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Source: *Wildlife Biology*, 9(1) : 29-36

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.2003.005>

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Sex ratio variation in reindeer *Rangifer tarandus*: a test of the extrinsic modification hypothesis

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Weladji, R.B. & Holand, Ø. 2003: Sex ratio variation in reindeer *Rangifer tarandus*: a test of the extrinsic modification hypothesis. - *Wildl. Biol.* 9: 29-36.

Evolutionary theories based on adaptive modification of maternal investment are generally suggested to explain variation in offspring sex ratios, but general concordance with empirical data is rare. Recently, factors beyond the control of the mother, such as density and climate, were reported to affect offspring sex ratios, and the extrinsic modification (EM) hypothesis has been advanced to explain such variation. The EM hypothesis states that offspring sex ratios in sexually dimorphic vertebrates may vary with extrinsically induced changes in maternal condition during pregnancy. We investigated sex ratio variation and inter-cohort calf live weight variation in 5,509 reindeer *Rangifer tarandus* calves during an eight-year period. Using separate models, we also tested whether offspring sex ratio covaried with density, and, respectively, summer weather before conception and winter weather (measured by the North Atlantic Oscillation (NAO)) when calves were *in utero*. Offspring sex ratios in mid-July differed from parity only in one year. Calf live weight varied among cohorts and males were heavier than females. The proportion of male calves in the herd decreased significantly with an increasing NAO index when calves were *in utero*. Density in the year of birth only affected calf sex ratios by increasing the negative effects of the NAO index. The proportion of males in the herd also declined with increasing summer temperature, summer precipitation, and density in the year of conception, suggesting potential for pre-conception environmental effect. Because the reported environmental variables affected negatively the proportion of male calves in the herd, we suggest that their effects may be associated with nutritional stress caused to the mother before conception, which have not been shown previously, and during pregnancy. Evidence of extrinsic sex ratio adjustment was conclusive and our findings therefore support the EM hypothesis of sex ratio variation.

Key words: climate, density, extrinsic modification, nutritional stress, *Rangifer tarandus*, sex ratio

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Received 14 December 2001, accepted 5 August 2002

Associate Editor: Marco Festa-Bianchet

Several studies have reported offspring sex ratio variation in ungulates (see reviews by Clutton-Brock & Iason 1986, Frank 1990, Festa-Bianchet 1996, Hewison

& Gaillard 1999), but many provide contrasting results even within the same species (see Hewison & Gaillard 1999 for examples). Adaptive modifications of mater-

nal investment (e.g. Trivers & Willard 1973) are generally suggested to explain the variation in offspring sex ratios but do not always fit the data (Clutton-Brock & Iason 1986, Frank 1990, Festa-Bianchet 1996, Hewison & Gaillard 1999), possibly because the mechanisms influencing sex ratio variation are also affected by environmental conditions (Kruuk, Clutton-Brock, Albon, Pemberton & Guinness 1999).

Clutton-Brock & Iason (1986) reported evidence for relationships between maternal condition and offspring sex ratios in mammals. Climatic variation (local and global) has been reported to affect several population parameters of northern ungulates (see reviews by Putman, Langbein, Hewison & Sharma 1996, Forchhammer 2001, Weladji, Klein, Holand & Mysterud 2002a), including female condition (Albon, Clutton-Brock & Guinness 1987). It is therefore likely that factors influencing maternal condition, such as environmental conditions, may also affect offspring sex ratios (Kruuk et al. 1999, Post, Forchhammer, Stenseth & Langvatn 1999b, Mysterud, Yoccoz, Stenseth & Langvatn 2000). Climate may act directly on ungulates' offspring sex ratio through effects on maternal condition. For example, severe cold or chilling due to rainfall may increase the costs of thermoregulation (Parker & Robbins 1985, Putman et al. 1996), and increasing snow depth may increase the costs of locomotion (Parker, Robbins & Hanley 1984) and cratering (Fancy & White 1985). Climate may also act indirectly on ungulates through its effect on plant quality and biomass production in summer (Bø & Hjeljord 1991, Van Soest 1994), and forage availability in winter as this might be limited by snow condition.

