© 2015 Universities Federation for Animal Welfare
The Old School, Brewhouse Hill, Wheathampstead,
Hertfordshire AL4 8AN, UK
www.ufaw.org.uk

Animal Welfare 2015, 24: 173-183
ISSN 0962-7286
doi: 10.7120/09627286.24.2.173

*Calf mortality in semi-domestic reindeer (*Rangifer tarandus*) in a Scottish herd: the impact of maternal age and individual differences between cows*

MW Jorgensen†, S Jarvis‡§, MJ Brewer# and PJ Goddard¶*

† 380B Haecker Hall, 1364 Eckles Ave, University of Minnesota, St Paul, MN 55108, USA
‡ University of Edinburgh, Royal (Dick) School of Veterinary Studies, Easter Bush Veterinary Centre, Easter Bush, Roslin EH25 9RG, UK
§ Scotland's Rural College, The Roslin Institute Building, Easter Bush EH25 9RG, UK
# Biomathematics and Statistics Scotland, Craigiebuckler, Aberdeen AB15 8QH, UK
¶ Ecological Sciences Group, The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH, UK
* Contact for correspondence and requests for reprints: jorge505@umn.edu

Abstract

*High calf mortality rate is a significant problem facing semi-domestic reindeer (*Rangifer tarandus*) production around the world. Mortality rates, commonly due to predation, can range from 5 to 70%, which constitutes a great welfare concern. This study examined the influence of quantifiable maternal characteristics on reindeer calf survival. Data were compiled from 18 years' worth of records on the survival of calves in the Cairngorm reindeer herd (Scottish Highlands, UK). Overall, mortality rate of calves (n = 635) in the herd was 34.9% to six months old, rising to 47.8% by one year old. For both Total Calf Survival (including perinatal losses) and Post-natal Calf Survival (excluding perinatal losses) of calves up to six months old, the only maternal trait found to significantly influence calf survival was the age of the cow at calving. Calves of very young and old cows showed higher mortality rates. Only 40% of the cows were associated with 77% of calf deaths and it was demonstrated that there were significant individual differences between cows in relation to their ability to consistently rear calves successfully. These findings can be applied to reduce calf mortality within herds, guiding selection towards females with successful reproductive histories and with ages falling in the prime productive range (3–11 years old). Additionally, annual variation had a highly significant influence on calf survival with rising mortality over the recorded period, indicating a role of environment on survival and an avenue for further research to investigate the impact of external factors, such as climate and pathogen load on post-natal loss.*

Keywords: *animal welfare, individual, maternal care, mortality, post-natal, reindeer*

Introduction

Post-natal (pre-weaning) mortality rates vary in extensively raised domestic species: 10–40% in sheep (*Ovis aries*: Eales *et al* 1983; Binns *et al* 2002), 10% in red deer (*Cervus elaphus*: Guinness *et al* 1978), approximately 9% in beef cattle (*Bos taurus*: Cundiff *et al* 1982). Semi-domestic reindeer (*Rangifer tarandus*) display mortality rates from around 5% (Nieminen *et al* 2011) to a relatively high 31% (under one year of age; Nybakk *et al* 2002), to 50% (six months; Chetkiewicz & Renecker 1994), up to 70% (six months: Bjärvall & Franzén 1981). In most populations, these heavy losses are largely attributed to the impact of predation, with brown bear (*Ursus arctos*), wolf (*Canis lupus*), lynx (*Lynx lynx*), wolverine (*Gulo gulo*) and golden eagle (*Aquila chrysaetos*) among the most common predators (Norberg *et al* 2006; Nieminen *et al* 2011). These post-natal losses have a strong negative impact on farm profitability and efficiency in extensively raised species, such as sheep (Everett-Hincks & Dodds 2008) and the processes leading to mortality are regarded as having negative impacts on animal welfare in a range of farmed species, including sheep, goats, cattle and deer (Mellor & Stafford 2004). With broadly similar husbandry systems and functional biology, these issues certainly pertain to less-studied farmed species, such as reindeer. Though proximate causes of mortality in young reindeer have previously been described, with predation (Nybakk *et al* 2002; Nieminen 2010; Nieminen *et al* 2011), insect harassment (Helle & Tarvainen 1984) and environmental conditions (Kumpula & Colpaert 2003) the most common factors regarded as impacting post-natal mortality, such external factors, are largely outside producer control.

High quality maternal care increases survival of young in extensively raised species, such as cattle (Reynolds *et al* 1980), red deer (Guinness *et al* 1978), and sheep (Everett-Hincks & Dodds 2008), by increasing the young's ability to cope with a challenging environment. This trait is manipulable in ways that external factors are not. Some work has been conducted on cow-calf interactions in reindeer (eg Espmark 1971) and the connection of maternal traits to calf survival (Eloranta & Nieminen 1986; Weladji *et al* 2008), but the maternal impact on calf survival and, subsequently, farm productivity is not fully understood.

This study investigated productivity and losses in a herd of semi-domestic reindeer in the Scottish Highlands, UK to determine the influence and importance of cow traits, calf traits and external factors on post-natal survival.

Materials and methods

Animals and study area

The Cairngorm reindeer herd was introduced into the Cairngorm Mountain Range in the Scottish Highlands in 1952 by the Reindeer Company Ltd (originally from Swedish stock). Prior to calving in the spring of 2011, the herd numbered approximately 150 animals — 44 adult females and around 82 castrated males (between two and 15 years old), and 24 yearling calves. In a given year there are also 5–7 breeding bulls present (between three and seven years old). Cairngorm reindeer are kept for educational and tourism purposes, and the small size of the herd does not allow for harvest of meat or furs. Despite purpose differences, similarities between this herd and larger commercial herds elsewhere — along with a relatively high control over risk of predation, a major factor in other locations — makes the herd a useful model for calf survival with fewer variables. The animals are essentially free ranging at one of two sites (Site One: 57°12' N/3°50'W, Site Two: 57°19'N/3°24W) for the great majority of the year, though they typically stay within 16 km of each area. Animals are brought into a series of enclosures for regular husbandry procedures (eg annual immunisation, health checks, controlled breeding) one or more times per year depending on their health status. The primary enclosed area, located at Site One, measures approximately 405 ha in total, surrounded by a perimeter fence. This complex is divided into five smaller areas, ranging from 1–135 hectares — and covers upland hills ranging from 425–640 m in altitude. Plant cover is characterised as dwarf-shrub heath, with *Calluna vulgaris*, *Erica tetralix*, and *Trichophorum cespitosum* as the dominant species (Gilbert 1974); tree cover (primarily *Pinus sylvestris* ssp *scotica*) is present in some areas.

