Lifetime patterns in adult female mass, reproduction, and offspring mass in semidomestic reindeer (*Rangifer tarandus tarandus*)

Lars Rönnegård, Pär Forslund, and Öje Danell

Abstract: The objective of our investigation was to examine relationships between lifetime patterns of female mass, calving incidence, and offspring mass in semidomestic reindeer (*Rangifer tarandus tarandus*). The analyses were made on data recorded from 1986 to 1997 on semidomestic reindeer in the herding district of Ruvhten Sijte in Sweden. A female rearing a calf was shown to weigh 3.1 ± 0.3 kg (mean ± SE) less in winter than a female not rearing a calf. The difference in calving incidence between females rearing a calf in the previous year and those not rearing a calf in the previous year was small, but there was a tendency for old females to have a decreased calving incidence if they had reared a calf in the previous year. The average calving percentage for adult females was 73%. Calf masses were affected by both the mother's mass and her age. The regression coefficient of calf autumn mass on female mass the previous winter was 0.26 ± 0.02. Mothers aged 2–4 years had calves that weighed less than calves of older mothers. The average difference in autumn mass between male and female calves was 2.9 ± 0.2 kg, but the difference was less for calves with mothers aged 2–4 years. We obtained lifetime patterns of female mass, calving incidence, and offspring mass. We also gave an organized structure of relationships between these traits.

Résumé : Nous avons tenté de déterminer les relations entre les patterns de la masse des femelles, le nombre de mises bas et la masse des rejetons au cours de la vie. Les analyses ont porté sur des données recueillies de 1986 à 1997 chez des rennes semi-domestiques (*Rangifer tarandus tarandus*), dans le district d'élevage de Ruvhten Sijte, en Suède. Les femelles nourricières pèsent 3,1 ± 0,3 kg (moyenne ± erreur type) de moins que les femelles sans petit. La différence dans la fréquence des mises bas entre les femelles qui ont élevé un petit l'année précédente et celles qui n'en ont pas élevé est peu importante, mais la fréquence des mises bas a tendance à être plus faible chez les femelles âgées qui ont élevé un petit l'année précédente. Le pourcentage moyen de mises bas est de 73 % chez les femelles adultes. La masse d'un rejeton est affectée à la fois par la masse de sa mère et par son âge. Le coefficient de régression de la masse des rejetons à l'automne sur la masse des femelles l'hiver précédent a été estimé à 0,26 ± 0,02. Les mères de 2 à 4 ans qui ont donné naissance sont de masse moins élevée que les femelles plus âgées. La différence moyenne entre la masse des rejetons mâles et celle des rejetons femelles à l'automne est de 2,9 ± 0,2 kg, mais cette différence est moindre chez les rejetons nés de mères de 2–4 ans. Nous avons pu obtenir les patterns de la masse des femelles, de la fréquence des naissances et de la masse des rejetons tout au long de la vie. Nous avons également pu établir une structure organisée des relations entre ces caractères.

[Traduit par la Rédaction]

Introduction

Knowledge of female reproduction in reindeer is important for the understanding of reindeer population biology. Female fecundities vary with age, and in long-term investigations of reindeer populations, lifetime patterns of fecundity can be examined (Eloranta and Nieminen 1986; Lenvik 1988). Further, if energy is limiting, then there ought to be a trade-off between present reproduction and future growth

L. Rönnegård[1] and Ö. Danell. Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Box 7023, S-750 07 Uppsala, Sweden.
P. Forslund. Department of Conservation Biology, Swedish University of Agricultural Sciences, Box 7002, S-750 07 Uppsala, Sweden.

[1]Corresponding author (e-mail:Lars.Ronnegard@hgen.slu.se).

(Roff 1992). Thus, female growth is desirable to examine in connection with fecundity.

Pregnancy and calving rates in reindeer have been shown to increase with female mass, and to be lower in younger females (1- to 3-year-olds) than in older ones (Reimers 1983*b*; Eloranta and Nieminen 1986; Lenvik et al. 1988; Cameron et al. 1993; Cameron and Ver Hoef 1994; Gerhart et al. 1997). Furthermore, calf mass has been shown to increase with the mother's mass, to be lower in young mothers, and to be higher in male calves than in female calves (Eloranta and Nieminen 1986; Lenvik 1988; Petersson and Danell 1993*b*; Skogland 1984; Weladji et al. 2002). Thus, adult female mass affects both calving incidence and calf masses. The development of female mass over age has been shown to increase up to an age of around 4–5 years, when female mass reaches a maximum and then slowly declines at older ages (Reimers 1983*a*; Reimers et al. 1983; Lenvik 1988; Kojola and Eloranta 1989). Females rearing a calf in winter weigh less the following autumn than females that have not reared a calf as an effect of the energetic cost of reproduc-

tion (Reimers 1972; Kojola and Eloranta 1989; Ropstad et al. 1991; Gerhart et al. 1997; Chan-McLeod et al. 1999).