Recently, climate variables have been demonstrated to affect offspring sex ratios in red deer *Cervus elaphus* populations (Kruuk et al. 1999, Post et al. 1999b, Mysterud et al. 2000). Evidence for potentially non-adaptive environmental effects on sex ratio is increasing, and has been explicitly formalised by Post et al. (1999b) as the 'extrinsic modification' (EM) hypothesis, which states that "offspring sex ratios in sexually dimorphic vertebrates may vary with extrinsically induced changes in maternal condition during pregnancy". None of the studies relating environmental effects to vertebrates' sex ratio variations have reported a pre-conception weather effect, yet the condition of the mother at rut could also be important.

The effects of environmental conditions on offspring sex ratios have not been investigated on other ungulates, such as reindeer/caribou *Rangifer tarandus* which inhabit extremely seasonal environments and for which environmental influences ought to be very pronounced (Klein 1999). *Rangifer* also constitutes a biological re-

source of vital importance to the physical and cultural survival of Arctic residents (Kofinas, Osherenko, Klein & Forbes 2000) and offers great potential to test environmental effects on ungulate population parameters because of the large data sets available on semi-domestic animals. In reindeer/caribou, climate influences calf mortality (Fancy & Whitten 1991), reproductive performance and body mass (Adams & Dale 1998). If maternal condition affects offspring sex, we hypothesised that offspring sex ratios at a population level may be influenced by climatic variability and/or population density, thus supporting the EM hypothesis.

In this paper, we first investigated sex bias and inter-cohort live weight variation in 5,509 reindeer calves during an eight-year period. We then tested the EM hypothesis by examining whether the proportion of male calves in the population each year was affected by population density, climate in the summer preceding conception and climate regime in winter (measured by the North Atlantic Oscillation (NAO) to allow our results to be compared with other recent studies) when calves were *in utero*.

Material and methods

Reindeer data

We used data from a study on one semi-domestic reindeer population conducted in Østre Namdal reindeer-grazing area in the county of Nord-Trøndelag, Central Norway. The local Reindeer Husbandry Administration Office in collaboration with local reindeer herders collected these data as part of a project aimed at investigating calf mortality during autumn. Following the calving period, reindeer are gathered for the usual calf marking (ear tagging) operation, mainly in mid-July. Live weight and sex of calves were systematically recorded in addition to 'weighing dates'.

Our sample includes 2,650 male and 2,859 female calves. Mating usually takes place during the two first weeks of October and calving occurs mainly during the last two weeks of May. Skogland (1986) did not find pre-weaning mortality among wild reindeer in good range, and Kojola (1989) did not find any significant sex bias in pre-weaning mortality in any age or body mass category of the Kaamanen experimental semi-domestic reindeer herd in Finnish Lapland. Important reindeer neonatal mortality is often observed in areas with high levels of predation, which was not the case in our study area during the study period. Also, during the calf-marking operation, the number of calves per 100 potential reproductive females is registered and used to

assess the herd's 'calving success', which was on average approximately 92% for the studied herd (A. Kosmo, pers. comm.). This means that early neonatal mortality, if any, was rather low. Additionally, range condition in the grazing district is relatively good (Anon. 1998). Consequently, our data on calf sex ratio probably reflect birth sex ratio and are at least as good as the data used to test environmental effect on sex ratio variation in red deer in Norway (Post et al. 1999b, Mysterud et al. 2000). In order to obtain an index for density, the population size (estimated from yearly censuses at the end of March during a roundup) was divided by total available area (Anon. 1998). During the study period, the density varied between 0.27 and 0.57 animals/km² (mean = 0.40, SD = 0.10), with no systematic temporal trend.

Weather variables

Primary production and nutritive content of food plants in summer are influenced by temperature, precipitation and solar radiation (Bø & Hjeljord 1991, Van Soest 1994). We selected total precipitation and average temperature during July-August of the year of conception as summer weather variables to test their effect on sex ratio variations. We selected average temperature, total precipitation and average snow depth for the period December-March to characterise winter severity, to investigate the relationship between local winter weather variables and the NAO index. We considered winter variables of the winter area and summer variables of the summer area as reindeer display migratory patterns within the study area. Values are means calculated from the Namdalseid weather station (using the Kjobli weather station in Snåsa to estimate missing data) for the winter area and from the Nordli-Holand station (using the Haran station to estimate missing data) for the summer area, all within the Østre Namdal reindeer grazing district. The selection of the station used to estimate the missing data was based on significant correlation among selected variables in both stations during a 21-year period (1979-1999). All data were obtained from the Norwegian Meteorological Institute (NMI), Oslo.