Breeding in the Cairngorm herd is relatively controlled in comparison to the traditional systems of northern Europe, in which multiple herds are stocked in designated reindeer herding districts. In these systems, breeding animals (and the respective breeding strategies of herd owners) are heavily mixed and diluted, with little direct management or selection (Rönnegard *et al* 2003). As a significantly smaller herd, the Cairngorm reindeer are managed in order to minimise inbreeding and to prevent impregnation of very young female animals (less than three years old), meaning that not all adult females will be covered in a given year. The herd maintains 5–7 breeding bulls, most of which have been imported from Sweden in order to prevent inbreeding. Bulls are generally allowed access to groups of females during the rutting season (late September to early October). While in any part of the enclosure complex, all animals are provided with supplemental concentrate feed (a combination of hay mix, rolled oats, brewers' grain, lamb and ewe mix, and lichen), though this does not replace grazing as the primary food source. Once the rut has ended, females and the current year's calves are turned out onto free range in the Cairngorm Mountain foothills, while males are removed to a separate area at Site Two. The female group is checked regularly while on the free range and continues to receive some supplemental feeding throughout the winter. Though this feed is primarily used as a husbandry tool to attract free-ranging animals for closer physical inspection, it is available as an emergency ration in times of heavy snow, though this use is not recorded. Gestation in reindeer lasts approximately 225–235 days (Ropstad 2000).

Females are brought into the primary enclosure complex at Cairngorm (described above) in mid-April in preparation for calving. Historically, calving has occurred primarily at Sites One and Two, and at low levels at three other sites, all of which are within a 60-km radius and share climate, altitude and plant distribution traits with the primary sites. At Site One, pre-parturient animals have access to the two largest enclosures and are kept with a herd of pregnant females and yearling calves until parturition. Once a female has given birth and the calf is strong enough to be moved (usually within 2–3 days), cow-calf pairs are shifted to a smaller (50 ha) enclosure which houses only new mothers and their calves. This smaller enclosure features a wooded area, but is primarily open hillside. Calves are typically born in late April to mid-May, although there are occasionally births before and after this period and these may occur outside the enclosure. New calves are caught by hand within the first 24 h after birth (after the mother has licked them dry) for normal care procedures, including sexing, navel disinfection, physiological condition check and examination of the dam (all of which occupies less than 10 min) before being turned loose and observed from a distance for any detrimental effects of handling or other health/developmental issues.

After the primary calving period has ended and new calves have become more mobile, the cow-calf group is turned out of the enclosure onto free range to graze for the summer, though they may be turned out in multiple groups if calving is protracted or if some calves are not yet strong enough to reliably follow their dam. Animals typically head for high mountain plateaux during the summer grazing season to escape warmer temperatures and insect pests found in the lower valleys. Cows and calves remain on the free range for the entire summer and are brought back into the enclosure in the early autumn for the rutting season. Calves born the previous spring are marked with an ear-tag at this time; all animals in the herd are individually identifiable by tag number following their first summer, though the herd is small enough that all animals are readily identified by herders using other physical characteristics.

Due to the relatively small herd size and governmental restrictions, the Cairngorm herd does not harvest animals for meat or hides as is the case in most semi-domestic herds. Animals in the Cairngorm herd typically live longer than those in production herds, with approximately 80% of adult animals dying of natural causes while grazing on free range and the remainder humanely euthanised for various reasons.

https://doi.org/10.7120/09627286.24.2.173 Published online by Cambridge University Press

Data compilation

The primary data set were compiled from farm records of the 145 individual females bred in the 18 years from 1993–2010. Calving events (including perinatal losses) were recorded, including the date of parturition, identity of the dam as well as her age, coat colour and the parity number, calf identity as well as calf gender and coat colour, site of birth, and survival to certain age landmarks: six months (weaning) and one year old. Sire was recorded where possible, but, as in most reindeer production systems, sire identity was often unknown.

Since calves often die while the herd is out on the free range, the accurate recording of dates and causes of death is very difficult; thus, survival to landmark ages (six months and one year) was recorded as a simple binary Y/N value. The death of a calf *in utero* or during parturition was recorded when a female gave birth to a dead calf, when a newborn calf carcase was found without signs of sucking, or when a previously pregnant female presented with signs of birth (bloodied genital region in conjunction with full teats) with no evidence of a calf being present. Specific times and causes of death were frequently unknown and could have occurred both before and after parturition; because of this, a combination of stillbirths and losses occurring during or soon after parturition are referred to in this study as perinatal losses.

Statistical analysis

Effects of cow traits, calf traits and external factors on calf survival

Generalized Linear Mixed Models (GLMMs) were fitted to the compiled binary survival data (reindeer calf either dead or alive at six months, the approximate age of weaning, or at one year) in order to identify individual traits which influence calf mortality. Analysis was completed for four distinct categories:

• Total Calf Survival rate to six months of age (with the denominator being all calves born [including perinatal losses]);

• Post-natal Calf Survival rate to six months of age (with the denominator being live calves born);

• Total Calf Survival rate to one year of age (with the denominator being all calves born [including perinatal losses]) and;

• Post-natal Calf Survival rate to one year of age (with the denominator being live calves born).

In all of the models (one for each category above), survival (either to six months or one year) was fitted as the response variable; maternal identity was fitted as a random effect in order to account for the repeated sampling of certain individuals. Potentially influential variables were entered into the model as fixed effects. Traits with wide numeric ranges (ie age at calving, parity, date of parturition, and year) were fitted as variates/covariates. The error distribution for each model was Binomial and a logit-link function was used throughout; because the response variables are binary, the dispersion parameter was fixed at one throughout. The combination of the need to account for maternal identity, and the Binomial error structure for the binary survival response variables, is what makes use of a GLMM necessary.

Previous research suggests that female reindeer typically achieve their peak reproductive efficiency between three and 8–12 years old, and that births during the calving season are typically concentrated over a period of just a few weeks with only a small number of calves born earlier or later (Eloranta & Nieminen 1986). Considering this, as well as patterns observed in the initial review of the data, the relationships between survival and both maternal age at calving and date of parturition were fitted as quadratic functions, with the expectation that these would provide a better fit. There did not seem to be justification for a further generalisation of the response function beyond quadratic — this would in any case be difficult to justify biologically.

As expected, there was a strong correlation between parity number and cow age ($r = 0.921$; $P < 0.001$). Despite this very strong correlation, the statistical analysis suggested that cow age was a more important predictor of survival than parity, and hence in what follows we concentrate on maternal age. The statistical significance of each term in the model was calculated using Wald statistics. We also performed backward elimination on the model containing all the possible explanatory variables to produce 'minimal subsets' of significant terms, and present estimated effects for these. All statistical analyses were conducted using the GenStat statistical software (VSN International 2011).

Effects of individual cows on calf survival

To determine the importance of individual cows to the occurrence of calf survival we ran the four models with and without cow fitted as a Random Effect (using IRREML within GenStat). The changes in deviance were assessed using a Likelihood Ratio Test producing a statistic to be compared with a Chi-squared distribution with one degree of freedom.

