.

I am grateful for my sons, wife and parents for their endless support and forbearance of the sulky me during all those years.

My sincere gratitude belongs to my colleagues Peep Männil, Inga Jõgisalu, Raido Kont and Marko Kübarsepp from the department of game monitoring for their continuing support and forbearance.

I thank also Margo Tannik, Merit Kreitsberg, Lauri Laanisto, Tanel Tärna, Sander Säde, Priit Kilgas, Tiit Randveer, Kaarel Roht, Harri Valdmann, Marko Kohv, Hendrik Haljas and Siiri Kolka for their help and support.

I am also thankful for all Estonian hunters who have participated in collection of the research materials during all these years.

Finally, I also want to thank all the persons who have helped me during my PhD studies, but whose contribution I have forgotten to mention.

## **PUBLICATIONS**



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