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Authors: Flydal, Kjetil, and Reimers, Eigil

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Kjetil Flydal & Eigil Reimers

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Time of calving in reindeer *Rangifer tarandus* varies between populations, but takes place around the start of the green season to ensure a stable food supply for doe and calf. Causes of variation in calving time was investigated by studying the three adjacent populations of North Ottadalen, South Ottadalen and Snøhetta, in Norway. The peak calving time was 12-14 May during 1996-1998 in North Ottadalen, 10 May in 1997 and 11 May in 1998 in South Ottadalen, and 22-26 May during 1996-1998 in Snøhetta. Comparing these results with recordings from 1969-1972, 1978 and 1985, peak calving time has been delayed by 6-8 days in North Ottadalen, and has advanced by 2-6 days in Snøhetta. In South Ottadalen, the peak calving time has remained almost constant. Analyses of covariance showed that calving time was negatively related to autumn dressed weight ($P < 0.05$), but not to mandible length ($P = 0.15$), and that calving happened later in Snøhetta than in North Ottadalen for the same level of autumn dressed weight ($P < 0.05$; 11.5 days) and mandible length ($P < 0.05$; 14 days). These results strengthen the hypothesis that delayed conception and calving is a consequence of relatively poor doe condition in autumn.

Key words: calving, oestrus, pasture, physical condition, Rangifer tarandus, reindeer, snow depth

Kjetil Flydal & Eigil Reimers, University of Oslo, Department of Biology, Division of General Physiology, P.O.Box 1051, Blindern, 0316 Oslo, Norway - e-mail addresses: kjetil.flydal@bio.uio.no (Kjetil Flydal); eigil.reimers@bio.uio.no (Eigil Reimers)

Corresponding author: Kjetil Flydal

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Peak calving time, i.e. the day when 50% of the pregnant does in a population have given birth, has been found to vary between 6 and 27 May in the various populations of wild reindeer *Rangifer tarandus tarandus* in Norway (Holthe 1975, Reimers 1983a, Reimers 1997, Skogland 1984). Reimers (1983a,b) suggested that female reindeer do not ovulate until they have reached a certain body mass or body composition in autumn. Differences among populations in time of calving may be influenced by different pre-rut body weights and body compositions (Reimers 1983a, Lenvik 1988), different pasture availability during winter influencing the length of gestation (Bergerud 1975), different sex ratios, with large bucks initiating earlier ovulation (Holthe 1975, Verme, Ozoga & Nellist 1986), or genetically fixed adaptations to different start dates of the growing season (Skogland 1989). We examined the above-mentioned hypotheses by comparing three populations in southern Norway: North Ottadalen, South Ottadalen and Snøhetta, for five specific periods covering 28 years.

North Ottadalen (2,700 km^2), South Ottadalen (1,500 km^2) and Snøhetta (3,295 km^2) are adjacent geographical areas located at 61°30-62°35N, 7°15-9°30E in southern Norway. Habitat types and climate are similar in the three areas, with alpine terrain at altitudes of 1,000-1,500 m a.s.l. Wild reindeer populations in the three areas are controlled by hunting. In North Ottadalen, and especially in Snøhetta, the population densities have varied greatly due to varying management policies (Fig. 1). High densities in the 1960s caused severely overgrazed winter pastures in Snøhetta (Gaare 1968), resulting in small reindeer with low body mass (Reimers 1968). Concurrently, the small but growing reindeer population in North Ottadalen (Reimers 1972) enjoyed good pastures and had high body weights. During the last 25 years, the situation was reversed; body weights and winter pasture for the Snøhetta reindeer had improved (Strand, Jordhøy & Holmstrøm 1996), whereas they had deteriorated in North Ottadalen (Reimers & Sørumgård 1995). In South Ottadalen, the population has remained at 300-400 animals, with no apparent changes in pasture quality or physical condition for the last 30 years (K. Granum, pers. comm.).