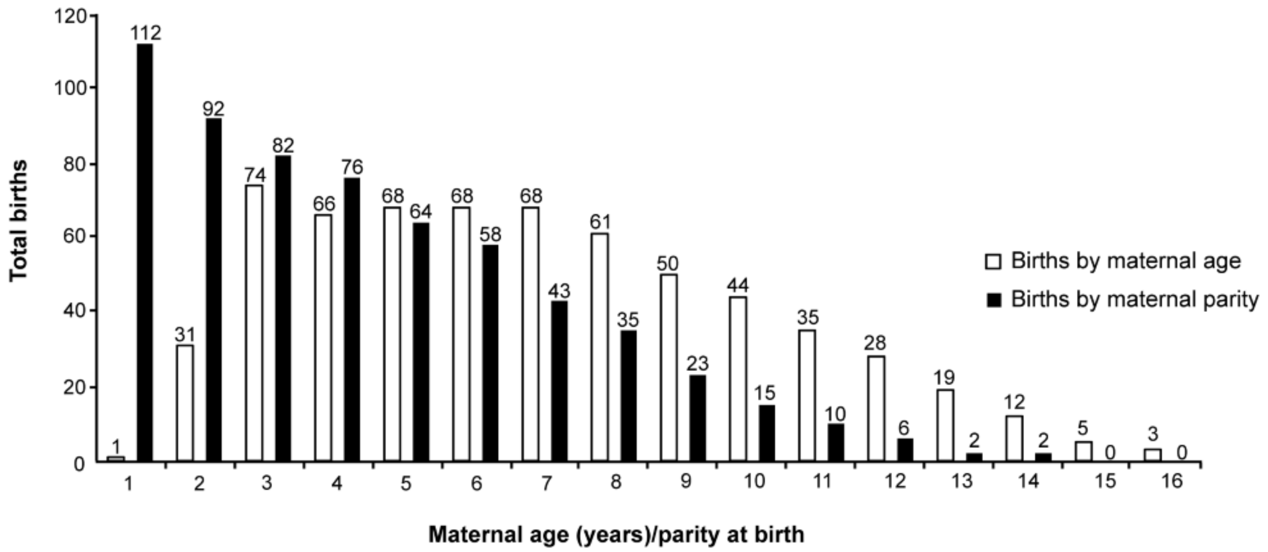
Results

Overall productivity and survival

From 1993–2010, 145 individual reindeer cows from the Cairngorm herd gave birth 634 times (including perinatal losses), producing 635 calves (Figure 1). The mean number of calves born per season was 35.2, the highest number born was 48 (2010) while the lowest was 14 (2001). For the herd overall, the median age of cows at calving was seven years (minimum = one year, maximum = 16 years) and the median parity (number of times a cow gave birth) reached in the individual productive life was four (minimum = one, maximum = 14).

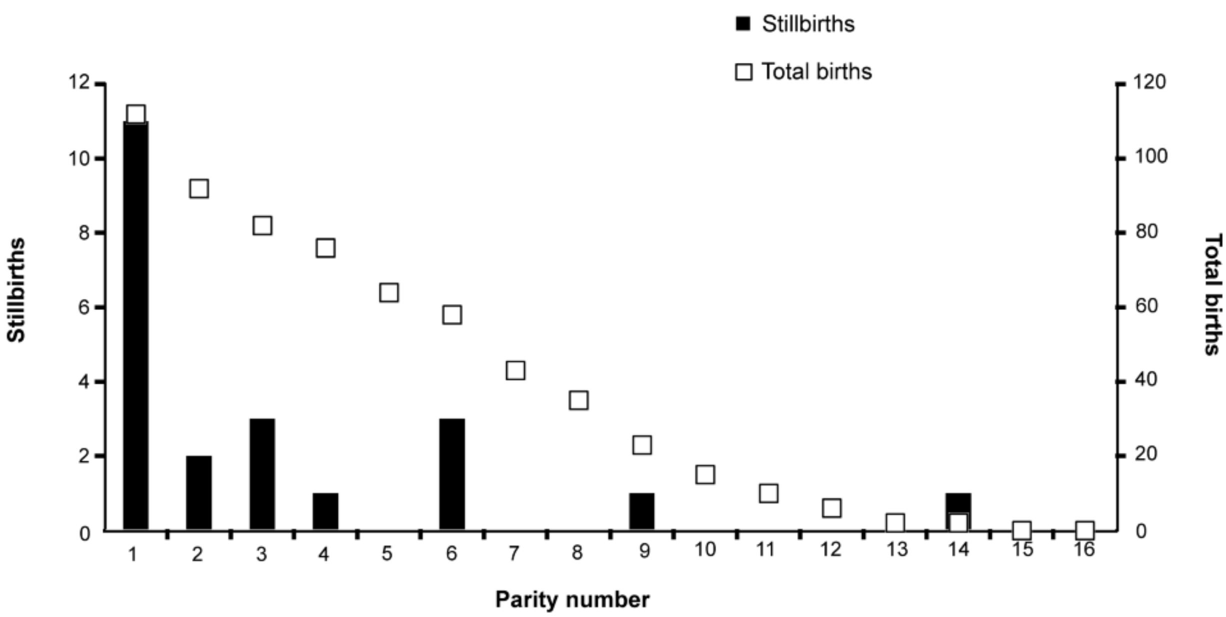
Of all births in the Cairngorm herd during this period, 311 were female calves, 295 were male calves, with 27 calves of unknown gender (born and died on free range before they could be checked) and one set of mixed gender twins. Of the 635 calves born to the herd (including perinatal losses), survival rate was 0.651 to weaning (six months) and 0.522 to

Figure 1



Distribution of individual births by maternal age and parity number at the time of calving. Maternal age/Parity data were not available for 14 births.

Figure 2



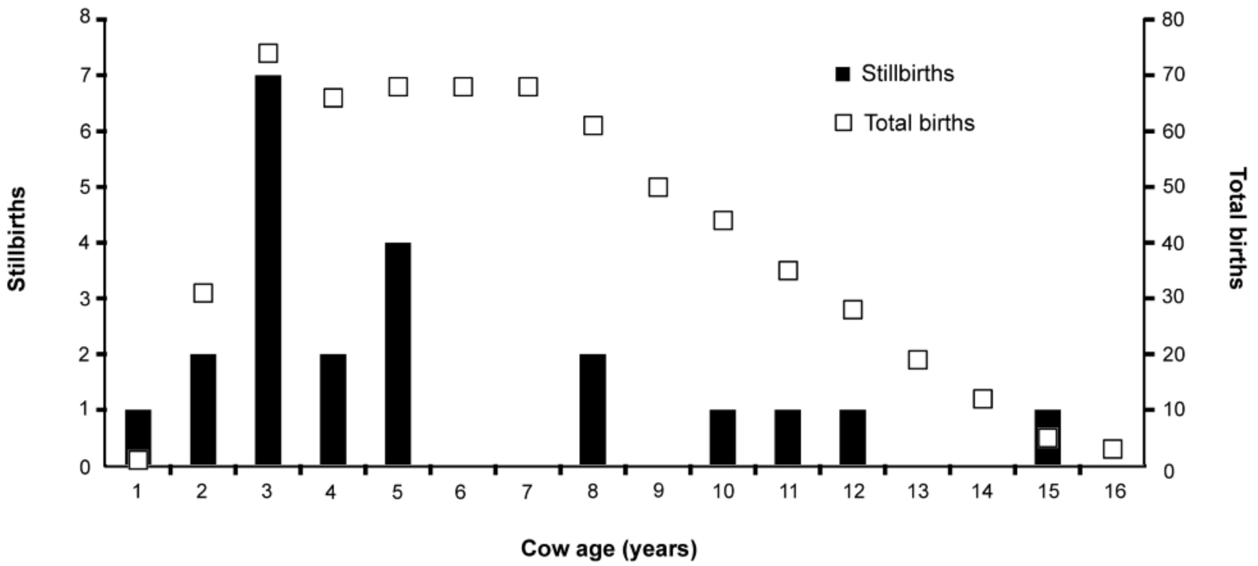
Total occurrence of perinatal loss (1993–2010) by parity number (1 = primiparous, etc).