In the North Atlantic region, winter climatic variability is, to a large extent, explained by a large-scale alternation of atmospheric pressure called the North Atlantic Oscillation (NAO) (Hurrell 1995). Because the signature of the NAO is strongly regional, its state is quantified annually by a simple index based on the mean deviation from the average sea-surface pressure between the Azores and Iceland from December through March. In northern Europe, positive values of the NAO index characterise warm, wet winters while negative values characterise cold, dry winters (Hurrell 1995). Because

the NAO accounts for most of the year-to-year fluctuations in winter precipitation in northern latitudes (Hurrell 1995, 1996) as well as variations in wintertime temperatures on the scale predicted by theoretical models of climate change (Hurrell 1996), the NAO clearly has the potential to affect the ecology of plants and animals in the Northern Hemisphere (Post, Forchhammer & Stenseth 1999a, Forchhammer 2001). However, as the effect of this large-scale climatic index may result in different local weather patterns in different areas (Mysterud et al. 2000), these interactions are inherently complex. We used the Hurrell's winter (December-March) NAO index, as a large-scale measure of global winter weather (<http://www.cgd.ucar.edu/~jhurrell/nao.html>; Hurrell 1995). There was a significant relationship between the NAO index and both winter precipitation ($r = 0.82$, $P = 0.01$) and winter temperature ($r = 0.83$, $P = 0.01$), but not winter snow depth ($r = 0.34$, $P = 0.41$). The winter weather station was located at approximately 80 m a.s.l.

Data analysis

We calculated the proportion of male calves registered each year during the marking operation (hereafter termed calf sex ratios). The departure from parity was tested using binomial tests, while χ^2 -tests were performed to assess the difference among years. Variation in calf live body weight was analysed with general linear models (GLM procedure in SAS version 8; SAS 1999), including the following predictor variables: calf's sex ('sex'), weighing date (to account for temporal change in calf mass), year, and the interaction between sex and year. The variables sex and year were defined as categorical, weighing date as continuous. The least-square estimates for means of live weight by 'year' and by 'sex' were generated from the model and used as predictors in the following generalised linear models.

We used generalised linear models (McCullagh & Nelder 1989) to determine the relationship between the proportion of male calves and climatic variables, density and the least-square estimate means of male calves' live weight by year ('average weight of male calves'). This last term was included to account for some of the initial density-dependence contribution, given the significant relationship between dam weight in spring and calf weight in mid-July in reindeer (Weladji, Mysterud, Holland & Lenvik 2002b). The interaction terms between density and climate variables were tested, but are not reported unless significant. We used density in the year of conception when dealing with the climatic variables pre-conception and density in the year of birth otherwise, as the roundup occurs after the slaughter, hap-

pening often just before the rut. Because of our limited time series, we ran two separate models (one for summer weather and one for winter weather) using the GENMOD procedure in SAS version 8 (SAS 1999), with a logit link function as our response variable was binomial (proportion of male calves, proportion of female calves). In case of overdispersion, an empirical scale parameter was adjusted using the deviance divided by the residual degrees of freedom (SAS 1999) for GENMOD models. The significance of the explanatory variables was assessed using the F-tests rather than the likelihood ratio-based chi-squares that tend to overestimate statistical significance (see Krackow & Tkadlek 2001).

Results

Sex ratios and live weight variation

The proportion of male reindeer calves in the herd varied between 0.468 and 0.493 with a mean of 0.482 (SD = 0.011; Table 1). Calf sex ratios did not vary significantly among years ($\chi^2 = 2.317$, df = 7, $P = 0.94$) and differed from parity only in 1985 (male:female ratio: 46.8:53.2; N = 1450, $P = 0.015$; see Table 1). Over all years, i.e. when pooling the data for the entire study, there were more female than male calves (male:female ratio: 48.1:51.9; N = 5509, $P = 0.005$; see Table 1). Calf live weight varied significantly among years ($F_{7, 5481} = 64.41$, $P < 0.001$) and by sex ($F_{1, 5481} = 340.95$, $P < 0.001$), with a significant interaction between year and sex ($F_{1,5481} = 4.05$, $P < 0.001$). Male reindeer calves were on average 2.5 kg (SE = 0.21) heavier than females ($t = 12.08$, $P < 0.001$).

