Genetic and environmental effects affecting the variation in birth date and birth weight of reindeer calves

Kirsi Muuttoranta[1], Øystein Holand[2], Knut H. Røed[3], Miika Tapio[1], Mauri Nieminen[4] & Asko Mäki-Tanila[1]

[1] Biotechnology and Food Research, MTT Agrifood Research Finland, FI-31600 Jokioinen, Finland (Corresponding author: kirsi.muuttoranta@mtt.fi).
[2] Department of Animal and Aquacultural Sciences, Norwegian University of Life Science, P.O.Box 5003, N-1432, Ås, Norway.
[3] Department of Basic Sciences and Aquatic Medicine, Norwegian School of Veterinary Science, P.O.Box 8146, N-0033 Oslo, Norway.
[4] Finnish Game and Fisheries Research Institute, Toivoniementie 246, FI-99910 Kaamanen, Finland.

Abstract: The factors causing variation in birth date and birth weight were analysed from the data from an experimental reindeer herd consisting of 1136 calves with parental information. The traits had coefficient of variation of 37 and 14%, respectively. The variation in both traits was affected by year and sex (male calves heavier) and by management factors, such as the age distribution of females and males. Early calving results from the use of older breeding males and is most apparent in prime age females. In both traits the heritability was moderate (0.23 and 0.24) with a high proportion of maternal genetic variation (0.23) in birth weight. The North Atlantic Oscillation (NAO) indices, summarizing the major weather conditions prior to rut, explained part of the annual variation in the traits. The amount of total genetic variation in relation to trait mean, or the evolvability, was 21% in birth date and 10% in birth weight indicating that selection could successfully be used to improve herd productivity and that the traits have substantial potential for adapting to possible changing environmental conditions. The results on genetic correlations imply that selection on calf's birth weight leads on one hand to calves being born earlier and on the other hand to dams with later parturition.

Key words: birth weight; birth date; genetic correlation; heritability; maternal effect; *Rangifer tarandus*; reindeer.

Introduction

Birth date and birth weight affect reindeer calf survival and growth and therefore productivity. Birth date (BD) is important in the subarctic region to match with the vegetation burst of short growing season (reviewed in Holand *et al.,* 2003). Heavy birth weight (BW) is linked to a good survival and growth (Eloranta & Nieminen, 1986).

There is much evidence from ungulates demonstrating that the variation in calf traits is influenced by maternal effects (Rönnegård, 2003; Bijma, 2006; Clements *et al.* 2011). Analysis on calf growth and survival should therefore contain direct effect (calf) and maternal effect (dam) (Willham, 1972). The maternal effect can be separated into genetic effect and permanent environmental effect (Willham, 1972). As

a practical example of the permanent non-genetic effect, a dam could have grown large in a favourable environment and is therefore able to provide good support for the growth of calves (permanently) in different parities.

The estimates of heritability (h^2) for BD and BW are lacking in reindeer. In red deer, a species closely related to reindeer, Clements *et al.* (2011) have reported h^2 = 0.09 in BD and Archer *et al.* (2013) h^2 = 0.20 for conception date, and Kruuk & Hadfield (2007) have found heritability of 0.14 for BW.

In reindeer the major determinant for BD is the conception date (Holand *et al.,* 2003). Indeed, dam weight prior to conception affects the calving date with the well-nourished and heavy dams calving early (Holand *et al.,* 2003; Mysterud *et al.,* 2009). Shortened day length and weather in autumn have been found to affect the conception time (review by Ropstad, 2000). The North Atlantic Oscillation (NAO) index (Hurrell, 1995) is commonly used in summarising the weather conditions (*e.g.* Weladji & Holand, 2003).