The relationships distinguished in the studies above concerning female mass, calving, and calf mass in semidomestic reindeer (*Rangifer tarandus tarandus*) are summarized in Fig. 1. We have also added hypothetical relationships that have not been examined earlier. These are the effects of previous calving on calving incidence and calf masses (relationships *d* and *i* in Fig. 1). The studies on reindeer, referred to above, lack simultaneous analyses of the components in Fig. 1, and lifetime patterns have not been examined in detail because few of these studies span over a longer period of time.

Our objective is to examine relationships between lifetime patterns of female mass, reproduction, and offspring mass. In our attempt to fulfill this objective, we test the hypothetical relationships in Fig. 1. Furthermore, we quantify these relationships for use as input parameters in dynamic modelling of production in a reindeer herd (e.g., Danell and Petersson 1994) and the evaluation of selection response in reindeer herds (Rönnegård and Danell 2003).

Materials and methods

The study was conducted using data collected and recorded between 1986 and 1997 by three reindeer owner groups in the herding community of Ruvhten Sijte (formerly Tännäs Sameby) in Sweden (63°N, 12°E; area available for grazing is 926 km² during May–October and 2936 km² in winter). In the early 1980s, these reindeer owners introduced a recording system (Petersson et al. 1990; Petersson and Danell 1993a), which has been used since then. Use of individual ear tags began in 1980 and calves have been weighed since 1986.

We defined the production year of Ruvhten Sijte to begin at calving in May. At the annual calf marking in July, the reindeer in the whole herding district of Ruvhten Sijte were gathered. Less than 10% of the herd may have been missed in the gatherings (E. Rensberg in Ruvhten Sijte, personal communication), except for 1990 when the gathering failed and only a small proportion of the calves were marked. The calves were ear-tagged and their identities coupled with their mothers' at the calf markings, whereas sires were unknown. Further, the reindeer owners recorded late autumn mass (October–December, mean date 27 November) and adult female masses were recorded in winter (November–January, mean date 10 December). Between 1986 and 1997, no twins and only four 1-year-old mothers were recorded.

At autumn slaughter, the reindeer were gathered in groups of approximately 500–1500 animals and the reindeer owners used the recorded masses to select heavier calves. Between 1992 and 1993, the number of reindeer in the spring herd was reduced from 8000 to 4500 by increased slaughter. Owners applying the recording system culled adult females based on recorded calf production data by culling females with recorded low fecundity. Culling of adult females was on average less than 5% per year.

Definitions

In this paper, the following definitions are used.

Fig. 1. Hypothetical relationships between a female's age, winter mass, and calving incidence in two consecutive years, *t* – 1 and *t*, together with the relationships with offspring mass in autumn. A production year starts in May at calving. Arrows go from independent to dependent effects. Previously uninvestigated relationships are shown as broken arrows and correlated variables are connected by a double-headed arrow.
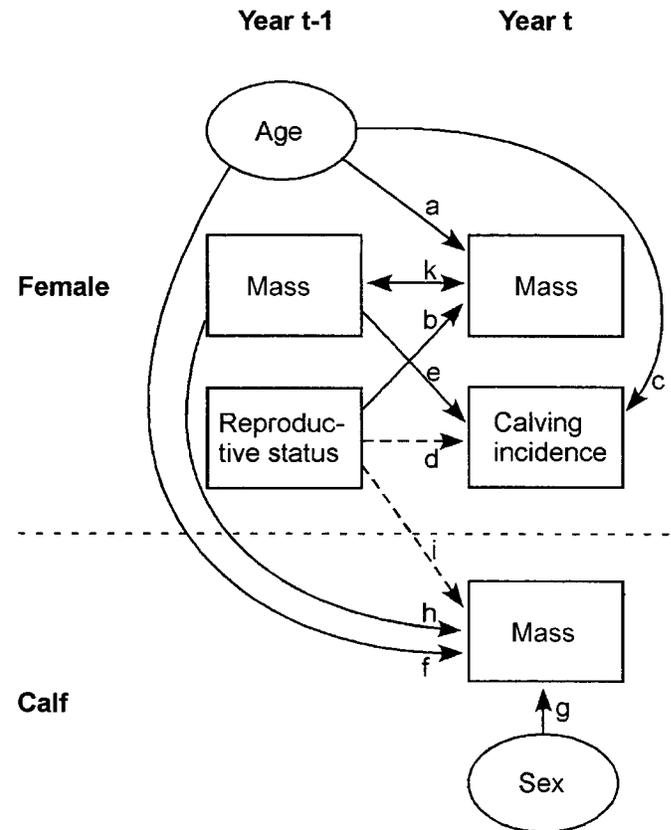
Calving incidence

Calving incidence is 1 if a female with recorded winter mass has a recorded calf at the calf marking in the following summer and 0 if a female with recorded winter mass has no recorded calf at the calf marking in the following summer. At the population level, calving incidence is given as a mean.

