

Genetic variation in meat production related traits in reindeer (*Rangifer t. tarandus*)

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Abstract: In reindeer husbandry, animal breeding could offer tools for improving productivity by selection. The traits affecting meat production efficiency are primarily related to calf growth and survival, and to dam's longevity and lifetime ability to raise heavy calves. Information on genetic (co)variation in these traits is scarce but needed in estimating the potential and effectiveness of selection as well as biological constraints. The objectives of the study were to estimate these genetic parameters from the data of an experimental reindeer herd at Kutuharju (Inari, Finland).

Heritabilities (h^2) and genetic correlations (r_g) among the average daily gain of calves (ADG), dams' age at maturity, individual fitness (λ_{ind}) and the cumulative sum of her calves' weaning weight over seven years (WW7) were studied with AS-Reml software using the dataset from the experimental herd. The pedigree included also sire information to allow the separation of the maternal effects.

Direct and maternal heritabilities of ADG were moderate (0.24 ± 0.09 and 0.18 ± 0.05 , respectively) and the direct-maternal correlation was highly negative (-0.73 ± 0.17). Indeed, selection on growth necessitates information on both calf and dam. The genetic correlation of growth with birth date and birth weight could not be detected with the data. The age at maturity and λ_{ind} had a small heritable component (0.07 ± 0.12 and 0.10 ± 0.06 , respectively), whereas the heritability value of WW7 was 0.23 ± 0.07 . Reindeer herders' empirical selection on calf's autumn weight favours fast growth (r_g between growth and autumn weight = 0.35 ± 0.24). Dam's weight in her first autumn was strongly correlated with her lifetime production expressed by her individual fitness ($r_g = 0.71 \pm 0.23$) and the cumulative sum of her calves' weaning weight ($r_g = 0.63 \pm 0.12$). Hence, the early information on the dam (her weight in her first autumn or her first calf's autumn weight) works as useful selection criteria for the traits related to lifetime production.

Key words: growth; lifetime production; individual fitness; heritability; maternal effect; genetic correlation; *Rangifer tarandus tarandus*.

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Introduction

In Fennoscandia, the profitability in reindeer husbandry is based on meat production. The majority of meat is produced from calves born in spring and culled in autumn, and the num-

ber and size of autumn calves determine herd productivity. From a herder's perspective the best females should mature early, have high reproductive rate and long productive life (Muuttoranta & Mäki-Tanila, 2011). In addition,

they should take good care of their calves facilitating rapid growth and high survival. This will lead to the effective use of the limited northern natural pasture areas for meat production.

Good calf growth over the summer implies heavy calf autumn weight. In practice herders use this autumn live weight as the main selection criterion (Muuttoranta & Mäki-Tanila, 2011), as fast-growing animals are thought to result in a rise in the number and quality of calves slaughtered (Muuttoranta & Mäki-Tanila, 2011). In reindeer, the heritability estimates (h^2) for growth are scarce: Varo (1972) reported an estimate of 0.6 based on very few animals, whereas Appel & Danell (unpubl., in Rönnegård & Danell, 2003) used a larger population and reported an estimate of 0.4. Later, Rönnegård & Danell (2003) estimated realized $h^2 = 0.2$ in the same population. All these estimates were based on dam-daughter pairs as none of the studies had information on sires. In reindeer, no maternal heritabilities in calf growth have been estimated and the effect of dam's permanent environment has not been studied.

Reindeer herders consider good dams vital and dam quality is among the major selection criteria (Muuttoranta & Mäki-Tanila, 2011; 2012). Quality of dam affects productivity via her reproduction rate, maternal care and survival (Tanida *et al.*, 1988; Brommer *et al.*, 2002; Martinez *et al.*, 2004a; 2004b). Herders expect the dams to have a calf at foot in every autumn round-up (Muuttoranta & Mäki-Tanila, 2011). The good dams should have a long productive life which facilitates less need of recruitment animals, and hence a higher annual proportion for culling or meat production (Tanida *et al.*, 1988; Martinez *et al.*, 2004a).

Most of the females start calving at the age of two to four years (Rönnegård *et al.*, 2002). Early maturation is related to a heavy body weight (see Reimers, 1983; Gaillard *et al.*, 2000; Rönnegård *et al.*, 2002, Weladji *et al.*, 2008) and it

is positively correlated with lifetime production (Weladji *et al.*, 2006; 2008). In addition, calving regularly and gaining experience in raising offspring improves the production performance of the reindeer female over the years (Weladji *et al.*, 2006; 2008).

The fitness related traits are commonly analysed in evolutionary ecology and in some species there are heritability estimates for lifetime reproduction success (*e.g.* Merilä & Sheldon, 2000) and for individual fitness (*e.g.* Blomquist, 2010). In livestock species lifetime production is gaining importance among breeders since it is related to profitability and animal welfare (Flint & Woolliams, 2008). In beef cattle the lifetime production is measured for example by the cumulative weaning weight of calves of beef dams at the age of 7 years. Heritabilities are reported to range from 0.06 to 0.18 (Martinez *et al.*, 2004a; 2004b). Lifetime number of offspring weaned has been reported to have h^2 varying from 0.05 to 0.21 (in beef: Tanida *et al.*, 1988; Martinez *et al.*, 2004a; 2004b; in sheep: Safari *et al.*, 2005). Dam quality, measured as number and weight of weaned offspring, can be assessed towards the end of her productive life only. The animals for breeding purposes are mostly selected as calves, therefore early-life indicators of future production ability are needed.