The gestation length in reindeer varies between 211 and 235 days (Ropstad, 2000; Mysterud *et al.,* 2009). The female calves are born earlier (Holand *et al.,* 2004) and male calves are carried longer (Mysterud *et al.,* 2009). Several studies provide evidence that the females adjust gestation length (*e.g.* Adams & Dale, 1998; Mysterud *et al.,* 2009). According to Mysterud *et al.* (2009), older and heavier females mate earlier and extend gestation length, whereas late conception may induce shortening (*e.g.* Holand *et al.,* 2006). The male calves are heavier at birth (Eloranta & Nieminen, 1986; Mysterud *et al.,* 2009). Ropstad's review (2000) shows that BW and calf survival are positively correlated with dam weight and condition. Low BW is connected to lowered survival and calf autumn weight (Eloranta & Nieminen, 1986).

In reindeer there are still only a few studies (Varo, 1972; Rönnegård, 2003) on the genetic variation of quantitative traits. At Kutuharju experimental reindeer field station in Finland data on individuals have been collected since the late 1960s (Eloranta & Nieminen, 1986), including the sire identification using DNA markers since 1997 (Røed *et al.,* 2002). By utilising the Kutuharju reindeer data we investigated the variation in calves' birth date and birth weight in detail, including the effect of environmental conditions, herd management factors, and direct and maternal genetic effect, as well as the permanent environmental effect of the dam. Further, we analysed the genetic correlations between the traits to understand how possible selection schemes would change the traits.

Material and methods
Data description
Study area
The data were collected at Kutuharju experimental reindeer research field station in Kaamanen, Finland (69°N, 27°E). The station, with a reindeer herd of about 100 individuals living in a fenced area of about 45 km², is owned and operated by the Reindeer Herders' Association. The Reindeer Research Station of The Finnish Game and Fisheries Research Institute maintains the data.

Study animals
The Kutuharju herd was founded in 1965 and the data collection started in 1969. Before 1970 there were 113 female and 51 male base animals; later 97 females and 79 males have been purchased from outside. Altogether 2980 calves have been born in 1969–2011, resulting in a total of 3320 individuals in the pedigree. During the winter the animals were supplemental fed in 1987-2011.

Available information
The variables in the analyses were BD, BW, dam weight prior to conception (DW), birth

year, sex and parity. The BD and BW were measured by daily observations and recordings of the herd during the calving season (Eloranta & Nieminen, 1986). BD was defined as the number of days since 1ˢᵗ of May. In years 1987, 1988, and 1990–1993 the marking harnesses were used to identify the sires of calves. From 1997 onwards the paternities have been confirmed at the Norwegian School of Veterinary Science using DNA markers giving sire information (Røed *et al.,* 2002). The April–September NAO indices (Climate Prediction Center Internet Team, 2013) prior to conception were used to detect the effect of weather on BD.

Exclusions
Calves without information on BD (N = 133) and paternity (N = 1700) were excluded. An additional 5 calves were removed as outliers for BD later than 1 July. Stillborn calves (N = 6) were not included in the analyses. The final analysed data contained 1136 calves. Of the dams, 1117 had information on DW.

Statistical analyses
Analysis of fixed effects
First, the significance of fixed classified effects was tested using a general linear model. Second, a regression analysis was used to find the monthly NAO indices explaining the variation in the traits.

The fixed effects (and their levels) were birth year, parity, sire age (2,…,6 y), sex (male or female) and calf at foot during rut (present =1 or absent = 0). Among parities 10–13 were combined due to the small number of records. The sire classes for age 1 and 2 years were merged, as were those for 6 and 7 years old.

In the regression analyses using the NAO indices, for the consistency the regression variables were also calf sex, sire age, dam parity (and its squared value) and presence of calf at foot at rut.

The statistical tests and preliminary analyses were performed with statistical softwares SAS EG®, version 4.2 (SAS Institute Inc., Cary, NC) and R, version 2.15.1 (R Development Core Team, 2012).