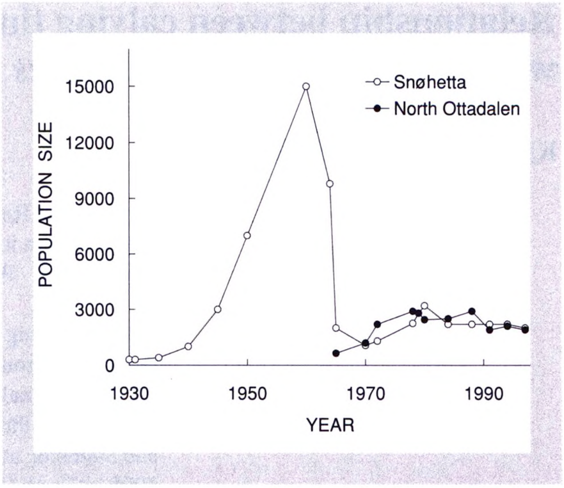

Figure 1. Approximate number of reindeer during winter in Snøhetta and North Ottadalen from 1930 until 1997. The wild reindeer population in North Ottadalen was established in 1964 (Reimers 1972). The curves are based on data from Hansen (1987), Jordhøy (1994), Jordhøy, Strand, Skogland, Gaare & Holmstrøm (1996), Hageland (1987), Heitkøtter (1981), Reimers (1968), Reimers & Sørumgård (1995), and K. Granum (unpubl. data).

Methods

Calving time in the three herds was determined for the following years: 1969-1972 (Holthe 1975), 1978, 1985, and 1996-1998. Calving data were acquired by calculating the cumulative proportion of births in consecutive days by counting 'does that have given birth' and 'pregnant does'. Two methods were tested:

1. The doe was classified as a 'doe that had given birth' if she had a calf in her vicinity, and as a 'pregnant doe' if she had antlers and no calf. Factors that bias such estimates are calf mortality in the first hours/days after birth, barren does with antlers, and pregnant does without antlers.
2. The newborn/female ratio for a day at the end of a calving season was used as an estimate for the proportion of breeding females (Caughley & Caughley 1974). For each counting day the total number of females was multiplied by this proportion to give the number of breeding females. The cumulative proportion of births was newborns/breeding females. Calf mortality causes bias in this method as the proportion of dead calves increases with time.

We compared the two methods mathematically, using estimated proportions of barren does with antlers and pregnant does without antlers at the start of the calving season (Espmark 1971), and calf mortality during the calving season (Aarthun Ims 1996). We found method 1 to be less biased, and thus only used method 1 in this study. Holthe (1975) used the same sampling method when estimating calving time for the years 1969-1972 in North Ottadalen, South Ottadalen and Snøhetta.

For 1996, 1997 and 1998, we used probit analysis with a significance level of 0.05 when estimating the calv-

Table 1. Mean reindeer calving time (Julian date) for the three Norwegian study populations, with 95% confidence intervals given in parentheses. Data are from the present study and Holthe (1976)[a] and E. Reimers (unpubl. data)[b].

Population	Year	Calving time	N
North Ottadalen	1969	126[a]	2640
North Ottadalen	1970	125[a]	2360
North Ottadalen	1971	126[a]	1370
North Ottadalen	1972	126[a]	1330
North Ottadalen	1978	132 - 134[b]	478
North Ottadalen	1985	129 - 131[b]	202
North Ottadalen	1996	132.0 (130.9, 132.6)	1061
North Ottadalen	1997	131.9 (131.1, 134.7)	2153
North Ottadalen	1998	134.2 (133.6, 134.8)	909
South Ottadalen	1971	132[a]	125
South Ottadalen	1972	132[a]	70
South Ottadalen	1997	129 - 131	236
South Ottadalen	1998	131.2 (128.7, 131.9)	458
Snøhetta	1969	149[a]	1325
Snøhetta	1970	148[a]	536
Snøhetta	1971	147[a]	181
Snøhetta	1996	142.3 (141.9, 142.9)	930
Snøhetta	1997	145.9 (145.1, 146.8)	601
Snøhetta	1998	143.2 (142.5, 144.1)	177