Reproductive status

Females were classified according to Clutton-Brock et al. (1987) as "first breeders" if they had not previously produced a calf, as "yeld" if they had produced earlier in life but not the previous year, or as "milk" if they had reared a calf the previous year. A female was classified as having reproduced if both mother and calf were gathered and recorded at the calf marking.

Female age class

The age of the adult female was rounded downwards to a discrete number of years, e.g., if offspring mass was recorded when the mother was 2½ years old, then the female age class of the mother was 2 years. Furthermore, females change age class directly before calving.

Table 1. Definitions of dependent and independent variables used in statistical models.

Variable	Definition
Dependent	
Mass	Adult female winter mass
Mdiff	Change in individual female mass between two consecutive years
Calving	Calving incidence
Calfm	Calf mass in late autumn
Independent of prior interest	
Age	Female age as fixed class effect
age, age^2	Female age and female age squared as continuous (fixed) covariates
Sex	Sex of calf as fixed effect
Rep	Fixed effect of reproductive status (first breeder, yeld, milk)
mss	Adjusted adult female mass as linear covariate
Other independent	
Year	Year of recorded mass as fixed class effect
D	Date of recorded mass as fixed class effect
f	Random effect of individual adult female, where $f \in N(0, \sigma_f^2)$
e	Residual term, where $e \in N(0, \sigma_e^2)$

Note: Fixed covariates and random effects are denoted by lowercased letters.

Table 2. Description of materials used in the analyses.

	Dependent variable			Calfm	
	Mass (Model 1a)	Mdiff (Model 1b)	Calving (Models 2a and 2b)	Model 3a	Model 3b
No. of observations	3449	827	1884	8056	1571
No. of individual females	1877	516	1009	3035	1117
Years included in analysis	1987–1991, 1994, 1996	1989–1992	1987, 1988, 1990, 1991, 1994, 1996	1986–1997	1988–1992, 1995, 1997
Female ages (years)	1–10	2–7	2–12	1–15	2–12

Statistical analyses

Dependent and independent variables are defined in Table 1. We analysed four different dependent variables: adult female mass (Mass), change in adult female mass between consecutive years (Mdiff), calving incidence (Calving), and calf mass (Calfm). The relationships between dependent and independent variables of primary interest are given in Fig. 1. Other independent variables were included to explain nuisance variation in data. The analyses were carried out using Proc Mixed and the GLIMMIX macro in SAS statistical software (Littell et al. 1996). Adult female was included as random effect, since several observations were made on the same individual females at different ages.

In the analyses of Mass and Calfm, effects of age were investigated without any constraint on the lifetime pattern by treating female age as fixed class effect. Smoothed and more parsimonious predictors of age dependency were subsequently obtained by fitting inverse polynomial regressions (Nelder 1966) of adjusted values of the dependent variables, y*, on age treated as a continuous covariate:

$$y* = (a + b \times age^{-1} + c \times age + d \times age^2)^{-1} + e$$

where *a*, *b*, *c*, and *d* are regression coefficients and *e* is a residual term. The adjusted values of the dependent variable were obtained by subtracting estimates of model terms, other than age, from the observed values. The inverse polynomials

were fitted using Proc NLIN in SAS (Freund and Littell 1991).

The statistical modelling is described in greater detail below. The materials used in the different models are found in Table 2.

Female mass patterns in relation to age and earlier calf production

The dependency of adult female mass (Mass) on age and reproductive status was analysed in Model 1a (Table 3). Only recorded masses from adult females with complete reproductive histories were included. Females older than 5 years and classified as first breeders were not included because the number of observations within age classes was low (two or less). The interaction term Age × Rep, where Rep is reproductive status in year $t - 1$, was found to be insignificant ($P = 0.49$) but was included because of the unbalanced structure of the data where all 2-year-old mothers were classified as first breeders.

Records of females with registered masses in two consecutive years were analysed in Model 1b to be able to draw conclusions on individual changes in mass caused by previous reproduction. The dependent variable, Mdiff, is the difference in adjusted female mass between year t and year $t - 1$ (see Fig. 1). Female masses in years t and $t - 1$ were ad-

Table 3. Description of models, significance of model terms, and variance estimates.