Growth is affected by genetic and environmental effects. The genetic effects can be separated to those due to the animal itself (direct) and those due to its dam (maternal). In addition to these genetic elements, both effects also include an environmental element (Willham, 1963). The correlation between direct and maternal genetic effects is often strongly negative in maternal traits, such as growth (*e.g.* Bijma, 2006), which, if biologically true, leads to a decline in maternal capacity if only direct growth is selected. Negative estimates have been questioned, as they may have arisen from the data structure (Meyer, 1992; Heydarpour *et al.*, 2008), the fixed effects (Meyer, 1997; Bijma,

2006) or an ignored correlation between residual, direct and maternal effects (Koerhuis & Thompson, 1997; Bijma, 2006; Eaglen & Bijma, 2009).

For contemplating the prospects of selective breeding of meat production in reindeer, it is important to estimate the genetic variation and correlation in the relevant traits. Such analysis requires appropriate phenotypic records. Due to the semi-domesticated nature of reindeer husbandry, individual records are rare. The exceptionally detailed long term data including information on sires (Røed *et al.*, 2002) from the Kutuharju experimental herd in northern Finland offers a unique possibility to perform genetic research in reindeer.

The objectives of the study were to estimate the genetic variation in the traits affecting meat production: calf growth (with related birth date, birth weight and weaning weight), females' age at maturity, and lifetime production of the dams without separating the effects of natural selection and herders' culling; and also quantify the influence of maternal effects on the variation and genetic and phenotypic correlations.

Material and methods

Data description and subsets

The Finnish Game and Fisheries Research Institute's Reindeer Research Station maintains data from the Kutuharju experimental herd, located in Inari, Finland (69°N, 27°E), and owned and managed by the Finnish Reindeer Herders' Association. Paternities have been confirmed at the Norwegian School of Veterinary Science using DNA markers giving sire information for the calves born since 1997 (Røed *et al.*, 2002). In addition, paternities were monitored using marking harnesses for calves born in 1987, 1988, and 1990-1993. The pedigree dataset contained 3320 animals, of which 101 were sires and 566 dams of the calves. The dataset has been described in Muuttoranta *et al.* (2013)

Calf data

The calves were weighed at birth in May (few born in June) and before selection in September. The weights are in kilograms and birth date is presented as days counting from 1st of May. Average daily gain (ADG, in grams), was calculated by subtracting birth weight from calf autumn weight and dividing the difference by calf age at autumn weighing. Calves lacking either birth or autumn weight record were excluded from the analyses for daily gain. The calf birth date is used to approximate the conception date (and gestation length). The other traits were calf birth date (BD), birth weight (BW) and calf autumn weight (AW1). The calf data consisted of 984 calves with known sires.

Dam data

The productive life of a dam starts at maturation, which is measured in practice as the age at first calving. Stillbirth or a calf that died during summer was counted as a calving. Females >3 y with no calving record were assumed to be late maturing and be included in the highest age class (7 years) for the age at maturation. Because data do not contain any culling reasons, there was no attempt to separate herders' voluntary culling from the involuntary mortality.

A Leslie matrix (Leslie, 1945) is a square matrix of order equalling the number of age classes. The (i,j)th cell in the matrix indicates how many individuals will be in the age class *i* at the next time step for each individual in stage *j* (Leslie, 1945). This transition matrix is constructed for each individual and the individual fitness (symbolised λ_{ind} and used as a trait in the study) is the dominant eigenvalue of the matrix (McGraw & Caswell 1996, used in reindeer by Weladji *et al.* 2006). The values were estimated with statistical software R, version 3.0.1 (R Development Core Team, 2013).

The lifetime production of a dam was measured also by the cumulative sum of her calves' weaning weight over seven years (WW7) (cf.

Martinez *et al.*, 2004b). Stillborn calves and calves that died before weaning were excluded. The trait reflects pre-weaning maternal care and is therefore in practice more important than the mere number of calves born. The weights of the calves were corrected by the birth year and calf sex. The calves with missing autumn weights were imputed by the autumn mean given the birth year and sex of the calf, instead more complicated methods (right-censored data or maximum likelihood) that could have been used. For the non-producing females the value of WW7 was 0 (similar to Kruuk *et al.* (2000), who estimated the number of offspring).

The dataset used for estimation of lifetime production contained 1165 females, born in 1964-2000. Only the complete age cohorts were used, as suggested by Tanida *et al.* (1988), hence the age cohorts with any living animals were excluded. This included the cohorts born after 2001. In the lifetime trait analysis, there were 555 female calves culled in their first autumn and 600 females aged one year or older. Age at maturity was estimated from the dataset spanning up to the year 2007 with 1404 animals. To study the correlations among lifetime production traits and traits related to growth, we also analysed the autumn weight of the first calf of the dam (CAW, as dam trait), dam's weight in her first autumn (DAW) and dam's ADG when she was a calf (D_ADG).