Models for variance component estimation
The univariate analyses contained:
1) The (direct) additive genetic effect of the animal (random) effect,
2) Both direct (calf) and maternal (dam) additive genetic effects, and
3) Direct and maternal additive genetic effects and maternal permanent effect (dam), so that the maternal impact on calf is made of three different effects: genetic, permanent (over parities) non-genetic and temporary non-genetic effect.

In matrix notation the models were:
1) $\mathbf{y = Xb + Z_a a + e,}$
2) $\mathbf{y = Xb + Z_a a + Z_m m + e,}$ and
3) $\mathbf{y = Xb + Z_a a + Z_m m + Z_c c + e,}$
where the vector **y** represented observations, **b** fixed effects, **a, m** and **c** were vectors for direct and maternal additive genetic effects and maternal permanent environmental effects, respectively, and **e** the random residual effect. $\mathbf{X, Z_a, Z_m}$ and $\mathbf{Z_c}$ were incidence matrices that relate the observations to **b, a, m** and **c**, respectively.

The residual effects were assumed to be independent, random variables identically distributed around mean 0 with variance σ^2_e. For the random effects $V(\mathbf{a}) = \sigma^2_a \mathbf{A}$, $V(\mathbf{m}) = \sigma^2_m \mathbf{A}$, $V(\mathbf{c}) = \sigma^2_c \mathbf{I}$, $V(\mathbf{e}) = \sigma^2_e \mathbf{I}$, where **A** is the additive relationship matrix of individuals and **I** is the identity matrix. The variance of direct additive genetic effect is denoted as σ^2_a, maternal genetic variance as σ^2_m, maternal permanent environmental variance as σ^2_c, and covariance between animal's own and maternal genetic effect as σ_{am}.

The birth year was used in the genetic analyses as it includes also management effects varying between years, together with the climatic effects. The random effects were tested using

likelihood ratio test (LRT) with and without the respective random effect; calculating twice the difference between the log-likelihood which is assumed to be distributed as X^2 with one degree of freedom, *i.e.* the difference in the number of unrestricted parameters fitted in the two models (Pinheiro & Bates, 2000).

Depending on the convergence, different types of multivariate analyses were carried out to detect the genetic (co)variation with the traits. The analyses were conducted using a Restricted Maximum Likelihood method (Patterson & Thompson, 1971). The actual estimation was carried out with statistical package ASReml version 3.0 (Gilmour *et al.,* 2009).

Results
Data
In the Kutuharju pedigree data there were altogether 3320 animals across more than 10 generations: 101 sires (21 sires of sires and 67 dams of sires) and 566 dams (44 sires of dams and 261 dams of dams). Of the dams, 39.5% had a record on BD and BW. Percentage of dams and sires with more than one offspring was 77 and 82%, respectively (Table 1).

The BD ranged from 2 May to 16 June (mean 18 May), the BW from 1.8 to 10.4 kg (mean 6.0 kg) and DW from 54 to 107 kg (mean 82 kg). The distributions of BD and BW followed approximately the normal distribution (results not shown). The coefficients of variation (CV) for the traits were 37% for BD and 14% for BW.

Fixed effects
The effects of birth year and parity were substantial in both traits (Table 2). In BD and BW, the effects of age of sire and calf sex were also significant. The lactation status of dam (*i.e.* the presence or absence of calf at autumn) seemed to have no effect on the studied traits.

When analysing the annual variation, only the NAOs prior to oestrus in the year before calving were considered (Table 3). The weather in late spring and early autumn may affect BD and DW (body condition), and hence the onset of oestrus cycling. The results for the other fixed effects were similar to those with classified factors (Table 2).