Table 2. Mean snow depth (in cm) in the period 1 March - 15 May for the three Norwegian study areas during the years 1969-1972, 1978, 1985 and 1996-1998. The first column (Mean) shows the overall mean for the period 1967-1999. Data are from the Norwegian Meteorological Institute's observational stations in Lesjaskog (North Ottadalen), Grov (South Ottadalen) and Ångårdsvatnet (Snøhetta).

		Year								
Study areas	Mean	1969	1970	1971	1972	1978	1985	1996	1997	1998
North Ottadalen	53.2	41.2	92.3	55.8	63.7	52.8	57.7	66.4	89.4	57.8
South Ottadalen	50.9			72.9	79.9				53.8	43.5
Snøhetta	70.1	62.4	130.4	56.5				89.1	133.4	84.7

ing time from cumulative birth proportions (Finney 1971, SAS 6.11). For 1978, 1985 and South Ottadalen 1997, the calving time was estimated qualitatively based on confidence intervals for the cumulative birth proportions because the number of counting days were too low to do a probit analysis.

The physical condition in autumn was measured as dressed weight and mandible length for does ≥2 years old (Reimers 1968). Physical condition estimates with 95% confidence intervals are given for the years preceding the years for which estimates of calving time exist. Data are lacking for some years. The relationship between calving time and autumn dressed weight, and calving time and autumn mandible length was calculated by analyses of covariance with two groups, North Ottadalen and Snøhetta, and a significance level of 0.05 (S-PLUS 2000). South Ottadalen was not included in the analyses due to low sample size.

Snow depths during late winter (1 March - 15 May) were registered at meteorological stations in Lesjaskog (North Ottadalen), Ångårdsvatnet (Snøhetta), and Grov (South Ottadalen), located in valleys adjacent to the reindeer areas. We tested for correlations between snow depth and time of calving in the different populations.

Results

In the period from 1970 until 1996-1998, the estimated calving time had been delayed by about six days in North Ottadalen, had advanced by about four days in Snøhetta, and had remained almost unchanged in South Ottadalen (Table 1). The changes in Snøhetta and North Ottadalen are probably significant, but unfortunately, Holthe's (1975) data were not available for treatment. Calving time in Snøhetta was significantly later than in North Ottadalen and South Ottadalen for all testable years. In 1998, calving time in North Ottadalen was significantly later than in South Ottadalen, reversing the situation in 1970. In Snøhetta, calving time was significantly later in 1997 than in 1996 and 1998. This coincided with large amounts of snow during late winter 1997 in Snøhetta (Table 2).

From around 1970 until 1995-1997, dressed weights and mandible lengths for does ≥2 years old increased significantly in Snøhetta by 2.6-2.9 kg and 4.4-8.0 mm, respectively, decreased significantly in North Ottadalen by 7.9-8.4 kg and 1.8 mm, respectively, and decreased in South Ottadalen by 2.6-4.9 kg (Table 3). For the years 1995-1997, only small differences in body weight among the populations was recorded (see Table 3).

Analysis of covariance showed a significant negative

Table 3. Mean reindeer autumn dressed weight and mandible length for the three Norwegian study population with 95% confidence intervals for does ≥2 years old. Data are from E. Reimers (unpubl. data)[a], K. Granum (unpubl. data)[b], Jordhøy et al. (1996)[c] and P. Jordhøy (unpubl. data)[d].