In summary, the analysis covered the following traits: birth date, birth weight, calf's average daily gain and calf's autumn weight; dam's age at maturity, individual fitness and the cumulative sum of dam's calves' weaning weight over seven years and the autumn weight of the first calf of the dam.

Methods

Fixed effects

For analysing the genetic variation in ADG we tested the model for the following fixed effects (classes in parentheses): sex of calves (male and

female); year of birth (21 classes across the years 1987-2011); parity of dam (parities 1,2,...9, with the last class including also parities 10-14); sire age (ages 1-2, 3, 4, 5, and 6-7); and calf at foot (a variable describing the reproductive status of dam, 0 or 1 for absence or presence of calf during the summer prior to calving).

For the lifetime production traits (age at maturity, λ_{ind} and WW7) the fixed effect was birth year (36 year classes, across the years from 1964 to 2000). For the autumn weight of the dam's first calf, the effects of calf sex and birth year were tested.

Models for variance component estimation

Because of the complete pedigree information, at least for the information since 1987, the genetic variation in the population was studied analysing the differences among individual animals using so called animal model. Three different animal models were used to estimate the genetic parameters in the ADG:

- 1) the only random effect was additive (direct) genetic effect of the animal,
- 2) direct (calf) and maternal (dam) additive genetic effects, and
- 3) direct and maternal additive genetic effects and maternal permanent environmental effect (dam). The different models were used to find out the best model for random effects.

In the matrix notation the models were

- 1) $\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{e}$,
- 2) $\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{e}$, and
- 3) $\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_m\mathbf{m} + \mathbf{Z}_c\mathbf{c} + \mathbf{e}$,

where \mathbf{y} was a vector for observations; \mathbf{b} was a vector for fixed effects; \mathbf{a} , \mathbf{m} and \mathbf{c} were vectors for direct and maternal additive genetic effects and maternal permanent environmental effects, respectively; and \mathbf{e} was random residual effect. \mathbf{X} , \mathbf{Z}_a , \mathbf{Z}_m and \mathbf{Z}_c were incidence matrices that relate the observations to \mathbf{b} , \mathbf{a} , \mathbf{m} and \mathbf{c} , respectively.

For the random effects the assumptions were as follows:

$$V(\mathbf{a}) = \sigma_a^2 \mathbf{A}, V(\mathbf{m}) = \sigma_m^2 \mathbf{A}, V(\mathbf{c}) = \sigma_c^2 \mathbf{I} \text{ and } V(\mathbf{e}) = \sigma_e^2 \mathbf{I},$$

where \mathbf{A} was the additive relationship matrix between individuals and \mathbf{I} the identity matrix. The variance of direct additive genetic effect was denoted as σ_a^2 , maternal genetic variance as σ_m^2 , maternal permanent environmental variance as σ_c^2 , and covariance between animal's own and maternal genetic effect as σ_{am} .

In the lifetime production analyses, an animal model (for the dams) was used to estimate the variance components in the age at maturity, λ_{ind} and WW7. The model and the related assumptions were similar to the model 1 for ADG. In addition to the genetic maternal effect, there may be non-genetic effects in the dam causing advantage or disadvantage on calf's performance. There may be a correlation between the maternal permanent environmental effect and the residual effect in calf's performance. Falconer (1965) proposed using a regression of calf's record on dam's record in the trait for estimating such a correlation. In the multi-generation data the estimation is problematic and Koerhuis & Thompson (1997) suggested including the respective covariance in the Willham's (1963) model. With a small amount of data such addition would not usually lead to satisfactory convergence. The existence of correlation between the residuals of the direct and maternal effects could simply be detected by comparing the variance components of the animal model with direct and maternal effects to the sire-maternal grandsire model (S-MGS), because the latter has no respective residual covariances (Eaglen & Bijma, 2009). The sire-maternal grandsire model was $\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_s \mathbf{u}_s + \mathbf{Z}_{mgs} \mathbf{u}_{mgs} + \mathbf{e}$, where \mathbf{Z}_s and \mathbf{Z}_{mgs} were the incidence matrices that relate the observations to \mathbf{u}_s and \mathbf{u}_{mgs} (additive genetic effects of sires and grandsires), respectively. Other terms are similar to those in the animal models. The direct and maternal variance components of the respective animal model were calculated ac-

ording to Steinbock et al. (2003) and Eaglen & Bijma (2009): $\sigma_a^2 = 4\sigma_s^2$, $\sigma_{am} = 4\sigma_{s,mgs} - 2\sigma_s^2$, and $\sigma_m^2 = 4\sigma_{mgs}^2 + \sigma_s^2 + 4\sigma_{s,mgs}$. The subscripts s and mgs represents the sire and maternal grandsire effects.

Fitting of the animal models were tested using the likelihood ratio test with a threshold value of 0.05 (Pinheiro & Bates, 2000). The bivariate analyses were conducted using the best model for ADG together with BD, BW and AW1. Age at maturity, λ_{ind} and WW7 were all analysed in a bivariate context together with CAW, DAW and D_ADG. For presenting graphically the relationship between the lifetime traits and indicator traits, the predicted breeding values were computed.