Analyses of the genetic effects
Single-trait analyses
Estimates of (co)variance components, heritabilities and correlations for the direct and maternal effects in BD and BW together with log likelihood values (logL) are summarised in Table 4. The model (1) with no maternal effects revealed moderate to high heritabilities. Fitting maternal genetic effects (model 2) increased logL values markedly (LRT test value was 3.02, *P* = 0.08 for BD and 45.80, *P*<0.001 for BW). The further addition of maternal permanent environmental effect (model 3) resulted in a non-significant improvement (LRT test value was 0.5, *P* = 0.48, for BD and 0.43, *P* = 0.84, for BW). Consequently, the best model for both traits was model 2 that included the direct genetic effect of animal and the maternal genetic effect. In BD the maternal heritability was small with high standard error, suggesting that genetically dam has little influence on the variation. In both traits the direct-maternal genetic correlations were smaller than their standard errors.

Bivariate analysis
The (co)variances from the bivariate analyses are shown in Table 4 and the respective correlations in Table 5. The estimates were similar to those from the univariate analyses, with a slight increase for σ^2_m of BD and σ^2_d of BW, and considerable change of σ_{am}. Among the genetic correlations only the ones related to direct effects of BW were larger than twice their standard error. Also phenotypic correlation between BD and BW was smaller compared to its standard error.

Table 1. The distribution of dams and sires over progeny in the Kutuharju pedigree data in the years 1987–2011.

Calves	1	2	3	4	5	6	7	8	9	10-14	15-19	20-24	25-34	35-44	45-54	71
Dams	62	35	43	34	16	18	26	23	9	7						
Sires	18	6	9	6	3	7	4	1	2	14	12	8	3	2	2	1

Table 2. The fixed effects for birth date (BD), birth weight (BW) and dam weight (DW) in the Kutuharju reindeer herd in 1987–2011. The level values of each factor are expressed as deviations from the last level.

Parameter	BD		BW		DW	
	Estimate	P-value	Estimate	P-value	Estimate	P-value
Intercept	10.09	<.0001	5.78	<.0001	84.82	<.0001
Birth year		<.0001		<.0001		<.0001
Parity		0.33		<.0001		<.0001
1	2.61		-0.91		-8.24	
2	1.59		-0.46		-4.24	
3	0.90		-0.10		2.63	
4	0.81		-0.15		-1.99	
5	0.62		0.08		-1.58	
6	0.67		0.12		-0.70	
7	0.86		0.23		-0.54	
8	0.31		0.10		-0.39	
9	-0.18		-0.08		-0.43	
10–13	0.00		0.00		0.00	
Sire age		<.0001		0.81		
1–2	4.52		0.05			
3	4.25		-0.03			
4	2.18		0.06			
5	1.69		0.01			
6–7	0.00		0.00			
Sex		0.45		<.0001		
male	0.29		0.05			
female	0.00		0.00			
Calf at foot		0.64		0.47		0.97
absent	-0.28		0.07		0.02	
present	0.00		0.00		0.00	

Table 3. Regression analysis on calf birth date (BD), birth weight (BW) and dam weight (DW) of the NAO indices at the Kutuharju reindeer herd in 1987–2011.

| Factor | Regression coefficients | | |
	BD	BW	DW
Intercept	24.40***	5.43***	75.08***
Parity	-0.36	0.38***	2.18***
(Parity)^2	0.01	-0.03***	-0.14***
Sire age	-0.99***	0,00	0.00
Sex	-0.31	-0.31***	0.00
Calf at foot	0.11	0.02	0.91
NAO, April	-2.98***	0.15***	1.31***
May	1.36***	0,00	0.17
June	0.04	-0.07**	-0.03
July	2.11***	0.05	-1.89***
August	1.24***	-0.15***	-0.31
September	-1.01***	0.03	0.61**

The significances of coefficients are * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. P is the probability for a type I error.

The (co)variance structure of the DW at the autumn prior to calving together with BW and BD was analysed with two separate bivariate analyses. When BD was analysed together with DW, its direct genetic variance slightly increased (from 10.22 to 11.95) and the direct-maternal covariance changed from negative to positive value (from -0.38 to 0.18) compared to analysis of BD together with BW. In BW there were no changes. In DW the heritability was (σ^2_a / σ^2_p = 28.61 / 41.44 =) 0.69 (±0.044). The correlations between DW and BD (including maternal effects) ranged from -0.07 to 0.06 with high standard errors (from 0.04 to 0.17). The only significant correlation between DW and BW was the phenotypic correlation, 0.16 (±0.046).

