The relationship between the fat content of Svalbard reindeer in autumn and their death from starvation in winter.

N.J.C. Tyler[1]

Abstract: The relationship between body fat reserves in autumn and age-specific mortality in winter were examined in Svalbard reindeer *(Rangifer tarandus platyrhynchus* Vrolik). Total dissectible fat (TDF) was measured in 17 females, 1-12 years of age, shot on Spitsbergen (78°N lat.) in autumn 1980-1981. TDF declined with age in reindeer 2 years and older. The youngest females which died in winter, with the exception of calves, were aged 7 years old. A direct causal link between low autumn TDF and mortality in winter seemed unlikely. Mortality was clearly associated with the degree of wear of molariform teeth. Perhaps severe tooth wear results in inefficient mastication of low quality forage and a decline in the rate of passage of digesta, thereby restricting the amount of food that reindeer can eat. A simple model of the energy balance of female Svalbard reindeer in winter shows that they must obtaine not less than about 74% of their total energy requirements from forage. Consequently, differences in the ability of individual reindeer to feed in winter are potentially more important for survival than differences in their fat content in autumn.

Key words: body composition, energy balance, mortality, reindeer, *Rangifer*, starvation, Svalbard, tooth wear

[1] Research Group in Mammalian Ecology and Reproduction, University of Cambridge Physiological Laboratory, Downing Street, Cambridge CB2 3EG, England.

Rangifer, Special Issue No. 1, 1986: 311 - 314

Introduction

Reindeer and caribou (*Rangifer tarandus)* store fat during summer and autumn which they use in winter when the quality and abundance of their forage declines. In some wild populations starvation is an important cause of natural mortality. However, although there is usually considerable variation in the size of fat reserves within a population (Dauphiné, 1976; Leader-Williams and Ricketts, 1981), it is not clear to what extent the fat content of an animal in autumn predjudices its chances of surviving winter. Fat may be an important source of energy but it is not their principal one. Individual differences in the ability to find food in winter, or actually to feed, might also be expected to have an important effect on survival.

Most natural mortality in Svalbard reindeer *(R.t. platyrhynchus* Vrolik), a sub-species known to have large amounts of subcutaneous fat in autumn (Reimers, *et al.*, 1982), is due to starvation in winter (Tyler, 1986). In this paper, age-specific patterns of variation in (1), the fat content of female Svalbard reindeer in autumn and (2), the condition of their molariform teeth, are compared with age-specific patterns of natural mortality.

Methods

Fat content and energy store.

Total dissectible fat (TDF) was measured in a sample of 17 females aged 1-12 years old shot in September and October 1980 and 1981 on Nordenskiold Land, Spitsbergen (78°N lat.)

(Tyler, 1986). The total amount of retrieval energy contained in this was calculated assuming that dissectible adipose tissue was composed of 92% triacylglycerol, by weight (Reimers, Ringberg and Sørumgaard, 1982), which yielded 9.4 kcal·g^{-1} on complete oxidation.

Energy budget in winter.

The average daily energy expenditure (DEE) of a non-pregnant, adult female reindeer during winter was estimated from the mean live body weight of females during winter (55 kg, Tyler, 1986), assuming a resting metabolic rate (standing) of 4.03 W (Watt) kg$^{-0.75}$ (Nilssen, *et al.*, 1984) and adding on increments for different activities. Activity patterns in winter were measured by watching reindeer continuously for periods of ≥24 hours (Tyler, 1986). Total energy expenditure during winter was calculated by multiplying DEE by 211 days (21 October to 29 May).

Age-specific pattern of mortality.

A discrete sub-population of between 400-800 reindeer lives all the year round in the valley of Adventdalen and its associated side valleys (Tyler, 1986). There is usually negligible net dispersal of reindeer either into or out from this area. The entire area was searched each summer (1979-1984) for carcasses of reindeer which had died during the preceding 12 months. Age at death was determined by counting annulations in the cementum of first incisor teeth (Leader-Williams, 1979).

Tooth wear.

The degree of wear of the first mandibular molar, m 1 (normally the most worn tooth), of each dead reindeer was measured using a dimensionless index devised for this purpose (Tyler, 1986).

Analysis of data.

The homogeneity of samples collected in different years was examined by analysis of variance. The degree of association between TDF, tooth wear and reindeer's age (in whole years) was measured using Spearman's rank correlation coefficient. Comparisons between age classes were made using the Mann-Whitney 'U' test (Siegel, 1956). The null hypothesis was rejected in all cases at the 5% level.

Results

Fat content and energy store.

There were no significant differences in the mass ($F_{(1,15)}=3.19$) or TDF ($F_{(1,15)}=2.36$) of reindeer shot in 1980 and 1981, so results from the two samples were combined. TDF increased with age up to 2 years but declined after that. The correlation between TDF and increasing age was weak, though, and not significant in females aged 4 years and older (females ≥2 years old, r_s= —0.58, n = 15, P <0.05); females ≥4 years old, r_s= —0.35, n = 13, n.s. (P >0.05).