The preliminary analyses were done using SAS EG[®], version 4.2 (SAS Institute Inc., Cary, NC) and R, version 3.0.1 (R Development Core Team, 2013). The (co)variance components were computed by Restricted Maximum Likelihood (REML) method (Patterson & Thompson, 1971). The significances of all genetic parameters with log likelihood tests were carried out with a statistical software package ASReml, release 3.0 (Gilmour *et al.*, 2009).

Results

Data

The data structure related to the calf traits has earlier been described in Muuttoranta et al. (2013). The summary statistics of the studied traits are given in Table 1. The first calf was lighter than those born in the later parities (CAW1 < AW1). The female calves which were selected for breeding were also lighter (DAW1 < AW1) due to the sex difference in the trait. The variation was moderate (CV about 0.15-0.25) in the growth and weight traits, higher (0.43-0.51) in birth date and age at maturation and very high (1.27-1.59) in the lifetime production traits.

Fixed effects

The birth year was the major factor causing

Table 1. The summary statistics of the studied traits in the Kutuharju reindeer herd in 1987-2011 (calf traits) or 1964-2000 (dam traits).

trait	N	mean	min	max	SD	CV
<i>Calf traits:</i>						
BD (days)	984	18 May	2 May	16 June	7.80	0.43
BW (kg)	984	6.06	3.4	10.4	0.89	0.15
AW1 (kg)	984	45.29	24	68	6.76	0.15
ADG (g/d)	984	315.70	156	493	54.04	0.17
<i>Dam traits:</i>						
age (y) at maturation	575	3.08	1	7	1.58	0.51
λ_{ind}	1165	0.46	0	1.62	0.58	1.27
WW7 (kg)	1165	49.36	0	301	78.58	1.59
DAW (kg)	694	41.94	25	70	6.25	0.15
D_ADG (g)	693	236.78	98.51	409.4	59.99	0.25
CAW (kg)	259	40.87	25	62	6.97	0.17

BW = birth weight, AW1 = calf autumn weight, BD = birth date, ADG = average daily gain, λ_{ind} = individual fitness, WW7 = cumulative weaning weight of calves over seven years, DAW = dam's weight in her first autumn, D_ADG = average calf daily gain of a female, CAW = the autumn weight of dam's first calf. N = number of records, SD = standard deviation, and CV = coefficient of variation.

variation in all the calf traits. All the studied fixed effects were significant in the calf traits except the lactation in the previous year (Table 2). The birth year was the only significant factor for the dam traits (results not shown).

Analyses of the genetic effects

Single-trait analyses

Calf traits

ADG was analysed using three different animal models. The best fit, according to the likelihood ratio test, proved to be the model including the direct and maternal genetic effects, but the addition of the maternal permanent environmental effect was not significant ($P = 0.88$, Table 3). Including a maternal effect had some effect on the variance estimates (model 1 vs. 2 and 3) but not on the direct heritability. The direct-maternal genetic correlation (r_{am}) was strongly negative, although with a high standard error.

In addition to the animal model, a sire-ma-

ternal grandsire model (S-MGS) was used to test the effect of correlated residuals in ADG. The genetic parameters from the S-MGS analysis were very similar to the ones from the animal model analysis with slightly higher standard errors (Table 3).

Age at maturity and lifetime production

The genetic parameters of the lifetime production traits are presented in Table 4. For age at maturity the heritability was smaller than its standard error. Both λ_{ind} and WW7 had a significant heritability. However, the heritability for λ_{ind} was only half of that of WW7; most likely because the latter has a scale with a much higher resolution.

Bivariate analyses

Calf traits

ADG and the related calf traits were also analysed in a bivariate context using the best-fitting

Table 2. The significance (F test) of fixed effects for birth date (BD), birth weight (BW), calf autumn weight (AW1) and average daily gain (ADG) in the Kutuharju reindeer herd in 1987-2011. The estimated level values of fixed effects (except year) are expressed as deviations from the last level.

Parameter	BD		BW		AW1		ADG	
	Estimate	<i>P</i> value	Estimate	<i>P</i> value	Estimate	<i>P</i> value	Estimate	<i>P</i> value
Birth year	<.0001		<.0001		<.0001		<.0001	
Sex		0.39		<.0001		<.0001		<.0001
male	0.37		0.33		3.91		31.19	
female	0.00		0.00		0.00		0.00	
Parity		0.89		<.0001		<.0001		<.0001
1	1.75		-0.79		-4.94		-31.95	
2	1.36		-0.38		-1.73		-13.61	
3	1.18		-0.21		-1.91		-11.93	
4	0.86		-0.19		-1.08		-10.08	
5	0.84		0.01		-0.10		-1.34	
6	0.82		-0.02		-0.21		-4.11	
7	0.98		0.13		-0.49		-10.80	
8	0.52		0.01		-0.39		0.49	
9	0.00		0.00		0.00		0.00	
Sire age		<.0001		0.42		0.00		0.07
1-2	4.96		-0.01		-2.43		-8.52	
3	4.43		-0.11		-1.44		-4.64	
4	2.11		0.11		0.00		-6.26	
5	1.83		0.01		-0.32		4.68	
6-7		0.00	0.00	0.00	0.00			
Calf at foot		0.85		0.73		0.85		0.93
absent	0.12		0.03		0.09		0.32	
present	0.00		0.00		0.00		0.00	

model with animal and maternal effects. When analysed with BW and AW1, which are the components of ADG, the heritability estimates of ADG were similar or higher compared to the univariate analysis (Table 5). There was a strong negative direct-maternal genetic correlation in ADG, as it was in the univariate analysis, whereas in the other traits the correlations were not significant.

