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Temporal patterns of juvenile body weight variability in sympatric reindeer and sheep

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The debate over whether winter or summer grazing conditions are more important for reindeer (*Rangifer tarandus*) growth and reproduction is not settled. We used long-term weight data of sympatric semi-domesticated reindeer and domestic sheep (*Ovis aries*) in Sør-Fosen, Norway, to address indirectly the above-mentioned debate, by assessing the temporal patterns, variation and covariation of juvenile body weights. We further examined the relative importance of winter and summer weather conditions in explaining variation in reindeer autumn weights. A positive relationship between autumn body weight of reindeer and sheep was found, suggesting that a "good" summer for reindeer is also a good one for sheep. Despite the sheep being fed indoors during winter, there was no difference in intrinsic variability between yearly mean juvenile body weights of the two species. These results suggest that (i) reindeer and domestic sheep may equally benefit, or suffer, from weather-related variation in summer forage conditions, and that (ii) either reindeer calf autumn body weights are not very sensitive to environmental conditions in the previous winter (i.e. when they were *in utero*), or that they are able, to some extent, to compensate for winter-related stress experienced by their mother. Furthermore, (iii) winter weather conditions may influence reindeer and sheep similarly, through indirect effects on the summer forage conditions. Direct analysis revealed that summer weather index explained more of the between year variance in reindeer autumn weights than the winter weather index. Hence, our results support the view that summer, rather than winter range conditions, are more important to juvenile body growth of reindeer.

Introduction

In populations of large herbivores, density-independence and density-dependence co-occur and have similar effects on various fitness components (Gaillard *et al.* 2000). For some northern ungulates, much of the variation in life history and population parameters is related to either winter (Skogland 1985, Kumpula 2001) or summer (Reimers *et al.* 1983, Reimers 1997, Hjeljord & Histøl 1999, Finstad *et al.* 2000) resource availability and accessibility. However, there is little consensus about which season plays the most significant role in influencing ungulate life history and population parameters (Weladji *et al.* 2002a). Since Klein (1968) proposed that the summer range quantity and quality determine the body size and reproductive success in reindeer/caribou (*Rangifer tarandus*), the debate over whether winter or summer grazing conditions are more important has raged. Gaare and Skogland (1980) suggested that the body size and reproductive performance in reindeer is primarily influenced by lichen biomass of the winter pasture (*see* also Skogland 1985). Alternatively, Reimers *et al.* (1983) and Reimers (1983, 1997) argue that body size in *Rangifer* is determined primarily by grazing conditions during the summer.

Several wild and domestic ungulates overlap substantially in temporal and spatial habitat use (Skogland 1984, Gordon & Illius 1989, Putman 1996, Mysterud 2000). Information on overlap in resource use is central to understanding of inter-specific exploitation, competition, and resource partitioning (Mysterud 2000). Unfortunately, the relationship between niche overlap and competition is poorly understood (Litvaitis *et al.*1996).

On Norwegian rangelands, the domestic sheep is the most prevalent ruminant during summer, sharing alpine summer ranges with both wild and semi-domestic reindeer. Reindeer and sheep overlap in preferred habitat types (Skogland 1984, Ballari 1986, Gausemel 1988, Mysterud & Mysterud 1999, Mysterud 2000), and graze on many of the same plant species (Skogland 1984, Bergmann 1997, Mysterud 2000). Although several studies have addressed behavioural interactions between the two species (Warren & Mysterud 1995, Moe *et al.* 1999, Colman 2000), long-term temporal patterns of body weights of sympatric populations of reindeer and sheep have not been investigated.

Body weight is one of the most important life history traits (Calder 1984) and several ungulates' life history aspects are associated with body weight (Klein 1970, Sæther 1985, Reimers 1997). A number of temperate ungulate studies have demonstrated relationships between body weight and summer conditions (Klein 1965, Reimers 1983, 1997, Langvatn *et al.* 1996, Sæther *et al.* 1996, Hjeljord & Histøl 1999, Weladji 2001). It is also known that reindeer calf (Weladji *et al.* 2002b) and lamb weights (Steinheim *et al.* 2002) are, to some extent, dependent upon the pre-rut condition of the dam.