the age of one year; post-natal survival (excluding stillbirths) was 0.681 to weaning and 0.546 to one year. Live-born female calves were slightly more likely than males to survive both to weaning (male survival = 0.671, female survival = 0.690) and to one year (male = 0.535, female = 0.556), though this difference was not statistically significant.

Twenty-three calves were lost in the perinatal period over the study period, of which eight (36.36%) were single male calves, three (13.63%) were single female calves, one (4.54%) was a set of mixed gender twins, and the remaining ten (45.45%) were calves of unknown gender (mothers showing physiological signs of very recent birth were found on the free range without calves). The highest incidence of perinatal loss (50%) occurred in first-time mothers (parity one; Figure 2) all of which were four years old or younger, most of which (seven of eleven) were three years old (Figure 3). Parity was significantly correlated with incidence of perinatal loss ($r = -0.59$; $P = 0.02$), as was maternal age at calving ($r = -0.52$; $P = 0.04$). Maternal age was not a significant factor within first-parity losses. Maternal age at first calving did not significantly affect future incidence of stillbirth.

https://doi.org/10.7120/09627286.24.2.173 Published online by Cambridge University Press

Figure 3



Total occurrence of perinatal losses (1993–2010) by maternal age.

Individual differences between cows in calf survival

Forty percent of mothers were associated with 77.2% of calf deaths prior to weaning and 72.4% of calf deaths up to one year of age. As it appeared that some cows were consistently very unsuccessful in raising calves we investigated whether there were statistically significant differences between cows in their ability to rear calves.

For all four models, it was found that there were highly significant differences between cows, indicating that cows differ significantly from each other in whether their calves survive (LRT test statistic [df = 1] for Total Calf Survival up to six months = 649.63 [$P < 0.001$], for Total Calf Survival up to one year = 515.21 [$P < 0.001$], Post-natal Calf Survival up to six months = 640.63 [$P < 0.001$], for Post-natal Calf Survival up to one year = 503.04 [$P < 0.001$]).

Trait impacts on calf survival

Total calf survival (denominator including perinatal losses) to six months (weaning)

Cow age at calving was found to be the only *maternal* trait which significantly affected calf survival to six months ($P = 0.018$; Table 1). Female success (measured as calf survival to weaning) peaked in adulthood (equation $0.426 \times \text{Age} – 0.026 \times (\text{Age})^2$, maximal calf survival in offspring of nine year old females: 0.816 mean survival), with lower levels of success in both very young (cows aged two years or less at calving: 0.571 mean calf survival to weaning) and very old individuals (cows aged 12 years or older: 0.585 mean calf survival to weaning).

Post-natal calf survival (denominator live calves born) to six months

When the model was run on Post-natal Calf Survival data, dam age was once again the only maternal trait found to significantly influence calf survival ($P = 0.039$; Table 2). This model indicated that reproductive success (rearing calves to six months) peaked during adulthood (equation $0.352 \times \text{Age} - 0.022 \times [\text{Age}]^2$, estimated peak at age eight).

Total calf survival (denominator including perinatal losses) to one year

Total Calf Survival to one year old was not significantly affected by any maternal model component in the full model, but the quadratic part of the effect of the age of the cow at calving was marginally significant ($P = 0.063$) (Table 3). After backward elimination however, removing confounding variables, both the linear and quadratic terms for Age at Calving were strongly significant ($P < 0.001$ and $P = 0.002$, respectively), with quadratic relationship $0.378 \times \text{Age} - 0.023 \times (\text{Age})^2$, with peak survival at age 8.2 years.

Post-natal calf survival (denominator live calves born) to one year

None of the maternal traits tested showed a significant effect on Post-natal Calf Survival to one year old (Table 4).

Annual survival rates

The differing conditions between years was the most significant, and most consistently significant, factor affecting calf survival in all models (Total Calf Survival model: six months — effect = –0.064, SE = 0.018; $P < 0.001$; one year — effect = –0.035, SE = 0.017; $P = 0.038$; Post-natal Calf Survival model: six months — effect = –0.074, SE = 0.019; $P < 0.001$; one year — effect = –0.035, SE = 0.017; $P = 0.038$). Although the differences between annual survival rates are quite high (Figure 4: maximum survival to weaning; 0.88 in 1994, minimum survival to weaning; 0.36 in 2001; maximum survival to one year old; 0.75 in 1994, minimum survival to one-year old; 0.19 in 2004), the consistently negative influence of year on survival in each of these models indicates a downward trend in mean calf survival rate for the Cairngorm herd in the years between 1993 and 2010.

Table 1 Total survival to six months. GLMM model of traits associated with total calf mortality. Since certain traits (age at calving, parity, date of parturition, and year) were fitted as variates/covariates, back-transformed means were not calculated; the effect on the linear predictor scale is reported for all categories. Significant effects in bold.

Model terms	df	Wald statistic	*P*-value
Age at calving (overall)	**2**	**7.98**	**0.018**
Age at calving (linear)	1	4.37	0.037
Age at calving (quadratic)	**1**	**6.77**	**0.009**
Date of parturition (overall)	2	1.50	0.472
Date of parturition (linear)	1	1.39	0.239
Date of parturition (quadratic)	1	1.48	0.224
Parity number (experience)	1	0.68	0.411
Sex of calf (M, F, M & F twins)	2	0.49	0.783
Previous calf alive at six months	1	2.68	0.102
Previous calf alive at one year	1	2.51	0.113
Sex of previous calf	1	2.07	0.150
Site of birth	4	4.84	0.304
Year	**1**	**15.70**	**< 0.001**

Minimal model	Effect	SE	df	Wald statistic	*P*-value
Constant	0.575	0.097			
Age at calving (linear)	0.426	0.116	1	13.38	**< 0.001**
Age at calving (quadratic)	–0.026	0.007	1	12.58	**< 0.001**
Year	–0.064	0.018	1	13.07	**< 0.001**

Discussion

That just 40% of females in the Cairngorm reindeer herd were associated with over 70% of calf deaths prior to weaning indicates that maternal quality and ability vary between individuals and that an investigation into the traits affecting these relative success rates is justified. In evolutionary terms there would clearly be strong selection pressure for maximising calf survival through losing genetic lines predisposed to higher than average rates of loss. While predation is reported specifically to be responsible for significant losses in some semi-domesticated systems (eg Norberg *et al* 2006; Nieminen *et al* 2011), from this study and numerous other reports of high early life mortality rates under semi-domestication (Bjärvall & Franzén 1981; Chetkiewicz & Renecker 1994; Nybakk *et al* 2002) it appears that some non-random effect (or positive selection pressure) is predisposing particular females to higher than average calf losses. However, in the present study, information was not available about the precise cause of death of calves across the recorded period; instead our focus was on maternal effects.