Table 6 gives the correlations among the calf traits. Birth date was the only direct effect genetically related to growth rate. In birth weight dams with a low (or high) maternal effect on

birth weight had a high (or low) maternal effect on growth. The calves born heavy for non-genetic reasons would be expected to also grow fast. Fast growth leads to both phenotypically and genetically heavy calf autumn weight.

Age at maturity and lifetime production

Age at maturity, λ_{ind} and WW7 were analysed pairwise with the other traits. Gaining information from another trait resulted in an increment in the heritability of the studied trait (Table 7), which also meant obtaining significant estimates. However, the available amount of data

Table 3. Estimates of (co)variance components, and genetic and permanent maternal environment parameters (with their standard error in parentheses) for average daily gain (ADG) in the Kutuharju reindeer herd in 1987-2011. Models 1–3 have following random effects: 1 = direct genetic, 2 = direct genetic + maternal genetic, and 3 = direct genetic + maternal genetic + maternal permanent environmental effect. The best model among 1, 2 and 3 is indicated in bold. S-MGS is sire-maternal grandsire model.

	model 1	model 2	model 3	S-MGS
σ_a^2	405.53	449.59	450.61	482.12
σ_m^2	-	337.29	323.26	275.74
σ_{am}^2	-	-284.1	-279.92	-285.82
σ_c^2	-	-	10.63	-
σ_e^2	1194.66	1106.37	1103.72	1461.57
σ_p^2	1600.19	1893.25	1888.22	1609.71
h_d^2	0.25 (0.07)	0.24 (0.09)	0.24 (0.09)	0.30 (0.12)
h_m^2	-	0.18 (0.05)	0.17 (0.08)	0.17 (0.14)
c^2	-	-	0.01 (0.04)	-
r_{am}	-	-0.73 (0.17)	-0.73 (0.18)	-0.78 (0.24)
LogL	-4029.58	-4026.81	-4026.8	-

σ_a^2 = direct additive genetic variance, σ_m^2 = maternal additive genetic variance, σ_{am}^2 = direct-maternal additive genetic covariance, σ_c^2 = the variance of maternal permanent effect, σ_e^2 = residual variance, σ_p^2 = phenotypic variance, h_d^2 = direct heritability ($=\sigma_a^2 / \sigma_p^2$), h_m^2 = maternal heritability ($=\sigma_m^2 / \sigma_p^2$), 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.

relative to estimated parameters lead less often to significant correlations. The traits were correlated with each other and their early indicators. Genetic correlations implied that early

maturation is positively correlated with high survival and reproduction (λ_{ind}).

Table 4. The genetic parameters for age at maturity (dam age at first calving), individual fitness (λ_{ind}) and cumulative weaning weights of calves over seven years (WW7) in the Kutuharju reindeer herd in 1964-2000.

	Age at maturity	λ_{ind}	WW7
σ_a^2	0.12	0.03	1339.07
σ_m^2	1.69	0.26	4480.29
σ_c^2	1.82	0.28	5819.40
h^2	0.07 (0.12)	0.10 (0.06)	0.23 (0.07)

σ_a^2 = direct additive genetic variance, σ_c^2 = residual variance, σ_p^2 = phenotypic variance, h^2 = heritability (and its standard error in parentheses).

To demonstrate the relationship between the dams, we plotted the predicted individual genetic deviations from the population mean for dam's weight in her first autumn (DAW1) versus the cumulative sum of her calves' weaning weight over seven years (WW7) (Figure 1). The correlation between the traits is favourable, resulting in the genetic gain in WW7 when using her autumn weight as calf as selection criterion.

Discussion

Profitable reindeer husbandry rests on good calf growth and productive dams. Genetic variation in the traits facilitates the successful selection. The heritabilities in calf growth and dam productivity are moderate. However, the negative direct-maternal correlation in calf growth implies taking the dam properties into account in

Table 5. The estimates of direct (h^2_d) and maternal (h^2_m) heritabilities and direct-maternal correlations (r_{am}) of average daily gain (ADG), birth date (BD), birth weight (BW) and calf autumn weight (AW1) in the Kutuharju reindeer herd in 1987-2011.

trait	h^2_d	h^2_m	r_{am}	analysed with
ADG	0.47 (0.13)	0.31 (0.08)	-0.74 (0.11)	BW
ADG	0.27 (0.11)	0.22 (0.08)	-0.74 (0.17)	BD
ADG	0.52 (0.15)	0.24 (0.08)	-0.80 (0.09)	AW1
BD	0.28 (0.10)	0.09 (0.06)	-0.25 (0.34)	ADG
BW	0.24 (0.08)	0.35 (0.07)	-0.24 (0.23)	ADG
AW1	0.25 (0.12)	0.04 (0.07)	0.73 (1.39)	ADG

Standard errors are given in the parentheses.

selection criteria. The early information on the dam (her weight in her first autumn or her first calf's autumn weight) works as useful selection criteria for the traits related to lifetime production.