Discussion
The Kutuharju experimental herd provides unique data on reindeer calves' birth date and weight, life history of females and indispensable information on calves' sire (allowing the separation of maternal genetic effect). There is a moderate direct heritability in birth date and birth weight. The maternal heritability in birth weight is moderate and in birth date small. The evolvability (Houle, 1992), or coefficient of total additive genetic variation, including also maternal genetic variation ($\sqrt{(\sigma^2_a + 2\sigma_{am} + \sigma^2_m)}$) / mean) (Bijma, 2006), quantifies the potential for selection. It is 0.21 for birth date and 0.10 for birth weight, which are comparable to the expected responses in the economically relevant traits of farm animal species expressed in as a percentage of the mean (Smith, 1984).

Table 4. Estimates of (co)variance components and genetic parameters (standard error in parentheses) for birth date and birth weight in the Kutuharju reindeer herd in 1987–2011. Models 1–3 have following random effects: 1 = animal, 2 = animal + maternal genetic, and 3 = animal + maternal genetic + maternal permanent environmental effect. The best model is indicated in bold and used in bivariate context giving the (co)variance components of an analysis of BD and BW together.

	Model 1	**Model 2**	Model 3	Bivariate
Birth date				
σ^2_a	16.96	**11.98**	12.01	10.22
σ^2_m	-	**2.57**	0.48	3.84
σ_{am}	-	**0.04**	0.85	-0.38
σ^2_c	-	-	1.45	-
σ^2_e	28.45	**30.15**	29.01	30.77
σ^2_p	45.41	**44.70**	43.83	44.45
h^2_d	0.37 (0.07)	**0.27 (0.09)**	0.27 (0.09)	0.23 (0.09)
h^2_m	-	**0.06 (0.05)**	0.01 (0.07)	0.09 (0.06)
c^2	-	-	0.03 (0.04)	-
r_{am}	-	**0.01 (0.54)**	0.36 (2.02)	-
LogL	-2668.06	**-2666.55**	-2666.30	-
Birth weight				
σ^2_a	0.47	**0.16**	0.17	0.19
σ^2_m	-	**0.17**	0.14	0.17
σ_{am}	-	**0.017**	0.029	0.022
σ^2_c	-	-	0.026	-
σ^2_e	0.28	**0.37**	0.36	0.35
σ^2_p	0.75	**0.70**	0.70	0.74
h^2_d	0.63 (0.06)	**0.23 (0.08)**	0.24 (0.08)	0.26 (0.09)
h^2_m	-	**0.24 (0.06)**	0.20 (0.09)	0.23 (0.07)
c^2	-	-	0.04 (0.06)	-
r_{am}	-	**0.17 (0.34)**	0.19 (0.37)	-
LogL	-338.97	**-315.61**	-315.46	

σ^2_a = direct additive genetic variance, σ^2_m = maternal additive genetic variance, σ_{am} = direct-maternal additive genetic covariance, σ^2_c = the variance of maternal permanent effect, σ^2_e = residual variance, σ^2_p = phenotypic variance, h^2_d = direct heritability, h^2_m = maternal heritability, c^2 = the variance due to maternal permanent environmental effects as proportion of total variance, r_{am} = direct-maternal genetic correlation, LogL = the log likelihood value.