In Norway, sheep use mountain pastures during a 2–3-month summer period (Drabløs 1997, Skurdal 1997), while semi-domestic reindeer use the same pastures throughout the year. Both reindeer (Eloranta & Nieminen 1986) and sheep (Hellebergshaugen & Maurtvedt 1998) have synchronised spring birth peaks. While sheep are kept indoors throughout the winter and early spring and fed a diet that is stable between years, reindeer are subjected to weather related stochastic variations in range conditions during the same period.

Here, we used 12 years of data from a reindeer herd in mid-Norway, and from three sheep flocks — all grazing the same area — to analyse (i) temporal patterns and (ii) relative variability of juvenile autumn weights in sympatric reindeer and sheep. We further (iii) tested the relative importance of winter and summer weather conditions in explaining the variation in autumn weights of reindeer calves.

Material and methods

We selected a grazing district, Sør-Fosen, in Nord-Trøndelag County, where the reindeer and sheep range overlap during summer (Fig. 1) and where records of animal body weights were available. To detect overlap of summer grazing area by sheep and reindeer we used information from the Reindeer Husbandry Administration's Grazing Map (Reindriftsforvaltningen 2000), the National Database on Organised Grazing, and interviews with local grazing authorities and sheep farmers. The study area is close to the coast and within the vegetation section O2 (Moen 1998); that is: oceanic with relatively mild winters and a yearly precipitation above 1200 mm (Moen & Odeland 1993). The geology is mainly granite (and related types) and granitic gneiss, with a thin soil layer dominated by moraine materials and peats (Dahl *et al.* 1997).

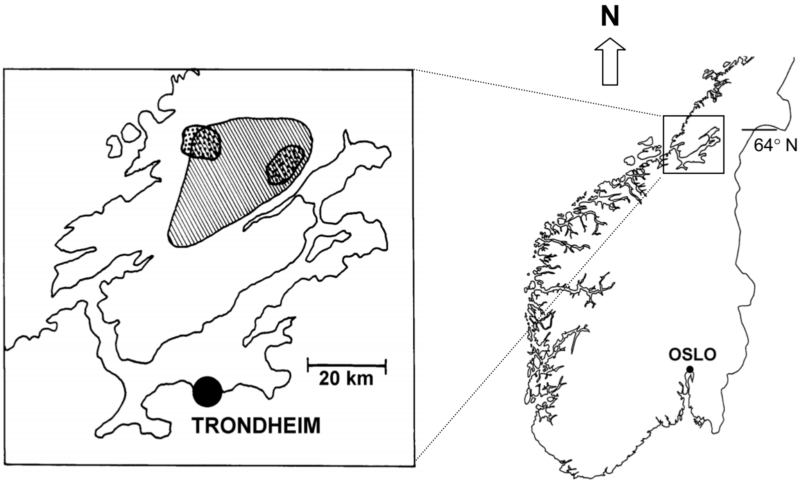

Fig. 1. Map of the study area in Sør Fosen displaying the reindeer grazing area (hatched) with the approximate home ranges of the sheep flocks used in the study (dotted).

Reindeer data

In Norway, semi-domestic reindeer are kept under very extensive farming systems, generally without additional feed during winter. The studied herd did not receive forage during winters. In autumn, when semi-domestic reindeer are gathered for slaughtering, carcass weight, sex and age, specified according to year, identity of the owner, corresponding herd and grazing area are recorded by the Reindeer Husbandry Office. Carcass weight is equivalent to live mass minus head, skin, viscera, blood and hoofs from the wrist down. Records from 1989 to 2000 were used and the number of carcasses weighted per year is displayed in Table 1. Estimates of population sizes are made during an annual census around the end of March. In the source file used, the population sizes of the Sør-Fosen and Nord-Fosen herds were pooled for the Fosen district and varied between 1528 and 1754 reindeers from 1989 to 2000, corresponding to an average density of about 0.38 reindeer km^{-2}. This pooled population size was used as a density index.

Sheep data

Of the five sheep flocks utilising the reindeer grazing area under study, three (one in the

Table 1. Least square estimates of mean (± SE) annual autumn weights (kg) of reindeer (based on a random sample of 96 calves per year) and sheep (based on a random sample of 200 lambs per year) in Sør Fosen, Norway. *N* = total available sample size.