The highly significant differences between individual cows in their ability to rear calves suggest that certain cows are consistently unsuccessful, or consistently successful in rearing calves. The cause of this variation between cows could be genetic, environmental or both, though the current data set are limited in deriving specific causes of consistent losses or heritability of inconsistent and consistently poor reproductive success. Previous work has linked the reproductive success of female reindeer to measures of individual quality, such as higher mature physical size, condition, and ability to withstand the challenges of gestation/lactation, traits which have genetic links (Weladji *et al* 2008; Hamel *et al* 2009). As in other species (eg pigs [*Sus scrofa*]), genetic factors outside of maternal physical quality are likely to influence other pertinent traits such maternal behaviour and early life mortality (Baxter *et al* 2011). Further research is needed to understand the impact of these potentially heritable behavioural and reproductive traits and the interaction of these traits with measures of individual quality, but there is potential to include these traits when considering culling or reproductive decisions. Since age at calving was the only maternal trait to achieve significance in any of the present models, it is unsurprising that this trait influenced the survival of calves to weaning age (six months) and confirms previous reports (Eloranta & Nieminen 1986; Weladji *et al* 2006, 2008). Maternal age at parturition is often linked to other factors, such as high individual quality (Gaillard *et al* 2000; Hamel *et al* 2009), elements of high physical condition and increased knowledge of local resources (Ortegareyes & Provenza 1993), increased social rank, increased experience in

Table 2 **Post-natal survival to six months. GLMM Model of traits associated with post-natal calf mortality. Significant effect in bold.**

Model terms	df	Wald statistic	*P*-value
Age at calving (overall)	**2**	**6.50**	**0.039**
Age at calving (linear)	1	2.31	0.128
Age at calving (quadratic)	**1**	**4.23**	**0.040**
Date of parturition (overall)	2	1.81	0.404
Date of parturition (linear)	1	2.02	0.155
Date of parturition (quadratic)	1	2.14	0.144
Parity number (experience)	1	0.79	0.373
Sex of calf (M, F)	1	0.61	0.436
Previous calf alive at six months	1	2.14	0.143
Previous calf alive at one year	1	2.23	0.135
Sex of previous calf	1	1.56	0.212
Site of birth	3	4.57	0.206
Year	**1**	**14.95**	**< 0.001**

Minimal model	Effect	SE	df	Wald statistic	*P*-value
Constant	0.677	0.101			
Age at calving (linear)	0.352	0.123	1	8.24	**0.004**
Age at calving (quadratic)	–0.022	0.008	1	8.26	**0.004**
Year	–0.074	0.019	1	15.33	**< 0.001**

Table 3 **Total survival to one year. GLMM model of traits associated with calf mortality. Significant effect in bold. Marginally significant effect in italics.**

Model terms	df	Wald statistic	*P*-value
Age at calving (overall)	2	3.97	0.138
Age at calving (linear)	1	1.53	0.216
Age at calving (quadratic)	*1*	*3.45*	*0.063*
Date of parturition (overall)	2	0.49	0.782
Date of parturition (linear)	1	1.01	0.315
Date of parturition (quadratic)	1	0.90	0.344
Parity number (experience)	1	0.98	0.323
Sex of calf (M, F, M & F twins)	2	0.34	0.844
Previous calf alive at six months	1	1.69	0.193
Previous calf alive at one year	1	1.50	0.221
Sex of previous calf	1	2.27	0.132
Site of birth	4	6.36	0.174
Year	**1**	**6.16**	**0.013**

Minimal model	Effect	SE	df	Wald statistic	*P*-value
Constant	0.067	0.092			
Age at calving (linear)	0.378	0.114	1	11.04	**< 0.001**
Age at calving (quadratic)	–0.023	0.007	1	9.99	**0.002**
Year	–0.035	0.017	1	4.29	**0.038**

Table 4 Post-natal survival to one year. GLMM model of traits associated with calf mortality. Significant effect in bold.

Model terms	df	Wald statistic	*P*-value
Age at calving (overall)	2	3.90	0.143
Age at calving (linear)	1	0.56	0.455
Age at calving (quadratic)	1	1.89	0.169
Date of parturition (overall)	2	0.51	0.774
Date of parturition (linear)	1	1.46	0.227
Date of parturition (quadratic)	1	1.33	0.249
Parity number (experience)	1	1.06	0.304
Sex of calf (M, F)	1	0.46	0.497
Previous calf alive at six months	1	1.46	0.227
Previous calf alive at one year	1	1.37	0.221
Sex of previous calf	1	1.84	0.175
Site of birth	3	5.23	0.156
Year	**1**	**5.61**	**0.018**

Minimal model	Effect	SE	df	Wald statistic	*P*-value
Constant	0.142	0.090			
Year	–0.041	0.016	1	6.10	**0.014**

maternal care, or an improved ability to minimise calf-mortality risks, all of which may enable long-lived females to be more successful in raising offspring. Longer lived cows are more successful in each individual reproduction event than their shorter lived counterparts (Weladji *et al* 2006). The reduction of success in older animals may be due to reproductive senescence, a progressive loss of function and reproductive performance in old age, or loss of body condition and competitive edge in resource acquisition which increases the relative cost of reproduction as reindeer cows reach their post-prime years (Weladji *et al* 2002).

Low birth weight significantly increases the likelihood of calf mortality (Eloranta & Nieminen 1986) and larger females (physical size and quality peaks within the range of 3–11 years), produce larger, more vital calves (Rognmo *et al* 1983). Both female body mass and age are related to social rank within the herd (Kojola 1989; Holand *et al* 2004). Higher social rank allows greater access to resources year-round, but is particularly important during the winter months when craters (feeding sites) are the most contested resource in the herd (Kojola 1989). High-ranking females are better able to defend these resources and retain access to important food sources through the winter (Holand *et al* 2004). While pre-weaning mortality is not dependent upon female social rank, this rank does significantly affect both early pre-weaning calf growth and the body mass and condition of calves at weaning (Holand *et al* 2004) which, in turn, affect survival over the winter season (Reimers 1982).