Data and methods

Including all data, also the calves lacking paternal information, led to upward biased estimates (results not shown). The exclusion of the maternal genetic effect in the analyses on the data with known sires gave direct heritability of 0.63 for birth weight, which is much higher than the estimate 0.23 from the analysis including maternal effect. This is resonated well with what Willham (1972) predicted it to be in such a case, *i.e.* $0.5h^2_d + 1.5 r_{am} + 0.5h^2_m = 0.61$. Data with multiple offspring across generations and sire information allow an efficient separation of direct and maternal genetic ef-

Table 5. Estimates of direct (dir) and maternal (mat) genetic correlations (standard errors in parentheses) of the bivariate analysis in birth date (BD) and birth weight (BW) of reindeer calves in the Kutuharju reindeer herd in 1987–2011.

	BD, mat	BW, dir	BW, mat
BD, dir	-0.06 (0.44)	**-0.46 (0.24)**	0.06 (0.31)
BD, mat		**0.76 (0.41)**	-0.19 (0.27)
BW, dir			0.12 (0.32)

The significant correlation estimates are in bold.

fects in the univariate analyses (*e.g.* Kruuk & Hadfield, 2007). Elaborated models, especially across traits, resulted in poor convergence of estimated variance parameters in REML analyses.

The variation in the gestation length could not be included in the analyses, because the oestrus or copulation dates were not available. Clements *et al.* (2011) reported in red deer a very high correlation (0.97) between the observed oestrus days and parturition date, dismissing the variation in gestation length. However, there is naturally high variation in birth date because oestrus in autumn is following a three week cycling (review by Ropstad, 2000). We did not see signs of multimodality in the birth date distribution.

Fixed effects
Sex. Despite the reported longer gestation for the male calves (Mysterud *et al.*, 2009), there was no evidence of calf sex effect on birth date. The results on birth weight agree with the common finding about male calves being heavier at birth (*e.g.* Eloranta & Nieminen, 1986).

Sire age is a very important trait from the management point of view with older males siring the earlier-born calves (Holand *et al.*, 2003). This is possibly accentuated by the prime-age females choosing to mate with heavier and older males (Holand *et al.*, 2006). The possible differences caused by management trials in Kutuharju (cf. Holand *et al.,* 2003) are taken into account using sire age and birth year as fixed effects.

Annual variation in birth date and weight was explained partly by the NAO indices of months between April and September of the previous year. The dam's condition depends on weather conditions such as temperature, precipitation and insolation, as they affect plant phenology and thereby availability of feed (review by Weladji & Holand, 2003). The NAO indices have earlier been considered in studies on reindeer herd productivity (*e.g.* Weladji & Holand, 2003). The season from spring to autumn prior to rut has greater effect on the timing of parturition of caribou than conditions at late gestation (Adams & Dale, 1998). There are comparable findings in reindeer (Holand *et al.,* 2004). The results suggest that there could be a way to predict the on-set of rutting from the weather statistics and consequently the optimum time for the herders to gather reindeer.

Parity affects both birth date and weight with the prime aged (4–10 years) dams having earliest calvings and the heaviest calves in accordance with Weladji *et al.* (2010).

Raising a calf during the summer before the rut had no influence on dam's weight in autumn or on calf traits in this study. This is in line with the findings of Holand *et al.* (2003) and Weladji *et al.* (2010) from the Kutuharju herd, but in contrast to a study by Bårdsen *et al.* (2010) with the difference being probably

explained by the supplementary feeding at Kutuharju herd.

Genetic variation

The considerable amount of evolvability (the coefficient of additive genetic variation) suggests that the trait will respond to both artificial and natural selection (cf. Smith, 1984). The genetic variation for birth date and birth weight is higher than in red deer (Kruuk & Hadfield, 2007; Clements *et al.,* 2011). Archer *et al.* (2013), however, found heritability 0.20 for the related conception date in the same species. The moderate $h^2{}_m$ in birth weight suggests considering dam quality when designing a selection scheme for the trait.