	Carcass weight of reindeer			Live weight of sheep		
Year	Adjusted means	SE	*N*	Adjusted means	SE	*N*
1989	20.696	0.305	309	40.469	0.876	209
1990				41.940	0.679	242
1991	19.863	0.245	141	36.495	0.647	248
1992	18.745	0.251	266	36.304	0.664	219
1993	21.307	0.243	96	40.971	0.550	201
1994	20.589	0.246	124	44.090	0.572	225
1995	21.320	0.254	120	40.955	0.506	250
1996	18.972	0.255	136	40.457	0.532	244
1997	19.641	0.244	116	37.115	0.556	235
1998	21.668	0.257	191	40.847	0.567	227
1999	19.890	0.256	119	39.569	0.540	214
2000	20.643	0.246	182	41.833	0.579	243

west, two in the east; Fig. 1) were registered in the Norwegian Sheep Recording System. All three flocks consisted of the Norwegian short-tailed "Spæl" breed (Drabløs 1997, Oklahoma State University 2002). Retrieved and calculated parameters were: identity of flock, sex of lamb, age of lamb (days) at weighing, date of weighing, live weight and litter size, all classified by year. To standardise the material, all hand-reared lambs were excluded. Furthermore, to be included in the analysis, lambs had to be weighed during September or October, with an age between 120 and 180 days. Records from 1989 to 2000 were used and the number of lambs weighted per year is displayed in Table 1. The lambs were born indoors during the spring, and shortly after released onto pastures together with their ewes, which they followed the entire outdoor season. In the large sheep grazing areas engulfing the study area, the sheep density was between 2.8 and 3.4 (adult) sheep per km^2 during 1992 to 1998 (National Database for Organised Grazing unpubl.). There was no additional information on sheep stocking rate. This may not affect our results, as Norwegian stocking rates of sheep on pastures are generally low (Mysterud 2000).

Climatic data

After identifying the summer and winter areas of the studied reindeer population, we obtained climatic records from the Norwegian Meteorological Institute in Oslo, for the nearest weather stations (Namdalseid and Ørland, respectively). Based on previous work relating weather to northern ungulates' phenotypic and demographic traits (review in Weladji *et al*. 2002a), we calculated: for winter (December–March), the average temperature (°C) and the average snow depth (mm) to characterize winter severity; and for summer (July–August), the total precipitation (mm) and the average temperature (°C). Selected weather variables were significantly correlated in winter (temperature and snow depth: $r = -0.88$, $n = 12$, $P < 0.001$) and summer (precipitation and temperature: $r = -0.71$, $n = 12$, $P = 0.009$). We, therefore, performed a principal component analysis (PCA) and used the score on the main axis as an index of winter or summer weather. The main axes explained 94% and 86% of the variation in winter and summer climate respectively. The winter and summer indices were not significantly correlated ($r = -0.45$, $n = 12$, $P = 0.14$).

Statistical analyses

We used general linear models (GLM) to estimate annual least square means (lsmeans) of autumn weight in juvenile reindeer calves (carcass weight) and sheep lambs (live weight). Predictor variables included for reindeer: *calf sex* (male/female), *weighing date* to account for temporal changes in calf body mass (1 to 91 days, starting 1 September), and *year* i.e. one of the years 1989–2000 (no data for the year 1990). For lambs, predictor variables were: *lamb sex* (male/female), *weighing age* of lamb (120–180 days), *litter size* i.e. number of offspring within the litter (one, two or three), *flocks* to account for potential differential management strategy applied by owner of any of the three flocks, *year* i.e. one of the years 1989–2000, and finally, the interaction between year and farm was included to account for between year variation in lamb weight of individual farmers, as the flocks are not herded together. In both models, all effects were defined as fixed, and all except *weighing date/age* as categorical variables.