Sex ratios and environmental conditions

The proportion of male calves declined with increasing NAO index during the winter when calves were *in utero* ($F_{1,3} = 39.76$, $P = 0.008$; Fig. 1A and Table 2A), after accounting for the effect of density and average

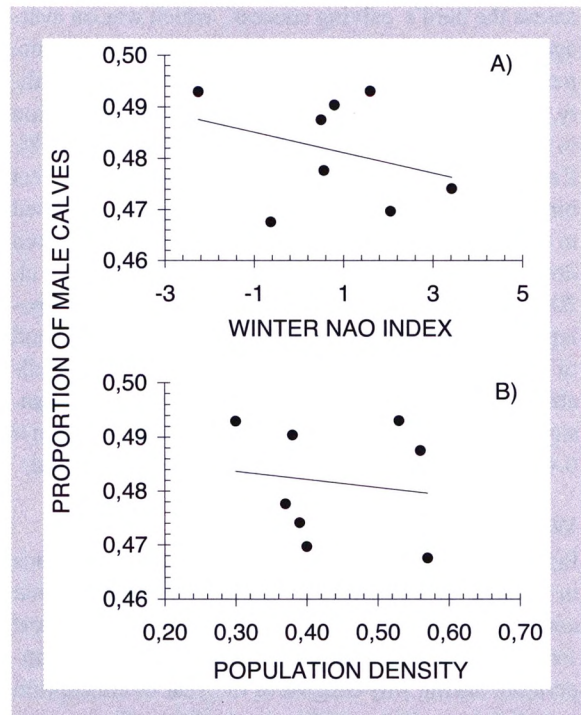


Figure 1. Proportion of male reindeer calves present in the herd each year in mid-July in relation to A) winter NAO index, and B) the population density in Østre Namdal, Norway.

weight of male calves. There was no main effect of density ($F_{1,3} = 0.70$, $P = 0.46$; see Fig. 1B), but the average weight of male calves had a positive effect ($F_{1,3} = 11.07$, $P = 0.045$; see Table 2A) on the proportion of male calves in the herd. Density only affected calf sex ratios by increasing the negative effects of unfavourable winter weather, i.e. the interaction between the NAO index and the density was positive and significant ($F_{1,3} = 38.34$, $P = 0.009$; see Table 2A).

Both precipitation ($F_{1,2} = 28.19$, $P = 0.034$; see Table 2B) and temperature ($F_{1,2} = 25.21$, $P = 0.038$; see Table 2B) in the summer prior to conception had a negative effect on the proportion of male calves. Increasing density in the year of conception decreased the proportion

Table 1. Annual weight of calves (in kg; mean \pm SE), number of male and female calves (N), binomial tests and χ^2 -test for inter-annual variation in sex ratios of reindeer calves in Østre Namdal, Norway.

Year	Average calf weight (kg)		Calf sex ratio			Binomial test		χ^2 -test	
	Male	Female	Male (N)	Female (N)	Proportion of males	P	χ^2	P	
1979	26.92 \pm 0.35	24.25 \pm 0.34	105	108	0.493	0.891			
1980	27.67 \pm 0.25	26.39 \pm 0.24	203	222	0.478	0.383			
1981	27.86 \pm 0.45	25.33 \pm 0.42	62	70	0.470	0.543			
1982	30.23 \pm 0.21	26.94 \pm 0.21	281	292	0.490	0.676			
1983	29.14 \pm 0.21	27.19 \pm 0.20	293	325	0.474	0.212			
1984	28.23 \pm 0.17	25.56 \pm 0.16	461	474	0.493	0.695			
1985	27.04 \pm 0.14	25.05 \pm 0.13	678	772	0.468	0.015			
1986	29.66 \pm 0.15	27.14 \pm 0.15	567	596	0.488	0.412			
Over all			2650	2859	0.481	0.005	2.317	0.940	

Table 2. Parameter estimates (point estimates) and standard errors (SE) for the generalised linear models of density and climate variables, on the proportion of male calves in reindeer. Only significant parameters were included when estimating coefficients in italics, the non-significant coefficients (not italics) being from models with only significant interaction terms. Interactions are denoted by * between terms. Degrees of freedom were 1 throughout.