	Model					
	1a*	1b*	2a†	2b†	3a*	3b*
Relationships in Fig. 1	*a*, *b*, and *k*	*a* and *b*	*c* and *d*	*c* and *e*	*f* and *g*	*f*, *g*, *h*, and *i*
Dependent variable	Mass	Mdiff	Calving	Calving	Calfm	Calfm
Age	<0.0001	0.007			<0.0001	<0.0001
age			<0.0001	<0.0001		
age^2			<0.0001	<0.0001		
Sex					<0.0001	<0.0001
Rep	<0.0001	<0.0001	0.036			—‡
mss				0.0014		<0.0001
Age × Sex					0.0024	—‡
Age × Rep	0.49§	0.15				—‡
age × Rep			0.003			
age^2 × Rep			0.0001			
mss × Sex						—‡
mss × Age						—¶
Year		<0.0001	0.032	0.032		
D	<0.0001				<0.0001	<0.0001
σ^2_f	17.8		0.40**	0.81**	4.6**	4.9**
σ^2_e	13.2	26.2	0.88	0.81	12.0	10.0

Note: Variables are defined in Table 1. Empty cells, not tested.
*Mixed linear model.
†Generalized linear mixed model with logit link function.
‡Not included in the final model due to Type 3 test, $P > 0.35$.
§Included because of the data structure.
¶Not included in the final model due to lower Akaike's information criterion without the interaction term.
**Mother identity as random effect.

justed to the mean day of the year when the masses (μ_{day}) were recorded using the following model:

$$\text{Mass} = \text{Year} + \text{Age} + b_1 \times \text{day} + b_2 \times \text{day}^2 + f + e$$

where day is the number of days since 1 January.

Masses were then adjusted as

$$\text{mss} = \text{Mass} - \hat{b}_1(\text{day} - \hat{\mu}_{day}) - \hat{b}_2(\text{day}^2 - \hat{\mu}^2_{day})$$

Effects of female age, mass the previous winter, and earlier reproduction on calving incidence

Calving incidence (Calving) was analysed by a generalized linear mixed model with binomial error distribution and logit link function. The analysis was made in two parts (Models 2a and 2b) because of the colinearity between female mass and reproductive status noted in Model 1a. Masses were adjusted for day of recorded mass in Model 2b in the same way as in Model 1b. Records of females weighed in the winter of 1989 were not included because only a small proportion of the calves in 1990 were marked. Females slaughtered between the date of recorded winter weighing and date of calf marking were excluded from the analyses. Furthermore, females born before 1984 were also excluded because of incomplete reproductive histories.

In a preliminary analysis, with age as fixed class effect, the effects of age within reproductive status were found to be close to a second-degree polynomial on the logit scale. The effect of age was subsequently included as a linear and second-degree covariate in the final model of the linear esti-

mator, as our aim was to obtain lifetime patterns of calving incidence.

Patterns in calf mass in relation to dam age class and mass

In Model 3a, calf masses (Calfm) were analysed to detect patterns in relation to female age. In a preliminary analysis, the interaction term of sex and year of observation was tested and subsequently excluded ($P = 0.61$).

Model 3b was used to analyse in greater detail dam-related factors that may influence calf masses. Not all mothers in Model 3a had recorded adult female mass. Consequently, fewer observations could be used in Model 3b than in Model 3a and the analyses included a shorter range of female ages. Furthermore, age classes 11 and 12 were merged into age class 11 because of the low number of observations. Masses were adjusted for day of recorded mass in the same way as in Model 1b.

In a preliminary analysis with Model 3b, the terms Rep, Age × Rep, mss × Sex, and Age × Sex were tested and subsequently excluded (backward elimination for $P > 0.35$). In a further preliminary analysis, the interaction term of dam mass and dam age (mss × Age) was found to be close to significant ($P = 0.062$), but there was no visible trend in estimated values of the regression coefficients over age. Therefore, the model was further analysed by studying the fit of the model with and without the fixed interaction term. Maximum-likelihood estimation was used instead of residual maximum-likelihood to enable comparisons of model fit of the two alternative models (Littell et al. 1996). The interaction term

was excluded from the final model because Akaike's information criterion (Akaike 1969) was not lower when the interaction term was included.

Results

Female mass patterns in relation to age and earlier calf production

Female mass was significantly affected by female age and reproductive status (Table 3). Female mass increased up to an age of about 7–8 years, where it reached an asymptote as shown by the fitted inverse polynomial functions (Fig. 2a, Table 4). Yeld and first breeder females did not differ significantly in mass ($P = 0.68$). When pooling these two categories of females, they were significantly ($P < 0.0001$) heavier (on average, 3.1 ± 0.3 (mean $\pm$ SE) kg) than milk females.

There tended to be individual differences in mass among females that were persistent over ages. The correlation of recorded masses from the same individual at different ages, after adjusting for fixed effects, was 0.57 (Table 3, $\sigma_f^2/(\sigma_f^2 + \sigma_e^2)$).

Individual changes in female mass were examined in Model 1b because the estimated effect of reproductive status in Model 1a (Fig. 2a) could not directly be interpreted as individual changes in mass caused by reproduction. The effect of reproductive status on female mass in Model 1a might be caused by individual changes in masses connected with reproductive status. However, if females that are persistently heavier have an overall greater probability of reproduction, the effect will be partly masked and not correctly estimated. To test this, we used Model 1b with Mdiff as the dependent variable.