Data and traits

The Kutuharju reindeer data are unique, including detailed production records and pedigree, both being valuable in genetic research. The quality and amount of data allowed uni- and bivariate analyses and, in particular, the evaluation of maternal effects. More data, like few thousand animals (cf. Kruuk *et al.*, 2000; Martinez *et al.*, 2004a; 2004b), could have improved the power of the analyses, but using incomplete cohorts would have led to biased

Table 6. The genetic [direct ($r_{g(d)}$) and maternal ($r_{g(m)}$)], phenotypic (r_p) and residual (r_r) correlations between average daily gain (ADG), and calf birth date (BD), birth weight (BW) and calf autumn weight (AW1) in the Kutuharju reindeer herd in 1987-2011.

Correlations	r_p	$r_{g(d)}$	$r_{g(m)}$	r_r
ADG/BD	-0.03 (0.04)	-0.39 (0.27)	-0.15 (0.36)	0.03 (0.08)
ADG/BW	0.17 (0.04)	-0.13 (0.24)	-0.44 (0.18)	0.23 (0.10)
ADG/AW1	0.61 (0.03)	0.35 (0.24)	-0.00 (0.62)	0.74 (0.07)

Standard errors are given in the parentheses.

heritability estimates (Tanida *et al.*, 1988; Martinez *et al.*, 2004b). Modelling the incomplete cohorts by treating them as censored data (*e.g.* Ducrocq & Sölkner, 1994) or as missing data with EM-algorithm (*e.g.* Ducrocq & Besbes, 1993) may have increased the power of the analysis. This was, however, not tried.

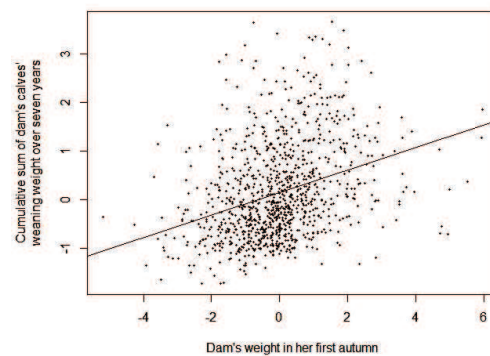


Figure 1. The predicted individual genetic deviations from the population mean for dam's weight in her first autumn (DAW1) versus the cumulative sum of her calves' weaning weight over seven years (WW7). The values are standardized by mean and standard deviation.

The similarity in the (co)variance components estimated among other species supports the biologically sound results.

The term λ_{ind} was used to measure lifetime production, as it includes information on survival and reproduction and takes into account also the gaps in reproduction (Brommer *et al.*, 2002). However, WW7 is most relevant from a meat production perspective, since it includes the calves' weights in autumn and allows

Table 7. The heritabilities (the range of the estimates from the analyses with different traits, on the diagonal in bold), and genetic (upper diagonal) and phenotypic (lower diagonal) correlations for the age at the maturity, individual fitness (λ_{ind}), cumulative weaning weight of calves over 7 years (WW7), dam's weight in her first autumn (DAW1), average daily gain of the dam (D_ADG) and her first calf's autumn weight (CAW1) in the Kutuharju reindeer herd in 1964-2000.

	Age at maturity	λ_{ind}	WW7	DAW1	D_ADG	CAW1
Age at maturity	0.05-0.17 (0.12-0.13)	0.16 (0.08)	-0.06 (0.08)	0.35 (0.34)	0.82 (0.44)	0.88 (1.45)
λ_{ind}	-0.98 (1.35)	0.07-0.13 (0.06-0.07)	0.86 (0.01)	0.71 (0.23)	0.56 (0.36)	0.95 (1.20)
WW7	-0.37 (0.69)	0.99 (0.05)	0.22-0.30 (0.07)	0.63 (0.12)	0.48 (0.22)	0.98 (0.65)
DAW1	-0.04 (0.07)	0.32 (0.03)	0.28 (0.04)	0.55-0.58 (0.08-0.09)	0.96 (0.09)	0.73 (0.59)
D_ADG	0.01 (0.07)	0.21 (0.04)	0.17 (0.04)	0.59 (0.03)	0.15-0.19 (0.08)	0.83 (1.08)
CAW1	0.07 (0.07)	0.21 (0.06)	0.31 (0.05)	0.21 (0.06)	0.15 (0.06)	0.04-0.08 (0.10-0.17)

The standard errors are given in the parentheses under the estimate.

the detection of differences among the dams. Therefore, the cumulative weaning weights (according to Martinez *et al.*, 2004a; 2004b) were also used. The lifetime production traits are highly correlated (Table 7), with WW7 being more variable, probably because of more continuous nature in its variation compared to λ_{ind} (cf. Brommer *et al.*, 2002).