We used Pearson correlation to assess the degree of synchrony between yearly lsmeans of the autumn weights of the two species. In order to be able to give an interpretation to our estimates (sample correlation or regression coefficient), it was appropriate to have balanced sample sizes of each species throughout the study period. We, therefore, generated a new data set for this analysis, using a computer based random selection procedure (SAS 1999b) to draw 200 lambs and 96 calves each year from the available data. The chosen numbers are determined by the minimum available annual sample size as we aimed at keeping the whole time series (*see* Table 1). To assess the relative variability in the yearly lsmeans of reindeer and sheep in the area, we compared the coefficient of variation of both species by combining the Lewontin (1966) approach and the Brown and Forsythe's test (Brown & Forsythe 1974). Lewontin (1966) has shown that a test of equality of two coefficients of variation is equivalent to a testing of equality of the variances of the logarithmic transforms, and that this could be used to assess the relative variation of a given character in two or more species, even of different body sizes (*see* Sokal & Rolf 1995: 58–59). Accordingly, lsmeans by year of calf carcass weights and lambs live weights were transformed by natural logarithms and subjected to a test of equality of variance. Although both the Levene's test (Levene 1960) and the Brown-Forsythe test (Brown & Forsythe 1974) are reasonably robust to the underlying distribution (SAS 1999a), we preferred the latter which is the best at providing power to detect differences of variance (Conover *et al.* 1981, Olejnik & Algina 1987), and has been shown to give accurate error rates even when underlying distributions for the raw scores deviate significantly from the normal distribution (Olejnik & Algina 1987). The year 1990 was excluded from statistical tests to allow for balanced time series. Statistical analyses were conducted using SAS version 8 (SAS 1999b).

Finally, to test effect of summer versus winter weather on reindeer carcass weight, we used mixed linear models with both fixed and random effects (Littell *et al.* 1996), using the *Mixed* procedure in SAS (1999b), with a 95% level of significance. Because of repeated sampling within a year, "year" was fitted as a random effect in the models (*see* Kruuk *et al.* 1999, Milner *et al.* 1999, Côté & Festa-Bianchet 2001). This also allowed accounting for stochastic between year variations. The following fixed independent variables were used: *weighing date*, *calf's sex*, *density*, *winter weather index*, *summer weather index*, and the interaction between *density* and weather variables. From these variables, we constructed the most parsimonious model on the basis of the Akaike's Information Criterions (AIC; Akaike 1973, Burnham & Anderson 1998), the best model being the one with the smallest value for the AIC.

Results

Correlation between sheep and reindeer juvenile body weight

The GLM models used to generate the lsmeans explained 33% ($F_{39,2360}$ = 29.35, P < 0.001) and 22% ($F_{12,1043}$ = 24.06, P < 0.001) of the inter-annual variation in autumn body weight of juvenile sheep and reindeer, respectively. Annual body weights of juvenile sheep and reindeer fluctuated significantly between years (sheep: $F_{11,2360}$ = 15.03, P < 0.001; reindeer: $F_{10,1043}$ = 15.52, P < 0.001; *see* also Fig. 2). Table 1 displays the lsmeans by years for the autumn weights with the corresponding standard errors, estimated from a random sample of 96 calves and 200 lambs each year for each species. The correlation (or linear relationship) between yearly weights in autumn (Fig. 2) of the two species was significant (Pearson correlation coefficient r = 0.60, n = 11, P = 0.05).

Relative variability in autumn body weight of reindeer and sheep

Mean (± SD) yearly lsmeans of autumn weights were, after a logarithmic transformation, 3.685 ± 0.061 (CV = 1.655) and 3.010 ± 0.048 (CV = 1.595) for sheep and reindeer, respectively. Brown and Forsythe's test ($F_{1,20}$ = 0.06, P = 0.80) revealed that the two species did not differ in terms of between-year weight variability.

Influence of weather on reindeer calf body weight

Autumn weights of reindeer calves were affected by density-dependent and climatic conditions in the cohort year of birth. The best model to predict between-year variations in calf autumn weight, as determined by the smallest AIC value (Table 2) included density and the summer weather index, in addition to weighing date and calf's sex. Including the winter weather index to this model, provided the second best model (Table 2, ΔAIC = 0.7), the effect of the