Using Model 1b, the estimated increase in mass for females without a calf (categories yeld and first breeders pooled) was 3.30 ± 0.72 kg more than for females with a calf (i.e., milk). The corresponding estimate on the same material using Model 1a was 3.48 ± 0.58 kg. Thus, there were no, or only small, differences between the estimates of reproductive status in Models 1a and 1b, and the estimate of previous reproduction in Model 1a was concluded to be caused mainly by individual changes in female masses.

Effects of female age, mass the previous winter, and earlier reproduction on calving incidence

Calving incidence was significantly affected by female age and reproductive status (Model 2a in Table 3). The calving incidence in the consecutive year for first breeder females decreased sharply after the age of 4, whereas the calving incidence for yeld females was kept at a nearly constant level (~80%) for ages 4–11 years (Fig. 2b). The differences between yeld and milk females were small for ages 6 and 7 years but increased for younger and older ages (Fig. 2b). First breeders had similar calving incidence as yeld and milk at 4 years of age, but at older ages, their calving incidence deviated increasingly from that of yeld and milk (Fig. 2b). The different effects of age on calving incidence among females of different reproductive status were evident as significant interaction terms between age and reproductive status (Table 3).

Calving incidence increased with female mass (Fig. 3), where the regression coefficient of the linear estimator was

Fig. 2. Female mass (*a*) and calving incidence (*b*) in relation to female age and reproductive status. The curves in Fig. 2a are smoothed values of female mass as inverse polynomials (estimated coefficients in Table 4), and the data points are least square means. The curves in Fig. 2b correspond to the regression coefficients estimated in Model 2a (data points and curves coincide), with calving incidence equal to $e^y/(1 + e^y)$ and $y = -3.44 + 2.61x - 0.39x^2$ for first breeders, $-1.59 + 0.94x - 0.075x^2$ for milk, and $1.33 + 0.047x - 0.006x^2$ for yeld, where x is the female's age class. Note that females in age class 1 are 1.5 years old at weighing. Furthermore, a mother in age class t at calving is in age class $t - 1$ when weighed the previous winter.
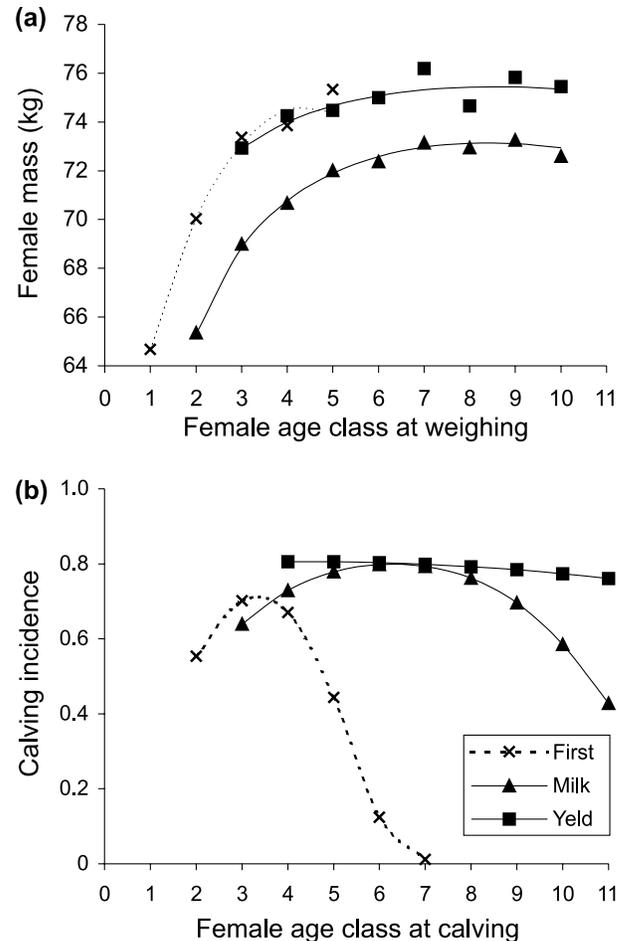
0.03 ± 0.01. For fixed female mass, calving incidence increased up to the age of 6 years, where it reached a maximum.

Patterns in calf mass in relation to dam age class and mass

The effect of mother's age on calf mass was highly significant in Model 3a (Table 3). Calf mass was highest for calves with mothers aged 6 years and slowly declined for older mothers (Fig. 4, Table 4).