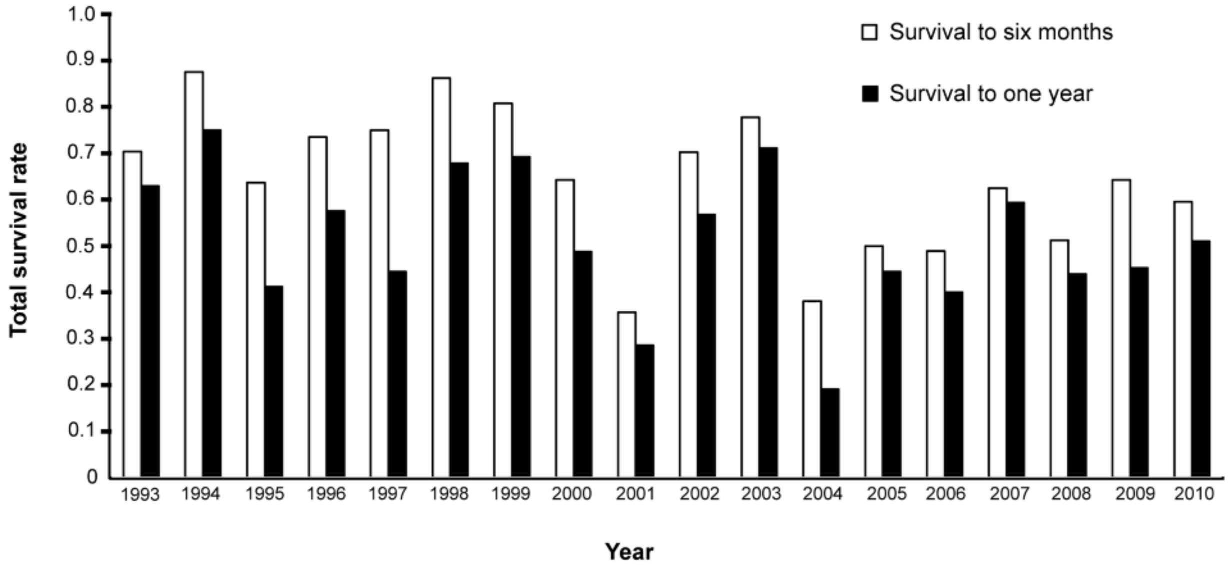
The absence of an effect of maternal age on calf survival to one year indicates a decrease in reliance on the dam following weaning in the Cairngorm herd. This may be due to a lack of competition for overwinter resources and could be partially attributable to availability of emergency feeding provided during winter months. While a wild calf would be more heavily dependent on the nutrient stores laid down from nursing during the summer months, the importance of such factors is substantially reduced for Cairngorm calves by supplementary feeding. In addition, supporting calves from family lines with a history of calf losses will tend to retain this trait in the genetic pool for the herd.

Age at calving has an effect both on the delivery of a healthy calf and on its subsequent survival. Perinatal losses represent a small fraction of total losses in the Cairngorm herd (3.6% of total births), but this factor is related to both cow age and parity, with young females experiencing the highest incidence. The rate of loss in females under three years old was 9.1%, with females between 3–11 years losing 3.1% and females 12 and older losing 3%. These rates are comparable to those seen in the herd at the Finland Reindeer Research Station at Kaamanen with stillbirths at 18.8% in cows under three years old and 3.8% in cows aged three years or more (Eloranta & Nieminen 1986).

In previous work considering the effects of maternal traits on reindeer calf survival (Weladji *et al* 2006, 2008), age and experience have been treated as synonymous terms yet it may be inappropriate to treat age and experience as a single term unless all females represented in the data set give birth every year. While experience was highly correlated with age in the present data set, it was not sufficiently so that the two could be readily substituted for one another. That experi-

https://doi.org/10.7120/09627286.24.2.173 Published online by Cambridge University Press

Figure 4



Annual total survival rates (including perinatal loss) for calves of the Cairngorm reindeer herd from 1993–2010.

ence, independent of age, was not significant as a factor in calf survival in the present study indicates that it is likely not mothering 'practice' that makes older females more successful mothers, but that physical quality and social implications that come with age might be more important.

Reproduction costs of gestation/lactation impact negatively on future reproduction (Rönnegard *et al* 2002), future growth and body condition (Gerhart *et al* 1997), and even future survival (Clutton-Brock *et al* 1996). Thus, high reproductive effort may prevent a female from recovering sufficient body condition to reproduce in a given year.

Though they are managed in a similar manner to the reindeer at Kaamanen (ie supplemental feeding is potentially available during harsh weather to support pregnancy) (Weladji *et al* 2008) the effects of reproductive costs in the Cairngorm herd were not clear. Indeed, the effect of success or failure in raising the previous year's calf to weaning in this study was found to be only marginally significant and, as such, does not definitively demonstrate an influence.

While maternal age was significant for calves up to six months of age, it is evident that the influence of this trait wanes as calves pass beyond weaning. Recognising that young animals are more susceptible to starvation in the winter months (Skogland 1985), management of herds with high proportions of overwintering calves should be adjusted to provide nutritional support to the younger animals as they develop full self-sufficiency. Neither the sex of the current calf, nor that of the previous calf, showed a significant effect on mortality rates in the Cairngorm herd. The costs of raising a male calf are higher than those required to raise a female (mothers with male calves display a greater weight loss between conceptions than their female-bearing counterparts [Kojola & Eloranta 1990]). Despite these effects, the findings of this study support previous work (Kojola & Eloranta 1990) which shows that the difference in resource requirement does not affect the frequency of reproductive failure.

In the Cairngorm herd, the most significant and consistent determinant of calf mortality rates was variation in conditions between years. Since local resource availability and herd husbandry procedures are consistent across years it is likely that climate/weather conditions and disease have the greatest effect on post-natal mortality. In 1997, managers of the Cairngorm herd noted the first cases of babesiosis — a tick-borne disease which is often fatal in reindeer (Nilsson *et al* 1965). The prevalence of babesiosis in the herd trends towards a moderately positive relationship with year ($r = 0.41$; $P = 0.06$), indicating that the problem may be increasing over time. While a longer data set is needed to determine the true impacts of babesiosis on the herd, managers perceive it to be increasingly problematic. The underlying causes of a potentially increased disease load are unclear in this situation, but it has been shown elsewhere that warmer years in Arctic and Subarctic regions, beginning in 1997, are introducing conditions which favour the expansion of bacterial, parasitic, and insect-borne diseases (Bradley *et al* 2005). Insect irritation is also a source of disturbance stress to reindeer calves (Helle & Tarvainen 1984). Adequately addressing the details of environmental factors (climate, weather, insect, and pathogen load) and their impacts on calf survival falls outside the scope of this paper, but the variation detected in survival between years merits a follow-up study investigating the impact on calf survival of yearly differences in climate, weather patterns, and the relationship between these factors and disease. Disturbance due to tourism may also be a factor. Sibbald *et al* (2011) showed that red deer were disturbed by walkers and may have altered their diet composition, even if walkers remained on defined tracks and Colman *et al* (2012) reported how readily reindeer were disturbed by snow-kiters and skiers, with potentially very negative population consequences.