Variable	Estimate	SE
A) Environmental conditions in winter when calves were <i>in utero</i>		
Intercept	-0.5702	<i>0.1380</i>
Density in the year of birth	-0.0495	<i>0.0591</i>
Average live weight of male calves	<i>0.0173</i>	<i>0.0049</i>
NAO index when calves were <i>in utero</i>	-0.1197	<i>0.0184</i>
Density * NAO index when calves were <i>in utero</i>	<i>0.2827</i>	<i>0.0440</i>
B) Environmental conditions in the summer preceding conception		
Intercept	<i>1.2289</i>	<i>0.1673</i>
Density in the year of conception	-1.9418	<i>0.2202</i>
Average live weight of male calves	-0.0009	<i>0.0064</i>
Summer precipitation	-0.0041	<i>0.0005</i>
Summer temperature	-0.0485	<i>0.0078</i>
Density in the year of conception * Summer precipitation	<i>0.0112</i>	<i>0.0014</i>

of male calves ($F_{1,2} = 36.60$, $P = 0.026$; see Table 2B). Moreover, the interaction between density in the year of conception and in precipitation the summer prior to conception was positive and significant ($F_{1,2} = 32.77$, $P = 0.029$; see Table 2B), implying that the negative effects of wet summers would be amplified by increasing density. The average weight of male calves did not have an effect in this model ($F_{1,2} = 0.02$, $P = 0.9$).

Discussion

Fisher (1930) argued that sex ratios are self-adjusting through frequency-dependent selection, which should favour even sex ratios if the fitness costs of producing males and females are equal. We found that calf sex ratio did not differ from parity in seven out of eight years among 5,509 semi-domestic reindeers. Kojola & Helle (1994) reported a slight non-significant male biased sex ratio in semi-domestic reindeer, whereas Kojola & Eloranta (1989) and Reimers & Lenvik (1997) in semi-domestic reindeer, and Reimers (1999) in wild reindeer, did not find any departure from parity. Our calculations did not account for variability in maternal age within the population (Thomas, Barry & Kiliaan 1989), but studies on both wild and semi-domestic reindeer found no age effect on the overall sex ratio (Kojola & Helle 1994, Reimers & Lenvik 1997, Reimers 1999). This supports the contrasting results reported regarding sex allocation in vertebrates (Festa-Bianchet 1996, Hewison & Gaillard 1999, Kruuk et al. 1999). This variability may suggest, among other reasons, that maternal strategies alone might not be the only driving force shaping offspring sex ratio. Other mechanisms may be important as well, e.g. climate which has been largely overlooked.

Our analyses show that both density-dependent and density independent factors have the potential to influ-

ence offspring sex ratios in reindeer. Kruuk et al. (1999), Post et al. (1999b) and Mysterud et al. (2000) recently demonstrated for red deer that extrinsic factors affecting body condition, such as density and climate, also affect offspring sex ratios. Our study corroborates these findings. An increase in the NAO index when calves were *in utero* decreased the proportion of male calves in the herd, as did density, summer precipitation and summer temperature in the year of conception.

During 1978-1986, winter precipitation was mainly rainfall (11.3%), snowfall (41%) and a mixture of rain, snow and sleet (44%), the rest being either dew or white frost (source: NMI, Oslo). That the winter NAO index is correlated with the mixture of rain, snow and sleet ($r = 0.82$, $P = 0.013$) may be important for understanding reindeer winter condition. When the temperature cools down, such a mixture favours the development of frozen crusts that are hard to break through. Cold weather following wet snow or rain, may lead to ice layers limiting the access of herbivores to vegetation (Miller, Edmonds & Gunn 1982, Forchhammer & Boertmann 1993). Thus, high NAO index values may indicate severe winters for reindeer in this area and may cause nutritional stress that may deteriorate the dam's condition during pregnancy. This could in turn cause sex-differential foetal loss or at least modify the sex ratio at implantation (Kruuk et al. 1999), thereby influencing population birth or juvenile sex ratio.