The time span in both of the lifetime traits was up to seven years of age. The cutting point was chosen as seven years to provide a sufficient amount of data for the study and enable to detect the differences among the prime-aged animals. The study was dictated by production and artificial selection purpose rather than survival and natural selection. Indeed, survival was primarily the outcome of herders' decisions with the objective of maximising meat production by selecting the female calves for reproduction. Individual fitness could, in retrospect, be

more appropriately called a selective advantage in production. Hence, it is not surprising that the correlations of the two lifetime production measurements with their early indicators are so high.

Fixed effects

The annual variation in growth and reproduction (Table 2) is probably due to the weather conditions in spring and summer (*e.g.* review by Weladji & Holand, 2003). Also the management regime affecting BD and BW has varied over the years. Growth of the calf depends on the dam weight in the autumn prior to calving (Lenvik *et al.*, 2008; Weladji *et al.*, 2003; Holand *et al.*, 2004). Although the dam winter weight has been reported lower after rearing a calf the previous year (Rönnegård *et al.*, 2002; Weladji *et al.*, 2010), this had no effect on the studied traits (Table 2). This supports the find-

ing of Weladji *et al.* (2008), how there is no evidence on reproduction costs in reindeer. The parity effect in the model takes into account that the very young and old females have smaller calves with lower growth rate (Lenvik *et al.*, 1988; Rönnegård *et al.*, 2002; Weladji *et al.*, 2002; 2003; 2010). Further, the male calves grew faster than the female calves (Table 2), which is in line with the earlier studies (cf. Weladji *et al.*, 2003), and calf sex was therefore included in the model.

Genetic variation

Growth

The estimated heritability for growth is close to the realised estimates for autumn weight reported by Rönnegård & Danell (2003). The maternal heritability for growth was smaller than the direct one, a common feature for the growth traits (*e.g.* Heydarpour *et al.*, 2008). Contrary to the birth weight of reindeer (Muuttoranta *et al.*, 2013), the inclusion of the maternal effect in the growth model did not cause reduction in the direct heritability, as also reported by Safari *et al.* (2005) for sheep. In reindeer this is due to the strongly negative direct-maternal genetic correlation in growth (Willham, 1972; Table 2).

Age at maturity

Genetic variation of age at maturity was detected in the bivariate analysis. The low heritability value for age at maturity is common among the domestic animals (*e.g.* Bourdon & Brinks, 1982), and is therefore difficult to predict. In reindeer, the coarse scale makes the analysis even more challenging. In cattle, the age at first calving is measured in days or months (*e.g.* Bourdon & Brinks, 1982), whereas in reindeer, due to seasonal breeding, the trait is measured in years.

Lifetime production

The trait combining survival and reproduction rate, individual fitness, λ_{ind} , is heritable and

hence selection results in genetic gain in dam quality (Table 7). We have found no previous study analysing genetic variation of λ_{ind} for reindeer or other livestock species, although estimates on the other lifetime production traits exist (*e.g.* Kruuk *et al.*, 2000). The found heritability for λ_{ind} is smaller than that estimated in macaques by Blomquist (2010), who also noticed that the exclusion of the females, who never produced an offspring, caused lower heritabilities. This is also seen in our results: without the non-produced females λ_{ind} was 0.01 (0.09) and WW7 was 0.12 (0.09). In cattle, the heritability for lifetime number of weaned calves has been estimated to be 0.16 (Tanida *et al.*, 1988) and in red deer to 0 (Kruuk *et al.*, 2000). Due to the coarse scale, the heritability value for λ_{ind} is smaller than that of another lifetime production trait, lifetime reproductive success (Brommer *et al.*, 2002), while WW7 is similar to it. In general, the low heritability values in the lifetime production traits, such as individual fitness, could be due to a high amount of non-genetic variation that masks the additive genetic variance (Merilä & Sheldon, 2000; Brommer *et al.*, 2002). Another explanation is that there is only little variation left in fitness after selection (Falconer & Mackay, 1997).

In cattle, Martinez *et al.* (2004a) reported the heritability values of cumulative weaning weight for different dam ages (2-7) ranging from 0.06 to 0.16 (the highest values are for the longest reproductive life). This may originate from an increased opportunity to express their genetic potential.

Correlations

Direct-maternal correlation

We found a strong negative direct-maternal correlation for growth of reindeer calves, commonly reported in livestock (*e.g.* Bijma, 2006). In contrast to what was found by Heydarpour *et al.* (2008), the proportion of dams with no record of the trait did not explain the high neg-

ative value (results not shown). As another explanation, Bijma (2006) suggested estimating the residual covariance between the maternal and direct effect. However, the computational challenges (Koerhuis & Thompson, 1997) and the limited size of the data allows only speculation on the impact of correlated residuals on the strongly negative direct-maternal correlation. As applied by Eaglen & Bijma (2009), we compared the results from an animal model and a S-MGS model. We found similar estimates for the genetic covariance in both models and, therefore, little room for the covariance due to non-genetic effects.

The negative direct-maternal correlation underlines the importance of including both maternal and direct effect for calf growth in future selection criteria (Holand, 2007; Heydarpour *et al.*, 2008). Selection on calf's growth leads to heavy dams with possible reduced milk production and consequently poorer growth of their calves (*e.g.* Meyer, 1997). In a controlled situation this could be compensated with additional feeding. We suggest using large data: Among very numerous animals the ones with the least negative or even positive direct and maternal genetic effects could be detected and selected for breeding.