The estimated difference in masses between male and female calves varied significantly over dam age ($P = 0.0024$) and tended to increase for calves with dams between ages 2 and 5 years (Fig. 5). The estimated effect of a calf being male was 0.65 kg less for 2- to 4-year-old dams than for 5-

Table 4. Estimates of coefficients of the inverse polynomial fitted to adjusted masses (kg), $y^* = (a + b \times \text{age}^{-1} + c \times \text{age} + d \times \text{age}^2)^{-1}$.

| Coefficient	Model 1a[a]			Model 3a[b]	Model 3b[c]
	First	Milk	Yeld		
$\hat{a}$	0.0153	0.0131	0.0132	0.0210	0.0311
$\hat{b}$	0.00107	0.00461	0.00201	0.00857	0.0177
$\hat{c}$	–0.00102	–0.00006	–0.00007	–0.00015	0.00030
$\hat{d}$	0.000121	0.0000075	0.000006	0.000025	0.000005

Note: These functions give the smoothed age effects as shown in Figs. 2a and 4 and Table 5.
[a] y^* = Mass adjusted for average effect of D and f.
[b] y^* = Calfm adjusted for average effect of Sex, D, and f.
[c] y^* = Calfm adjusted for average effect of Sex, D, and f and effect of mother's mass subtracted.

Fig. 3. Calving incidence in relation to female mass for 2- to 5-year-olds (Model 2b). The curve of calving incidence, for all age classes, is given by $e^y/(1 + e^y)$ with $y = -2.72 + 0.58x - 0.05x^2 + 0.03m$, where x is the female's age class and m is the female's body mass.
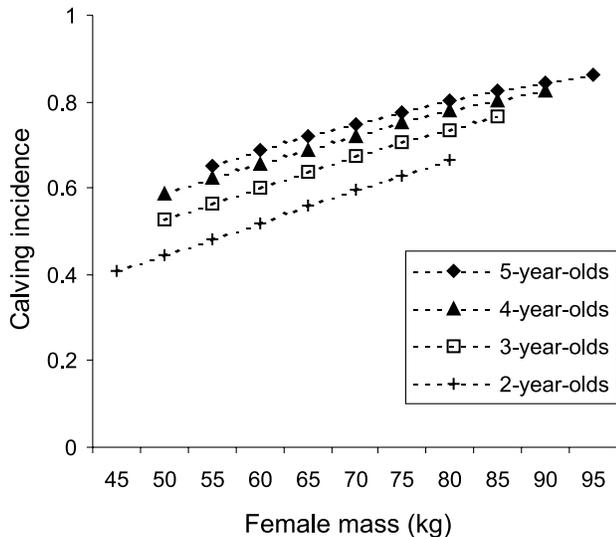
to 10-year-old dams ($P = 0.0004$). The mean effect of a calf being male was 2.52 ± 0.45 kg.

The variation of sex differences between dam ages could be caused by young mothers getting lighter calves, and the sex difference may be proportional to calf masses. To test this, the calf masses were log transformed (Sokal and Rohlf 1995), but the Age × Sex interaction remained significant ($P = 0.0093$). Thus, we concluded that the sex difference was not directly proportional to calf masses.

In Model 3b, the mother's mass was included as an independent variable, and calf mass was then found to be significantly affected by sex, mother's age, and mother's mass (Table 3). The regression coefficient for adjusted dam mass was estimated to be 0.26 ± 0.018 and the estimated difference between male and female calf masses (2.86 ± 0.20 kg) was close to the estimate in Model 3a. Pure age effects, i.e., separated from mass effects, showed patterns similar to the age effects estimated in Model 3a but with a lower increase from 2 to 4 years of age (Tables 4 and 5), where the masses of adult females increases considerably (Fig. 4).

Dam masses in Model 3b were adjusted to the mean day of the year when the dam's mass was recorded (mean day = 344.0, i.e., ~10 December, range 27 October to 20 January),

with regression coefficients for day of the year and day of the year squared equal to 0.43 and –0.00057, respectively (which gives a maximum mass for day 377.2, i.e., ~12 January). Thus, masses increased during late autumn and were close to constant in midwinter.

Discussion

The relationships in Fig. 1 were found to be significant, except for the effect of reproductive status on calf mass (relationship i). The effect of reproductive status on calf mass was tested in a model that also included the mother's mass. The effect of reproductive status may have appeared to be significant if tested without mother's mass included in the model because female mass and reproductive status were found to be closely related.

Calving incidence increased with female age and mass in the same way as in the studies by Eloranta and Nieminen (1986), although their calving incidence increased more steeply with female age and mass than in our results. This might have been because they studied an unselected population where female calves with low masses had not been systematically culled. According to Skogland (1983), young female reindeer with low mass delay reproduction to put on more mass, and consequently, calving incidence will increase more steeply with age in an unselected herd.

Our estimate of the effect of calving on female body mass (3.1 kg) is slightly higher than earlier estimates on semi-domesticated reindeer (~2 kg in Kojola and Eloranta 1989) and is also higher than that found in wild caribou (*Rangifer tarandus granti*) in the Porcupine Caribou Herd with a difference of approximately 1.5 kg between non-lactating and lactating females in November (Gerhart et al. 1997). However, the estimated effect of calving on female body mass will be reduced if the female's age is not accounted for because young females are light and have low calving rates. Thus, the estimates referred to may be underestimated because they did not make a joint analysis including effect of calving and effect of age on female mass.