In all reindeer herds, the vulnerability of calves to death by disease, exposure and predation make young animals a primary focus of welfare and production research with relatively little attention paid to the welfare of adult animals which die in similar circumstances. Since at least one-fifth of the adult animals in the Cairngorm herd are humanely euthanised at the end of life, there is a net welfare gain in the herd related to calf survival, though this could be enhanced through wider application of humane killing methods. Other meat- and hide-producing reindeer systems humanely slaughter significantly larger proportions of adult animals before they die naturally (Thompson Hobbs *et al* 2012), with the majority harvested by 18 months and an increasing proportion in the first autumn (Kojola & Helle 1993). It is in these herds, where harvest of relatively young animals reduces the likelihood of non-harvest deaths, that the current research has the most potential to improve animal welfare.

Animal welfare implications

When compared to traditionally farmed domestic species, modern reindeer production systems lose a relatively high proportion of offspring each year between birth and weaning. As this post-natal mortality causes significant economic loss and negatively impacts animal welfare, the potential gains from improving survival rates are considerable. By identifying animal traits which affect (and do not affect) calf mortality rates, the current paper can be used to direct the development of animal management techniques which minimise these losses and improve animal welfare.

Conclusion

Since reindeer are raised in highly extensive systems, attempts to manage environmental influences are likely to be economically taxing, politically challenging, and logistically complex, but improving maternal quality represents an alternative approach which may improve calf survival. With respect to maternal traits, there is sufficient variation in maternal quality and success within female reindeer to justify a deeper investigation. From our study, it appears that the identity and age of the mother are the maternal traits which most influence calf survival, and that maternal influence falls after weaning. Clearly, maternal predisposition to calf loss is an important factor. More work is warranted to identify specific causes of mortality and separate which aspects of maternal identity and age affect calf survival, be it social rank, resource access, improved maternal behaviour, or simply better physical condition.

In addition, we have demonstrated that cows show significant individual differences in rearing ability. As certain females are responsible for large proportions of calf losses, identifying and culling individual cows with consistently poor reproductive output would reduce herd-level calf losses. A deeper understanding of which traits affect reproductive consistency — and potentially heritability of this consistency — would be helpful in further refining the use of this information in management decisions.

Finally, this study demonstrates that the age of cows used for breeding affects perinatal loss rates and calf survival and can be used as a tool for guiding the breeding management of reindeer herds — age is a simpler and less time-consuming characteristic to identify than body condition or behavioural traits, and using age as a guide would enable herd managers to prevent females within high-risk groups (ie very young and old animals) from expending considerable energy in reproduction and nursing only to have the calf die before it reaches adulthood. Low calf survival rates are among the most significant problems facing reindeer production systems around the world — incorporation of these findings into current management systems could dramatically reduce economic losses and welfare issues associated with post-natal mortality.

Acknowledgements

Sincerest thanks to Tilly and Alan Smith (Reindeer Company Ltd), and to their staff, for their incredible flexibility, hospitality, and of course for access to the Cairngorm Reindeer Herd and herd records over the course of this research. Thanks to Dr Sue Mitchell for her statistical advice during project development and to Dr Stewart Rhind for his comments of an earlier draft of the manuscript. The James Hutton Institute and Biomathematics and Statistics Scotland receive support from the Scottish Government Rural and Environment Science and Analytical Services Division.

References

Baxter EM, Jarvis S, Sherwood L, Farish M, Roehe R, Lawrence AB and Edwards SA 2011 Genetic and environmental effects on piglet survival and maternal behaviour of the farrowing sow. *Applied Animal Behavior Science 130*: 28-41. http://dx.doi.org/10.1016/j.applanim.2010.11.020

Binns SH, Cox IJ, Rizvi S and Green LE 2002 Risk factors for lamb mortality on UK sheep farms. *Preventative Veterinary Medicine 52*: 287-303. http://dx.doi.org/10.1016/S0167-5877(01)00255-0

Bjärvall A and Franzén R 1981 Mortality transmitters: an important tool for studying reindeer calf mortality. *Ambio 10(1)*: 26-28

Bradley MJ, Kutz SJ, Jenkins E and O'Hara TM 2005 The potential impact of climate change on infectious diseases of Arctic fauna. *International Journal of Circumpolar Health 64(5)*: 468-477. http://dx.doi.org/10.3402/ijch.v64i5.18028

Chetkiewicz CLB and Renecker LA 1994 Reindeer calf productivity and survival on the Seward Peninsula, Alaska. *University of Alaska Fairbanks (AFES) Circular 100*: 1-8

Clutton-Brock TH, Stevenson IR, Marrow P, MacColl AD, Houston AL and McNamara JM 1996 Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *Journal of Animal Ecology 65*: 675-689. http://dx.doi.org/ 10.2307/5667

Colman JE, Lilleeng MS, Tsegaye D, Vigeland MD and Reimers E 2012 Responses of wild reindeer (*Rangifer tarandus tarandus*) when provoked by a snow-kiter or skier: A model approach. *Applied Animal Behaviour Science 142*: 82-89. http://dx.doi.org/10.1016/j.applanim.2012.08.009

Cundiff LV, Gregory KE and Koch RM 1982 Selection for increased survival from birth to weaning. *Proceedings of 2nd World Congress on Genetics Applied To Livestock Production* pp 310. 4-8 October 1982, Madrid, Spain

Eales FA, Small J and Gilmour JS 1983 Neonatal mortality of lambs and its causes. In: Haresign W (ed) *Sheep Production* pp 289-298. Butterworths: London, UK

Eloranta E and Nieminen M 1986 The effects of maternal age and body weight on reindeer calf birth-weight and survival. *Rangifer 6(1)*: 105. http://dx.doi.org/10.7557/2.6.1-App.623

Espmark Y 1971 Mother-young relationship and ontogeny of behaviour in reindeer (*Rangifer tarandus* L). *Zeitschrift für Tierpsychologie 29*: 42-81. http://dx.doi.org/10.1111/j.1439-0310.1971.tb01723.x

Everett-Hincks JM and Dodds KG 2008 Management of maternal-offspring behavior to improve lamb survival in easy care sheep systems. *Journal of Animal Science 86(14)*: 259-270. http://dx.doi.org/10.2527/jas.2007-0503

Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A and Toïgo C 2000 Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics 31*: 367-393. http://dx.doi.org/10.1146/annurev.ecolsys.31.1.367

Gerhart KL, Russel DE, van de Wetering D, White RG and Cameron RG 1997 Pregnancy of adult caribou (*Rangifer tarandus*): Evidence for lactational infertility. *Journal of Zoology 242*: 17-30. http://dx.doi.org/10.1111/j.1469-7998.1997.tb02926.x