Population	Year	Dressed weight (kg)	N	Mandible length (mm)	N
North Ottadalen	1968	44.4 ± 2.5[a]	20	245.1 ± 4.0[a]	18
North Ottadalen	1969	40.1 ± 3.1[a]	11	239.5 ± 6.7[a]	10
North Ottadalen	1970	46.6 ± 10.8[a]	6	245 ± 7.1[a]	7
North Ottadalen	1971	44.7 ± 1.6[a]	68	244.9 ± 2.5[a]	63
North Ottadalen	1977	37.4 ± 0.5[a]	490	239.7 ± 0.7[a]	429
North Ottadalen	1995	35.6 ± 0.8[b]	120	242.7 ± 1.2[b]	114
North Ottadalen	1996	35.7[b]	61		
North Ottadalen	1997	36.1[b]	163		
South Ottadalen	1971	40.9 ± 2.9[a]	28	239.5 ± 3.7[a]	21
South Ottadalen	1996	38.3[b]	42		
South Ottadalen	1997	36.0[b]	65		
Snøhetta	1969	31.9 ± 1.8[a]	37	232.1 ± 1.8[a]	73
Snøhetta	1970	33.1 ± 2.6[a]	22	231.5 ± 2.8[a]	29
Snøhetta	1995	34.9 ± 0.9[c]	79	236.4 ± 1.1[c]	144
Snøhetta	1996	35.2 ± 1.2[d]	91	239.2 ± 1.1[d]	162
Snøhetta	1997	35.1[d]	84	240.0[d]	135

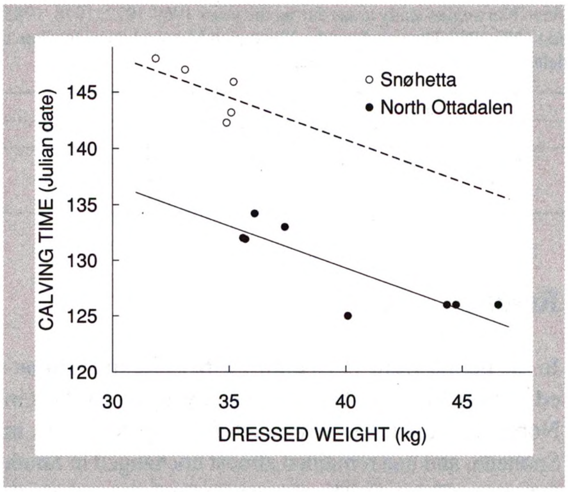

Figure 2. A significant linear relationship exists between calving time (Julian date) and autumn dressed weight (in kg) for does ≥2 years old ($y = -0.75x$, $P = 0.0009$), with a different level of 11.5 days for the two populations in Snøhetta and North Ottadalen ($P < 10^{-4}$). Ancova, $R^2 = 0.96$, $P = 1.5*10^{-7}$. Data are from 1969-1998.

linear relationship between calving time and autumn dressed weight ($y = -0.75x$, $P = 0.0009$), with a significantly later calving of 11.5 days in Snøhetta than in North Ottadalen for the same level of the covariate ($P < 10^{-4}$; Fig. 2). For mandible length the negative linear relationship with calving time was non-significant ($y = -0.46x$, $P = 0.15$), but calving in Snøhetta was significantly 14 days later than in North Ottadalen for the same level of the covariate ($P = 0.0007$; Fig. 3).

In Snøhetta, there was more snow in 1997 than in 1996 or 1998 (see Table 2) which agreed with our observations in the mountains during fieldwork. The tendency was clearest in Snøhetta, where pasture availability in May 1997 was low due to exceptionally large snowfalls in late April. For the whole data set, there were no significant correlations between snow depth and time of calving in the different populations.