The relationship between calving incidence and female mass causes a dynamic connection between reproduction and changes in mass throughout a female's lifetime. Growth up to maturity and, for mature females, variation in mass and condition between years are included in the mass changes. Our results showed that reproduction reduced mass gain (Fig. 2a) and that lighter animals had a lower probability of reproduction (Fig. 3). However, the effect of mass on reproduction was weak and a reproductive pause would give only

Fig. 4. Inverse polynomial function of dam age fitted to adjusted calf masses from Model 3a (mean ± 2 SE).
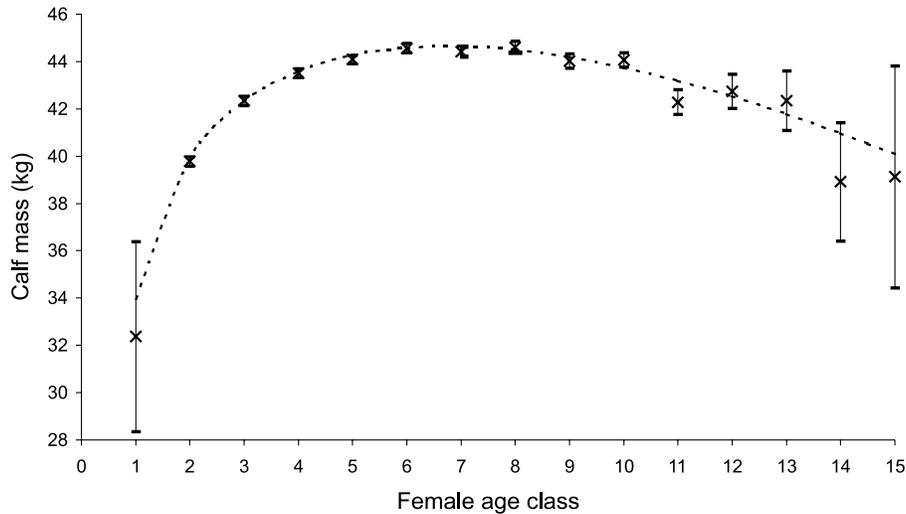

a small advantage in future reproduction in terms of higher calving incidence (Fig. 2*b*). Thus, the relationship between calving incidence and female mass was mostly one-way directed. The reason for this asymmetry was probably the high overall calving incidence in the population (Cameron and Ver Hoef 1994). If the environmental conditions (e.g., population density) of the studied herd had been less favourable, we would probably have found a greater advantage of reproductive pause on future reproduction because more animals would have been closer to their limit of reproductive ability. In red deer (*Cervus elaphus*), the difference in calving incidence between yeld and milk females increases with population density (Clutton-Brock 1984), and consequently, the advantage of a reproductive pause increases with population density. In Norwegian wild reindeer, a negative relationship between mean female growth rate up to maturity and calving rate has been reported (Skogland 1983), as could be expected with a trade-off between female growth and calving. Furthermore, wild reindeer females under poor environmental conditions are affected more by reproduction than females in a better environment (Skogland 1983). In reindeer husbandry, densities are generally kept considerably lower than the ecological carrying capacity and controlled by a 20–35% yearly harvest. Ruvhten Sijte most likely has a density that more or less corresponds to maximum harvest yield. Consequently, to obtain a better understanding of the trade-off between reproduction and mass in reindeer, we would need to investigate other populations under poorer environmental conditions.

Another interesting aspect of the relationship between calving incidence and female mass is that middle-aged first breeder females had a low calving incidence, although their masses were close to the masses of yeld females (Fig. 2). We interpreted these differences between first breeders and yeld females as a reproductive inability in old first breeders, since they had failed to reproduce year after year. It should also be noted that the number of old first breeders was low, either because there were few animals born with a reproductive inability or because a first breeder was culled as soon as the owner realized that it was not productive enough.