We found a negative phenotypic correlation between birth date and birth weight, as was found earlier by Weladji *et al.* (2010). The results on genetic correlations imply that selection on calf's birth weight leads on one hand to calves being born earlier and on the other hand to dams with later parturition. In traditional reindeer husbandry neither birth date nor birth weight is recorded, therefore the traits cannot directly be included in the selection criteria used by the herders. Before any recommendation are given on birth weight recording, it is important to understand how the current selection of breeding individuals based on autumn weight would be related to birth weight and date. There are empirical views (Muuttoranta & Mäki-Tanila, 2012) and results on the advantages of early birth and medium to high birth weight (Eloranta & Nieminen, 1986; Holand *et al.,* 2003).

With the available genetic variation, calf birth weight and timing of birth may be altered by natural selection as a response to changes in environmental conditions. Holand *et al.* (2004) is suggesting that there is stabilising selection in birth date, indicated by 90% of calves being born within two weeks.

Conclusions

Variation in birth date and birth weight of reindeer calves exists due to management, environment and genetic make up. The findings could be used to improve productivity by selection based both on calf and dam traits and by herd management (*e.g.* optimum age distribution of males and females), including even the timing of the herding operations by the deviations from the average weather pattern. The genetic variation enables reindeer to respond to natural selection caused by possible changes in environmental conditions.

Acknowledgements

References

Adams, L.G. & Dale, B.W. 1998. Timing and synchrony of parturition in Alaskan caribou. — *Journal of Mammalogy* 79:287-294.

Archer, J.A., Asher, G.W., Fisher, P.J., Ward, J.F., Scott, I.C., Bixley., M.J., Hickey., S.M. & Morris, C.A. 2013. Genetics of early concpetion and its relationship to growth traits in red deer (*Cervus elaphus*). — *Animal Production Science* 53: 1083-1087.

Bårdsen, B., Tveraa, T., Fauchald, P. &

Langeland, K. 2010. Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. — *Oecologia* 162: 627-639.

Bijma, P. 2006. Estimating maternal genetic effects in livestock. — *Journal of Animal Science* 84: 800-806.

Clements, M.N., Clutton-Brock, T.H., Guinness, F.E., Pemberton, J.M. & Kruuk, L.E.B. 2011. Variances and covariances of phenological traits in a wild mammal population. — *Evolution* 65: 788-801.

Climate Prediction Center Internet Team. 2013. North Atlantic Oscillation (NAO). http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml (Accessed 17 March 2013).

Eloranta, E. & Nieminen, M. 1986. Calving of the experimental reindeer herd in Kaamanen during 1970-1985. — *Rangifer* Special Issue 1: 115-121.

Gilmour, A.R., Gogel, B.J., Cullis, B.R. & Thompson, R. 2009. *ASReml User Guide* Release 3.0. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK. www.vsni.co.uk.

Holand, Ø., Røed, K.H., Mysterud, A., Kumpula, J., Nieminen, M. & Smith, M.E. 2003. The effect of sex ratio and male age structure on reindeer calving. — *The Journal of Wildlife Management* 67: 25-33.

Holand, Ø., Weladji, R.B., Gjøstein, H., Kumpula, J., Smith, M.E., Nieminen, M. & Røed, K.H. 2004. Reproductive effort in relation to maternal social rank in reindeer (*Rangifer tarandus*). — *Behavioral Ecology and Sociobiology* 57: 69-76.

Holand, Ø., Weladji, R.B., Røed, K.H., Gjøstein, H., Kumpula, J., Gaillard, J., Smith, M.E. & Nieminen, M. 2006. Male age structure influences females' mass change during rut in a polygynous ungulate: The reindeer (*Rangifer tarandus*). — *Behavioral Ecology and Sociobiology* 59: 682-688.

Hoyle, D. 1992. Comparing evolvability and variability of quantitative traits. — *Genetics* 130:195-204.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. — *Science* 269: 676-678.

Kruuk, L.E.B. & Hadfield, J.D. 2007. How to separate genetic and environmental causes of similarity between relatives. — *Journal of Evolutionary Biology*, 20: 1890-1903.