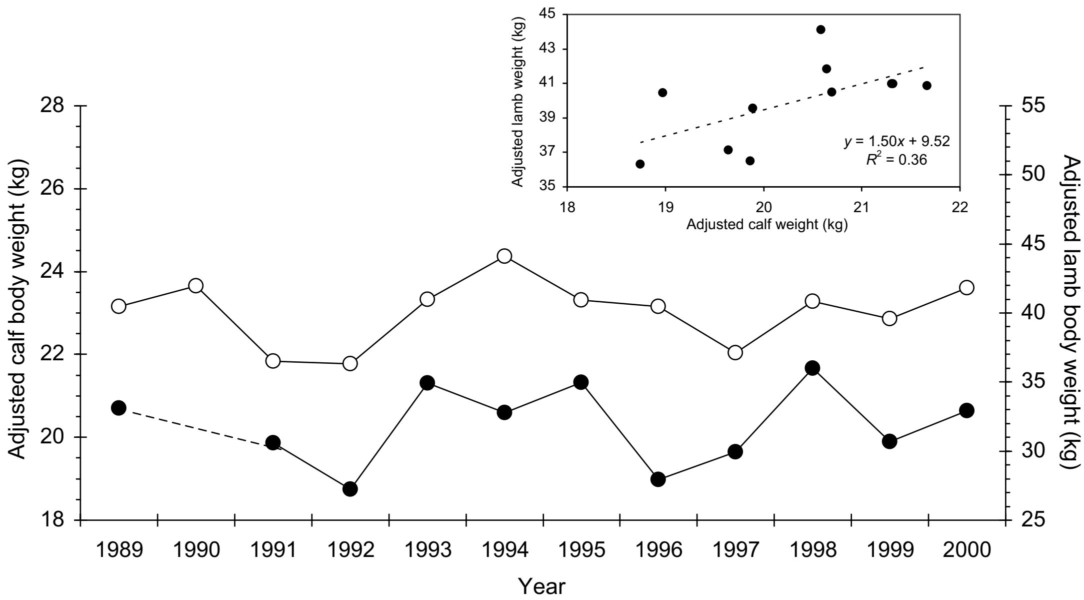

Fig. 2. Inter-annual variation in adjusted mean live weight of lambs (upper line) and carcass weight of reindeer calves (lower line) in Sør Fosen, central Norway in 1989–2000. Sample sizes per year are shown in Table 1. The inset scattergram shows the sheep/reindeer juvenile weight relationship.

winter weather index approaching significance ($F_{1,1793} = 3.21$, $P = 0.07$). This indicates that both winter and summer conditions are important for body size in reindeer, and probably other northern ungulates. The summer weather index had a significant effect on autumn weight of reindeer calves, the amount of explained variance being higher than that of the winter weather index ($F_{1,1793} = 55.46$, $P < 0.001$). The estimated variance components for "year" were consistently very small and not significant ($P > 0.2$) for all models.

Discussion

Our analysis shows that body weight of both reindeer and sheep vary from year to year, and that there is a positive relationship between autumn body weight of reindeer and sheep (Fig. 2). This

Table 2. Akaike Information Criterion (AIC) values for mixed linear models of reindeer calf's autumn weights with different combinations of predictor variables, including population size (D), winter weather index (WWI), and summer weather index (SWI), in addition to weighing date and calf's sex. Interactions are denoted by "×" between terms. Year was fitted as random factor in all models. The most parsimonious model (smallest AIC value) is shown in bold.

Model's independent terms	AIC
Weighing date + Calf's sex	8536.6
Weighing date + Calf's sex + D	8548.0
Weighing date + Calf's sex + D + SWI	**8498.7**
Weighing date + Calf's sex + D + WWI	8550.6
Weighing date + Calf's sex + D + SWI + D × SWI	8511.0
Weighing date + Calf's sex + D + WWI + D × WWI	8544.5
Weighing date + Calf's sex + D + SWI + WWI	8499.4
Weighing date + Calf's sex + D + SWI + WWI + D × SWI	8511.8
Weighing date + Calf's sex + D + SWI + WWI + D × WWI	8508.2
Weighing date + Calf's sex + D + SWI + WWI + D × SWI + D × WWI	8519.7

suggests that a "good" summer for reindeer may also be a good one for sheep. Moreover, despite the sheep being fed indoors during winter, there was no apparent difference in intrinsic variability between yearly-corrected mean body weights of the two species. We therefore suggest that:

Firstly, the known influence of climate on body mass of ungulates, for example through its effect on forage quality and quantity (*see* review by Weladji *et al*. 2002a), might explain the positive relationship between weights of the two co-existing species. The sympatric reindeer and sheep may equally benefit, or suffer, from weather-related variation in summer forage conditions. Further experimental studies under controlled conditions are needed to confirm this, and to investigate possible species-specific effects of climatic parameters (partly done in this study for reindeer). Also, although sheep are kept indoors during winter, winter climatic conditions may still influence both reindeer and sheep similarly, through indirect effects on the summer forage conditions (e.g. gradually snow melt in spring/early summer that affect the phenology of the forage plants, and wintering conditions for plants), as demonstrated by Mysterud *et al*. (2001) for red deer and domestic sheep along the west coast of Norway.

Secondly, summer weather conditions seem to be the major determinant of *Rangifer* autumn juvenile body mass, which is in accordance with findings by Reimers (1983) and Klein (1965, 1985). We expected reindeer, being exposed to environmental stochasticity all year round, to have a relative variation in yearly juvenile autumn weights different from that of the sheep. This was not the case, however, as there was no indication of a difference in the relative variability in yearly autumn body weights of reindeer and sheep. This suggests that the winters experienced by reindeer dams (i.e. when calves were *in utero*) between 1989 and 2000 did not substantially affect the weight of their calf in the following autumn, as compared with summer effect (but *see* Gaare & Skogland 1980 for wild reindeer). In addition, the reindeer might have been able to compensate for previous winter's effects on the juvenile weights, depending on the quality of the summer range, which concurs with Reimers (1983). Direct analysis revealed that, once summer effect was accounted for, there was no significant residual left to be explained by winter weather. We found the amount of variance explained by the summer weather index to be greater than that of the winter weather index. Similarly, Klein (1965) reported that summer forage determines the body condition of large herbivores. This does not, however, exclude the possibility that winter conditions are also important. This might be particularly true for the study area, where during the study period, winter (December–March) temperatures ranged between –1 °C and 3.1 °C (Mean ± SD: 1.39 ± 1.21), winter precipitation ranged between 366 mm and 776 mm (Mean ± SD: 594.1 ± 145.8), and winter snow depth ranged between 2.79 mm and 19.64 mm (Mean ± SD: 6.94 ± 5.46), whilst it is possible that reindeer body weights are more strongly influenced by winter conditions in areas with severe winters. Indeed, parameter estimates (± SE) from the second best AIC-based model provided negative effects of both the summer weather index (–0.6704 ± 0.090) and the winter weather index (–0.1133 ± 0.063). This suggests that both winters and summers may affect juvenile growth of reindeer in the study area. Again, the effect size was bigger for the summer than for the winter weather index.

We compared carcass weights (calves) and live autumn weights (sheep): this might have biased our results. The lambs' gut fill might vary, and thus boost the variation. Also, wet sheep are heavier than dry sheep, so local weather during lambs weighing may be important as well. In practise, this is not likely to be a serious problem: we expect the sheep farmers' routines for weighing their lambs to have been stable between years.

A marked increase in appetite, metabolic activity and hormones related to growth occur in cervids during spring and early summer (Ryg & Langvatn 1982, Kay *et al*. 1984, Regelin *et al*. 1985), and Reimers (1983) argued that free-ranging caribou and reindeer had a pattern of cyclic growth, with rapid growth in summer and slow growth or weight loss in winter. This view suggests that juvenile autumn weight in reindeer is an important determinant of over-wintering survival (which may lead to reduced variance), while sheep that have not experienced winter weather-related stress for many generations may have relaxed survival selection allowing greater variance in juvenile autumn weight. This may, however, be overridden by the heavy human breeding selection for sheep. Other similar studies argued that variation in nutritional levels in spring and summer should affect growth and body size more than variation during the period of winter growth dormancy when animals are "programmed" for survival, and less for growth and development (Klein 1985, *see* also Hjeljord & Histøl 1999).

Our study reports a positive relationship between, and similar variation of, autumn body weight of juvenile reindeer and sheep. The study also suggests that climatic factors influence body weight variation in the two ungulate species through effects on forage quality and quantity during the summer months. Finally, our results support the view that summer conditions are relatively more important than winter conditions to juvenile body growth of reindeer, and, most likely, other temperate and arctic large herbivores as well.

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