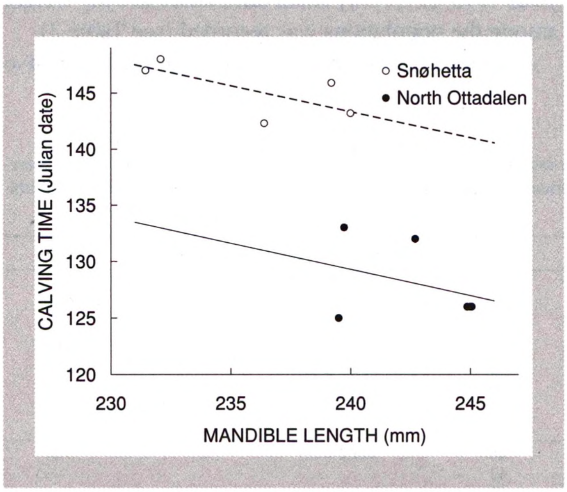

Figure 3. A non-significant linear relationship exists between calving time and mandible length for reindeer does ≥2 years old ($y = -0.46x$, $P = 0.15$), with a different level of 14 days for the two populations in Snøhetta and North Ottadalen ($P = 0.0007$). Ancova, $R^2 = 0.93$, $P = 2{,}7*10^{-5}$. Data are from 1969-1998.

Discussion

The negative relationship between autumn dressed weight and peak calving time suggests that breeding is delayed and/or gestation is prolonged when the physical condition of females is reduced, and *vice versa* when female physical condition improves. The insignificance of the negative relationship between mandible length and calving time may be explained by the combined effect of 1) higher growth priority of skeletal tissue, in particular in the body extremities and hence the mandible, than in muscular and adipose tissues (Langvatn 1977), and 2) fixed mandible length at 3-4 years of age (Reimers 1968).

For female reindeer, it would be adaptive to delay oestrus and conception until energy reserves are adequate to ensure successful gestation and early lactation. Lenvik (1988) found a negative relationship between autumn dressed weight and conception time among three populations of domestic reindeer, and Reimers (1997) found a negative relationship between autumn dressed weight and calving time for 11 populations of wild reindeer. In the experimental reindeer herd in Kaamanen, Finland, Eloranta & Nieminen (1986) reported that females calving before the peak of the calving period were significantly older and heavier than those calving after the peak. Except for Lenvik (1988), neither of the other two studies provided information on conception dates, and hence, could not exclude differences in pregnancy duration.

Studies on close phylogenetic species support the existence of a relationship between autumn physical condition and time of conception. In a study of two red deer *Cervus elaphus* populations in Scotland, Mitchell & Lincoln (1973) found a negative correlation between a kidney fat index and the date of conception. Correspondingly, Hamilton & Blaxter (1980) reported a distinct tendency for the heavier red deer hinds within an age cohort and a year to calve about one day earlier for every 4 kg of additional weight. Haagenrud & Markgren (1974) found a negative correlation between condition (measured by mandible length) and time of oestrus in moose *Alces alces*. In white-tailed deer *Odocoileus vir-*

ginianus, Verme (1965) found that extremely poor nutrition from October through the latter part of November resulted in a delayed and protracted rut. When offered a higher feed level in the treatment group, Verme (1969) found no difference from normal breeding time. In a food manipulation experiment on Scottish blackface ewes *Ovis aries*, the time of oestrus was delayed in the group of ewes that were in poor condition (Gunn & Doney 1975). In contrast, Dauphiné & McClure (1974) found that condition (weight and fat deposits) did not significantly influence the time of conception in Canadian barren ground caribou *Rangifer tarandus groenlandicus*. In conclusion, it appears that female oestrus, and thus breeding time, may be influenced by pre-rut physical condition.