Gilbert OL 1974 Reindeer grazing in Britain. *Lichenologist 6*: 165-167. http://dx.doi.org/10.1017/S0024282974000272

Guinness FE, Clutton-Brock TH and Albon SD 1978 Factors affecting calf mortality in red deer (*Cervus elaphus*). *Journal of Animal Ecology 47(3)*: 817-832. http://dx.doi.org/10.2307/3673

Hamel S, Gaillard JM, Festa-Bianchet M and Côté SD 2009 Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology 90(7)*: 1987-1995. http://dx.doi.org/10.1890/08-0596.1

Helle T and Tarvainen L 1984 Effects of insect harassment on weight gain and survival in reindeer calves. *Rangifer 4(1)*: 24-27. http://dx.doi.org/10.7557/2.4.1.488

Holand Ø, Gjøstein H, Losvar A, Kumpula J, Smith ME, Røed KH, Nieminen M and Weladji RB 2004 Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *Journal of Zoology 263*: 365-372. http://dx.doi.org/10.1017/S0952836904005382

Kojola I 1989 Mother's dominance status and differential investment in reindeer calves. *Animal Behaviour 38*: 177-185. http://dx.doi.org/10.1016/S0003-3472(89)80080-6

Kojola I and Eloranta E 1990 Reproductive investment by females in semi-domesticated reindeer. *Rangifer Special Issue 3*: 343-349. http://dx.doi.org/10.7557/2.10.3.877

Kojola I and Helle T 1993 Calf harvest and reproductive rate of reindeer in Finland. *The Journal of Wildlife Management 57(3)*: 451-453. http://dx.doi.org/10.2307/3809269

Kumpula J and Colpaert A 2003 Effects of weather and snow conditions on reproduction and survival of semi-domesticated reindeer (*R.t. tarandus*). *Polar Research 22(2)*: 225-233. http://dx.doi.org/10.1111/j.1751-8369.2003.tb00109.x

Mellor DJ and Stafford KJ 2004 Animal welfare implications of neonatal mortality and morbidity in farm animals. *The Veterinary Journal 168*: 118-133. http://dx.doi.org/10.1016/j.tvjl.2003.08.004

Nieminen M 2010 The impact of large carnivores on the mortality of semi-domesticated reindeer (*Rangifer tarandus tarandus* L) calves in Kainuu, southeastern reindeer herding region of Finland. *Rangifer 30(1)*: 79-88. http://dx.doi.org/10.7557/2.30.1.1218

Nieminen M, Norberg H and Maijala V 2011 Mortality and survival of semi-domesticated reindeer (*Rangifer tarandus tarandus* L) calves in northern Finland. *Rangifer 31(1)*: 71-84. http://dx.doi.org/10.7557/2.31.1.2029

Nilsson O, Nordkvist M and Rydén L 1965 Experimental *Babesia divergens* infection in reindeer (*Rangifer tarandus*). *Acta Veterenaria Scandanavica 6(4)*: 353-359

Norberg H, Kojola I, Aikio P and Nylund M 2006 Predation by golden eagle *Aquila chrysaetos* on semi-domesticated reindeer *Rangifer tarandus* calves in northeastern Finnish Lapland. *Wildlife Biology 12(4)*: 393-402. http://dx.doi.org/10.2981/0909-6396(2006)12[393:PBGEAC]2.0.CO;2

Nybakk K, Kjelvik O, Kvam T, Overskaug K and Sunde P 2002 Mortality of semi-domestic reindeer *Rangifer tarandus* in central Norway. *Wildlife Biology 8*: 63-68

Ortegareyes L and Provenza FD 1993 The amount of experience and age affect the development of foraging skills of goats browsing blackbrush (*Coleogyne ramosissima*). *Journal of Animal Science 71*: 380-383

Reimers E 1982 Winter mortality and population trends of reindeer on Svalbard, Norway. *Arctic and Alpine Research 14(4)*: 295-300. http://dx.doi.org/10.2307/1550792

Reynolds WL, DeRouen TM, Moin S and Koonce KL 1980 Factors influencing gestation length, birth weight and calf survival of Angus, zebu and zebu cross beef cattle. *Journal of Animal Science 51(4)*: 860-867

Rognmo A, Markussen KA, Jacobsen E, Grav HJ and Blix AS 1983 Effects of improved nutrition in pregnant reindeer on milk quality, calf birth-weight, growth and mortality. *Rangifer 3(2)*: 10-18. http://dx.doi.org/10.7557/2.3.2.476

Rönnegard L, Forslund P and Danell Ö 2002 Lifetime patterns in adult female mass, reproduction, and offspring mass in semidomestic reindeer (*Rangifer tarandus tarandus*). *Canadian Journal of Zoology 80*: 2047-2055. http://dx.doi.org/10.1139/z02-192

Rönnegard L, Woolliams JA and Danell Ö 2003 Breeding schemes in reindeer husbandry. *Rangifer 23(2)*: 45-55. http://dx.doi.org/10.7557/2.23.2.360

Ropstad E 2000 Reproduction in female reindeer. *Animal Reproduction Science 60-61*: 561-570. http://dx.doi.org/10.1016/S0378-4320(00)00100-7

Sibbald AM, Hooper RJ, McLeod JE and Gordon IJ 2011 Responses of red deer (*Cervus elaphus*) to regular disturbance by hill walkers. *European Journal of Wildlife Research 57*: 817-825. http://dx.doi.org/10.1007/s10344-011-0493-2

Skogland T 1985 The effects of density-dependent resource limitations on the demography of wild reindeer. *Journal of Animal Ecology* 54: 359-374. http://dx.doi.org/10.2307/4484

Thompson Hobbs N, Andrén H, Persson J, Aronsson M, and Chapron G 2012 Native predators reduce harvest of reindeer by Sámi pastoralists. *Ecological Applications 22(5)*: 1640-1654. http://dx.doi.org/10.1890/11-1309.1

VSN International 2011 *GenStat for Windows, 14th Edition*. VSN International: Hemel Hempstead, UK

Weladji RB, Gaillard JM, Yoccoz NG, Holand Ø, Mysterud A, Loison A, Nieminen M and Stenseth NC 2006 Good reindeer mothers live longer and become better in raising offspring. *Proceedings of the Royal Society of Biological Sciences 273*: 1239-1244. http://dx.doi.org/10.1098/rspb.2005.3393

Weladji RB, Loison A, Gaillard JM, Holand Ø, Mysterud A, Yoccoz NG, Nieminen M and Stenseth NC 2008 Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia 156*: 237-247. http://dx.doi.org/10.1007/s00442-008-0961-x

Weladji RB, Mysterud A, Holand Ø and Lenvik D 2002 Age-related reproductive effort in reindeer (*Rangifer tarandus*): Evidence of senescence. *Oecologia 131*: 79-82. http://dx.doi.org/10.1007/s00442-001-0864-6