Our estimate of the regression coefficient between the

Fig. 5. Difference in mass between male and female calves for different dam ages in Model 3a (mean ± 2 SE). A second-degree polynomial fitted to unweighted estimates for ages 2–10 is shown as a dashed line ($y = -0.029x^2 + 0.38x + 1.7$). Ages 11–14 are pooled into one age class, 11+.
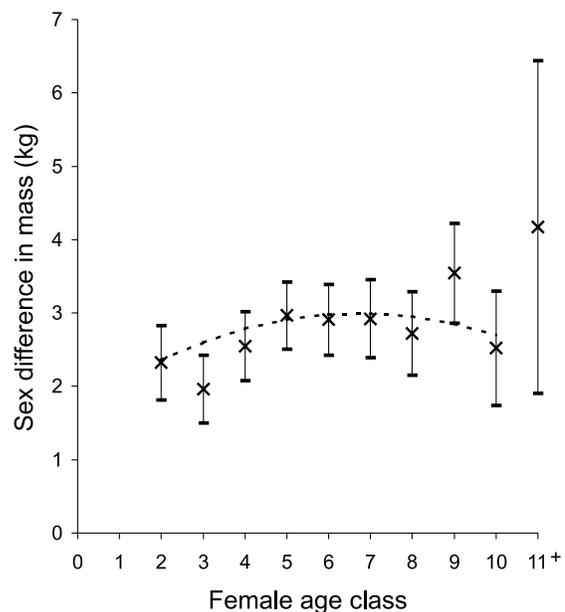
calf's mass in autumn and the mother's mass the previous winter (0.26) agrees with the estimate of between 0.2 and 0.4 obtained by Lenvik (1988) and that between 0.2 and 0.3 observed by Eloranta and Nieminen (1986). Although mother's mass is a major determinant of calf mass, we also found maternal age effects after accounting for mother's mass, which is supported by the recent study by Weladji et al. (2002) and also that by Lenvik (1988). Maternal age effects may be explained by an age-related improvement of some skill that positively affects reproductive performance (Forslund and Pärt 1995), e.g., breeding experience, ability to avoid predators, and ability to make optimal decisions for forage search and intake. An alternative hypothetical explanation is that the increase in maternal age effects for young females is a

Table 5. Estimates of independent variables in Model 3b where the dependent variable is Calfm.

Effect	Class	Estimate	Smoothed age effect[a]
Intercept		25.95	
Sex	Male	2.86	
	Female	0	
Age (years)	2	–2.71	–2.73
	3	–1.03	–1.02
	4	–0.13	–0.20
	5	0.03	0.21
	6	0.63	0.39
	7	0.32	0.43
	8	0.33	0.39
	9	0.24	0.28
	10	0.18	0.13
	11	0	–0.06
mss (kg)		0.26	

[a]Values from fitted inverse polynomial in Table 4.

consequence of an optimization of the lifetime reproductive effort, where the reproductive effort increases as the remaining number of years of potential reproduction decreases (Williams 1966; Curio 1983; Clutton-Brock 1984). In reindeer, this hypothesis has not been tested because it is difficult to test without making experimental manipulations of reproductive success (Roff 1992). Further, there is no evidence to support the hypothesis from nonmanipulated field data, since the body mass of calves decreases for old females and the energy allocated to maintenance and fattening decreases for old females due to a lack of ability to process food with worn-out teeth rather than an increased reproductive effort (Skogland 1988; Weladji et al. 2002). Further, as also found by Weladji et al. (2002) and Skogland (1988), our results suggest that there are effects of senescence in female reindeer after a prime age of approximately 7 years of age, since calving incidence and calf masses decrease for females older than 7 years, after adjusting for adult female mass.

We also found that the difference between male and female calf mass is smaller for young mothers than for older ones. This effect of maternal age on calf mass might be explained by the fact that when females mature (at about 5 years) and gain experience, they are capable of rearing larger male calves. For a deeper understanding of how young mothers gain in experience, it would be interesting to examine the development of predator avoidance and the improvement of forage search with age.

The selection of calves in the studied population may have influenced the analyses in two ways. First, the phenotypic mean of calf masses is increased directly after selection each year (average selection differential of female calves was 2.9 kg) (Rönnegård and Dannell 2003), and second, the selection will cause a genetic change in calf masses (the genetic increase in calf masses was less than 2 kg between 1986 and 1997, with a female generation interval of 6.4 years). (Rönnegård and Dannell 2003) The increment in calf masses directly after selection each year is comparable with advantageous cohort effects, and such effects should mainly cause changes of the levels of the lifetime patterns studied in this paper. A genetic

change, however, may influence the investigated lifetime patterns because the genetic level in young animals will be greater than in old ones as a consequence of the continuous genetic progress. We believe that this influence is small, since the genetic gain from selection was achieved gradually. Furthermore, the recorded identities of individual adult females were included as random effects in the analyses, which accounts for differences among females of different ages caused by selection, and the culling of adult females was on average less than 5% per year. The overall agreement of our results with earlier studies was also good. We conclude that even though we studied a selected population, our results should be applicable in modelling of population dynamics in other populations, after calibrating for environmental differences.

We have examined an organized structure of relationships between female mass, calving, and offspring mass, which gives us a better understanding of the connection between calving incidence and female mass throughout a female's lifetime in reindeer. Furthermore, we have obtained lifetime patterns of female mass, calving incidence, and offspring mass and estimates of the relationships between these traits that may be used as input parameters in dynamic modelling of the production in a reindeer herd.

Acknowledgements

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