Correlations between the traits

When there is a favourable genetic correlation among the traits, selection on one would result in a desired gain also in the other traits. Indeed, growth has a favourable genetic correlation with survival, calf autumn weight, carcass weight, dressing percentage and early maturation (in cattle: Bourdon & Brinks, 1982; in reindeer: Petersson & Danell, 1993; in sheep: Safari *et al.*, 2005). We found a positive genetic correlations between weight of a female in her first autumn and both her λ_{ind} and WW7, which are similar to the correlations in sheep between reproduction and growth (Safari *et al.*, 2005). Hence, the calf autumn weight of an individual can be used as an early indicator trait

for lifetime production. Apparently the herders are paying attention also to the dam information in selection. The selection intensity is very high, as only few females are needed as replacements. Knowing the negative direct-maternal genetic correlation it is retrospectively clear that the recruitment calves were from the favourable part in the distribution of selection candidate calves as the genetic correlation between the direct and maternal genetic effect in calf autumn weight is negative.

Early maturation could serve as an another indicator of lifetime production (Table 7), as also reported by Weladji *et al.* (2006; 2008), although some reindeer herders regard that relatively early calving, at the age of two years, leads to fewer calves in the subsequent years (Muuttoranta & Mäki-Tanila, 2012). A good environment physiologically favours the early maturation (Reimers, 2005); hence, winter feeding in Kutuharju may result in calving at too young age. However, the calves getting pregnant are very rare exceptions in Kutuharju (altogether six calves in data). Nevertheless, the difficulty in finding the correlation with age at maturity and lifetime production should be noted. Brommer *et al.* (2002) reported about a positive effect of age at maturity on λ_{ind} , but not on lifetime reproduction success. Rönnegård *et al.* (2002) discussed how the late maturing females have low calving rate (despite their good condition) and relates this to reproductive inability. Indeed, a herder will cull a female with a limited productivity (Rönnegård *et al.*, 2002; Muuttoranta & Mäki-Tanila, 2011).

Martinez *et al.* (2004a) reported very high correlations (0.94-0.96) between the early and later production, hence the successful production in the first parity can predict the lifetime performance. According to Weladji *et al.* (2008), calving at early age indicates phenotypically good lifetime production in reindeer. Our results suggest that selection of females according to their performance at the first calving can be fruitful (Table 7).

Conclusions

Genetic variation in growth of calves and lifetime production of dams occurs. In a female reindeer the favourable correlations between calf growth, calf autumn weight, age at maturity and lifetime production make selection straight-forward, since when selecting for growth, also the other traits will be improved. Autumn weight of a female calf could therefore be used as an early indicator of her lifetime production. The production capacity of a dam can further be estimated using her first calf's weight. In improving growth of reindeer, the maternal effects should be included in selection criteria due to the negative direct-maternal correlation to avoid undesirable consequences in dam quality. Intensive selection should be accompanied by parallel changes in management to compensate a possible impaired maternal care.

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Poron lihantuotanto-ominaisuuksien geneettinen vaihtelu

Summary in Finnish/Tiivistelmä: Porotalouden lihantuotannon tehokkuus paranee siitoseläinten valinnalla, jolloin voidaan tuottaa enemmän ja painavampia teurasruhoja. Lihantuotantoon vaikuttavia jalostettavia ominaisuuksia ovat vasojen kasvu ja emän elinikäistuotos. Elinikäistuotokseen vaikuttavat vaatimen sukukypsyytikä, yksilöllinen kelpoisuus (λ_{ind}) sekä vieroitettujen vasojen elopainojen summa seitsemän vuoden iässä (WW7). Jalostettavissa ominaisuuksissa olevan geneettisen vaihtelun selvittäminen on edellytys tehokkaalle jalostusohjelmalle. Selvitimme vasojen päiväkasvuun (ADG) sekä vaadinten sukukypsyyteen ja elinikäistuotokseen vaikuttavien ominaisuuksien geneettistä vaihtelua poroaineistosta.

Päiväkasvussa eläimen oman ja emävaikutuksen periytymisasteet olivat kohtalaisia (0.25 ja 0.18) ja korrelaatio eläimen oman ja sen emän välillä oli vahvasti negatiivinen (-0.73). Negatiivisen korrelaation vuoksi eläimen lisäksi sen emä tulee huomioida valintakriteereissä. Sukukypsyyden ja yksilöllisen kelpoisuuden periytymisaste on alhainen (0.07 ja 0.10), kun taas WW7 periytyy kohtuullisesti (0.23). Poromiehet suosivat valinnassa painavia vasoja ja tämä suosii nopeasti kasvavia yksilöitä, koska geneettinen korrelaatio kasvun ja vasan syyspainon välillä on 0.35. Emän oma vasapaino (DAW1) ja sen vasojen vieroituspainojen summa ovat korreloituneet positiivisesti (geneettinen korrelaatio DAW1, λ_{ind} = 0.71 ja DAW1, WW7 = 0.63), joten naarasvasan syyspainoa voidaan käyttää sen potentiaalisen elinikäistuotoksen indikaattorina.