Muuttoranta, K. & Mäki-Tanila, A. 2012. Regional differences in reindeer herding operations in Finland. — *Acta Agriculturæ Scandinavica, Section A – Animal Science* 62: 142-152.

Mysterud, A., Røed, K.H., Holand, Ø., Yoccoz, N.G. & Nieminen, M. 2009. Age-related gestation length adjustment in a large iteroparous mammal at northern latitude. — *The Journal of Animal Ecology* 78: 1002-1006.

Patterson, H.D. & Thompson, R. 1971. Recovery of inter-block information when block sizes are unequal. — *Biometrika* 58: 545-554.

Pinheiro, J.C. & Bates, D.M. 2000. *Mixed effects models in S and S-PLUS*. Springer Verlag. 530pp.

R Development Core Team. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org.

Ropstad, E. 2000. Reproduction in female reindeer. — *Animal Reproduction Science* 60: 561-570.

Røed, K.H., Holand, Ø., Smith, M.E., Gjøstein, H., Kumpula, J. & Nieminen, M. 2002. Reproductive success in reindeer males in a herd with varying sex ratio. — *Molecular Ecology* 11: 1239-1243.

Rönnegård, L. 2003. *Selection, maternal effects and inbreeding in reindeer husbandry.* Doctoral thesis, SLU, Uppsala. Acta Universita-

tis Agriculturae Sueciae, Agraria 370.

Smith, C. 1984. Rates of genetic change in livestock. — *Research and Development in Agriculture* 1:79-85.

Varo, M. 1972. Investigations on the possibilities of reindeer breeding II. — *Journal of the Scientific Agricultural Society of Finland* 44: 234-248.

Weladji, R.B. & Holand, Ø. 2003. Global climate change and reindeer: Effects of winter weather on the autumn weight and growth of calves. — *Oecologia* 136: 317-323.

Weladji, R.B., Holand, Ø., Gaillard J.M., Yoccoz, N.G., Mysterud, A., Nieminen, M. & Stenseth, N.C. 2010. Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? — *Oecologia* 162: 261-271.

Willham, R.L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. — *Journal of Animal Science* 35: 1288-1293.

Poronvasojen syntymäpainon ja -ajankohdan vaihteluun vaikuttavat perinnölliset ja ympäristötekijät

Summary in Finnish/Tiivistelmä: Vasomisajankohta ja vasan syntymäpaino vaikuttavat porokarjan tuottavuuteen. Tässä tutkimuksessa selvitettiin tekijöitä, jotka aiheuttavat vaihtelua vasomisajankohtaan sekä syntymäpainoon. Aineisto koostuu Paliskuntain yhdistyksen Kutuharjun koeporotarhalla syntyneistä vasoista (N=1136), joiden syntymäpaino ja–ajankohta sekä molemmat vanhemmat tunnetaan. Ominaisuuksiin vaikuttivat syntymävuosi sekä emän vasomiskerta, lisäksi vasomisajankohtaan vaikutti isän ikä, ja syntymäpainoon vasan sukupuoli. Vuoden vaikutus tarkentui edelleen käytettäessä kiimaa edeltävän kesän ja syksyn säätilaa kuvaavaa NAO-indeksiä (North Atlantic Oscillation).

Vasomisajankohdassa eläimen oman vaikutuksen heritabiliteetti oli 0.23 ja emävaikutuksen 0.09. Syntymäpainossa vastaavat luvut olivat 0.25 ja 0.24. Tulosten mukaan niin syntymäajankohdan kuin syntymäpainon suhteen valinnalla voidaan saada aikaan geneettistä edistymistä. Käytännössä suora valinta on hankalaa, koska ominaisuuksia ei mitata. Perinnöllisen vaihtelun olemassaolo helpottaa porokarjan sopeutumista muuttuvaan ympäristöön.