Differences in length of gestation could affect the time of calving. Estimates of gestation length in reindeer differ from 192 to 246 days (Skjenneberg & Slagsvold 1968). Autumn body weights of females were similar in Snøhetta in 1995, 1996 and 1997 (see Table 3), and yet, calving time was significantly later in 1997 than in 1996 and 1998. The snow conditions and pasture availability in late winter - early spring, and especially in May, were markedly worse in 1997 than in 1996 and 1998 (see Table 2). This period coincides with the major growth of the foetus in reindeer (e.g. Krog, Wika & Savalov 1979, Roine, Nieminen & Timisjarvi 1982). During the last week of March, the Snøhetta area received large amounts of snow and local farmers could not remember similar snow depths in late April-May (P. Fale, pers. comm.). The reindeer in Snøhetta grazed in smaller groups during calving in 1997 than in 1996, probably because pasture could only be reached on a few patchy wind-exposed ridges. Lengthened gestation rather than delayed breeding may have caused the late calving in Snøhetta in 1997. However, the lack of any significant correlation between snow depth and calving time for the whole data set suggests that other variables affecting pasture availability, like snow hardness and wind exposure in rugged terrain, may be more important.

McEwan & Whitehead (1972) measured the gestation length of reindeer (208.0 ± 2.9 days) and caribou (216.4 ± 1.7 days) fed *ad libitum*. These gestation periods are considerably shorter than the average of 225-227 days reported by Skjenneberg & Slagsvold (1968). Bergerud (1975) concluded that breeding dates of Newfoundland caribou *Rangifer tarandus caribou* vary little between years, and that the variable calving dates may result from differences in gestation length related to pasture availability. Espmark (1980) conducted a nutrition experiment with two groups of reindeer from the same population, and found a non-significantly longer gestation period of four days in the poorly fed group. More female than male foetuses in the food restricted group (7:2 vs 2:7 in the unrestricted group) may have contributed to the calving time differences. However, Varo (1972) found that male calves are born later or at the same time as female calves. Skogland (1983) reported later calving by wild reindeer in Snøhetta following winters of deep, persistent snow, but supplied no data. In a more recent study, Cameron, Fancy, Gerhart & White (1992) suggested that maternal undernourishment late in the gestation period might delay parturition. However, Thomson (1977) found the same gestation length of 225-228 days in wild reindeer in North Ottadalen and Hardangervidda even though winter pastures and physical condition in Hardangervidda were markedly worse than in North Ottadalen (Gaare 1968).

The results from studies on other ungulates suggest that gestation can be lengthened by reduced nutrition and physical condition. In a study on penned white-tailed deer, Verme (1965) found a 4-6 day shorter gestation length in high- than in low-diet groups. In a study of bison *Bison bison*, late-breeding cows in good condition produced calves at the normal time, whereas late-breeding cows in poor condition had significantly longer gestation than cows in good condition (Berger 1992). In an experimental study on sheep, Holst & Allan (1992) found that a period of nutritional restriction in the last part of the gestation period lengthened this. In horses *Equus caballus*, well-fed mares had shorter gestation than mares on a maintenance ration (Howell & Rollins 1951). Exceptions are Cox (1964), who found that the gestation length in pigs *Sus scrofa* was unrelated to the live weight and backfat thickness of the sows, and Alexander (1956), who found that undernutrition during late pregnancy shortened the duration of gestation in sheep.

If the adaptive time of calving varies with climate, and if populations have evolved in different climatic regions, a difference in calving time among populations could be developing genetically through natural selection (Skogland 1989).

Røed (1985, 1986) showed that wild and semi-domestic reindeer in southern Norway are genetically different. The geographic origin of domesticated reindeer is unclear because different herds have been mixed and moved by man several times through history. The Ottadalen populations are mainly of domestic origin (Reimers & Sørumgård 1995), probably from the forested areas in Trøndelag and Sweden (Mølmen 1991). According to Skogland (1989), the reindeer at Snøhetta are descendants of the original wild reindeer of southern Norway that are adapted to high mountain areas. However, immigration of escaped domestic reindeer and reindeer from North Ottadalen has occurred (Ø. Mølmen, pers. comm.). Our study shows that the Snøhetta population is calving later than the North Ottadalen population at the same level of physical condition. The difference may be genetically determined, caused by different adaptive calving times in different geographical areas in the past. More data are needed to test this hypothesis.

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