The fact that summer conditions prior to the rut negatively affected calf sex ratio may be generated either by the resulting variability in forage availability and quality caused by the combined effect of temperature and precipitation, or by the level of insect harassment that is weather-related (see Weladji et al. 2002a). Warm summers may decrease reindeer condition (Weladji, Holand & Almqvist in press), particularly that of females (Gerhart 1995). Summer weather and the resulting behaviour-

al/nutritional stress on reindeer before the rut may alter the birth or juvenile sex ratio in Østre Namdal, most likely through manipulation of sex at conception or sex-differential foetal mortality. Crête & Huot (1993) reported that summer nutrition seemingly regulated the Rivière George caribou through a combination of decreased fecundity and survival.

Our results concur with Trivers & Willard's (1973) prediction that increased favourable conditions for the mother should lead to more male calves being produced. That calf weight varied significantly with year may suggest that their mothers have experienced variable environmental conditions, given that reindeer calf weight depends on the condition of their mothers (Weladji et al. 2002b). Even after accounting for density, there was an effect of abiotic factors in altering sex ratios. This may, at least partly, explain the inconsistency in adaptive modification theories of sex ratio adjustment in reindeer as in several other ungulates (Festa-Bianchet 1996, Hewison & Gaillard 1999). We here report evidence of extrinsic modification of calf sex ratios by climate, which may or may not be adaptive (Kruuk et al. 1999, Post et al. 1999b, Mysterud et al. 2000). Summer weather variables may be influencing more the pre-rut condition (rut occurs in early October) of the mother and thereby either the sex at conception or the sex-dependent early foetal mortality, whereas winter variables may be acting during pregnancy through a sex-dependent foetal mortality, or later through post-natal mortality. Indeed, NAO exerts its greatest influence on winter severity during the two first trimesters of gestation (Hurrell 1995), a period when most sex-differential foetal mortality occurs in cervids (Robinette, Gashwiler, Low & Jones 1957). However, the proportion of males only changed by about 3% during our study period, which covered much of the range of the NAO index. Moreover, there were more female than male calves throughout the entire study. Therefore, although significant, the reported climate effects have not caused a major shift in the sex ratios of the studied population. There may be some overriding factors, not accounted for here, rendering a major shift in the sex ratio of the population unlikely in the near future.

The negative effect of density on the proportion of male calves could also be attributed to nutritional stress of the mother (Kruuk et al. 1999, Mysterud et al. 2000). Density could affect foetal mortality during winter, as well as conception rates in autumn (Kruuk et al. 1999), or accentuate the negative effect of severe weather conditions. Our results concur with those of Kruuk et al. (1999) who reported that female red deer in poor winter condition produce fewer sons. However, both Post

et al. (1999b) and Mysterud et al. (2000) reported a positive relationship between the NAO index and the proportion of male red deer calves shot in one population in a coastal area in Norway, which may be attributed to the opposite correlation between the NAO and local weather. The NAO affects local weather differently and, hence, cervid populations differently.

An understanding of population ecology is essential to wildlife managers (Bolen & Robinson 1999), and sex ratio is one of the basic population attributes. Furthermore, statistically sound monitoring of basic demographic parameters is needed to develop sustainable harvesting strategies (Sæther 2001). Investigations of environmental effects on population sex ratios are relevant to wildlife management because they may affect population growth potential, and thus population dynamics and optimal harvesting strategies. A male-biased sex ratio may allow more opportunities for trophy hunting (e.g. Clutton-Brock, Coulson, Milner-Gulland, Thomson & Armstrong 2002), whereas a female-biased sex ratio may favour population growth by increasing the recruitment rate.

Acknowledgements - we thank Loeske Kruuk, Atle Mysterud and Eric Post for very useful comments and discussions on the manuscript. We gratefully acknowledge the financial support of the Norwegian Reindeer Husbandry Development Fund. Marco Festa-Bianchet, Mark Hewison and two anonymous referees provided critical and constructive remarks that improved this article. Thanks are also due to Jos Milner and Nigel Gilles Yoccoz for insightful discussions regarding analytical tools and to Ansgar Kosmo for the data. T.S.K. Skaget of the Nord Trøndelag reindeer region has been helpful throughout with organising the data.

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