Two 2-year olds each had 16.0 kg TDF in autumn. Females aged 4 years and older had a mean of 10.6 kg TDF (range = 6.4 - 14.5 kg, n = 13). In autumn, therefore, full grown females carried sufficient dissectible fat to yield, on average, approximately 92 000 kcal standard free energy. Their gross energy store (including intramuscular fat and protein) was approximately 105 000 kcal (Tyler, 1986).

Energy budget in winter.

The total energy expenditure of non-pregnant female Svalbard reindeer during winter was approximately 400 900 kcal. Hence, in autumn, females had reserves of energy sufficient to contribute, on average, 26% of their total requirement for winter, not including the cost of gestation. They must, therefore, have had to obtain not less than 295 900 kcal, or 74% of their requirement, by feeding.

Age-specific pattern of mortality.

The youngest females found dead (excluding calves) were 7 years old (N = 127). Age-specific rates of mortality increased almost linearly from the age of 8 years (Tyler, 1986). No reindeer lived more than 15 years.

Tooth wear.

The degree of wear on the first mandibular molar increased linearly with age up to 8 years old after which there was no significant increase in tooth wear (females aged 2-7 years: r_s= 0.84, df = 44, t (one tailed) = 10.27, (P <0.005); females ≥9 years: r_s = —0.12, df = 35, t (one tailed) = —0.72, n.s. (P >0.1). The m1 of females aged 8 years and older was invariably badly worn: in most cases, for example, the infundibulum between the anterior and posterior cusps had disapeared completely (Tyler, 1986).

Fat content and mortality.

Females aged 4 to 7 years old (i.e. those which normally survived winter) were fatter in autumn than females aged 8 years and older but the difference was only just significant ($z = -1.68$, $P = 0.047$). There was no sign of a marked decline in fatness in the latter group, corresponding with the onset of mortality.

Tooth wear and mortality.

All reindeer which starved to death had badly worn molar teeth. The first mandibular molars of reindeer which had starved were significantly more worn than those of animals of the same age which had been shot ($z = -1.90$, $P = 0.029$).

Discussion

Svalbard reindeer undoubtedly need fat in winter but their principal source of energy, nevertheless, is their food. Consequently, individual differences in fat content in autumn are likely to have less significance for survival than differences in rates of food intake in winter. Adult females, for example, would need approximately 6.5 kg more fat (an increase of 60% on the mean autumn value) to compensate for a 20% reduction in their average daily intake of energy from food. However, they would need to eat only about 6% more food per day to compensate for a 20% reduction in autumn TDF.

Both the onset of mortality and age-specific differences in the survival of adult females were associated with increasing wear of the first mandibular molar teeth. Ruminants have evolved hypsodont (high crowned) teeth for grinding forage and the efficiency of mastication presumably decreases as their teeth wear down. The importance of thorough mastication has been demonstrated indirectly in both wild and domestic species (Dean *et al.*, 1980, Freer and Campling, 1963; Campling *et al.*, 1963). Cattle eat less when fed bulky, low quality roughage than when the same ration is finely ground and pelleted (Campling and Freer, 1966). Sheep eat less when their jaw-movements are restricted artificially during rumination (Pearce and Moir, 1964). In both of the above cases voluntary food intake was thought to have been limited by the rate of passage of digesta from the reticulo-rumen, a rate which itself is related to the specific gravity of particles (Campling and Freer, 1962). Conceivably, reindeer whose teeth are in good condition are able to masticate coarse winter forage better, pass the digesta through the gut more rapidly and, hence, eat more than those whose teeth are worn.

An alternative explanation for reduced survival after 7 years of age is that there exists a threshold fatness above which reindeer are safe from starvation. Females 1-7 years old, inclusive, had 10 or more kg dissectible fat in autumn and suffered negligible mortality; most females aged 8 years and older, by contrast, had less than 10 kg fat and many died. The minimum amount of fat a reindeer needs in winter depends on how much food it can find, eat and digest. Consequently, the decline in fatness with increasing age is likely to be sufficient by itself to explain the pattern of mortality *only* if all adult reindeer had the same rate of food intake. This is almost certainly not the case. An individual whose teeth are in good condition is likely to be able to eat more and, hence, to need less fat than one whose teeth are worn. Thus, it does not necessarily follow that reindeer with less than 10 kg TDF suffered increased rates of mortality because their reserves were too small *per se*. The main conclusion from this study is that it is misleading to assume a direct causal link between mortality in winter and body fat content alone.

Acknowledgements

This work was carried out as part of the Norwegian MAB (UNESCO Programme on Man and the Biosphere) project on Svalbard, managed by the Norwegian Polar Research Institute. A Special Research Grant awarded to me by the Eco-Sciences Division of NATO provided additional support. I am grateful to the Cambridge Philosophical Society, the Lightfoot Fund of Selwyn College, Cambridge and especially to ARCO Alaska Inc., for grants which enabled me to attend this meeting. Dr. M.G. Murray kindly read an earlier draft of this paper.

References

Campling, R.C. and **Freer, M.** 1962. Rate of Passage of Inert Particles through the Alimentary Tract of the Cow. *Nature (London)* 188:670-671.

Campling, R.C. and **Freer, M.** 1966. Factors affecting the voluntary intake of food by cows. 3. Experiments with ground, pelleted roughage. *British Journal of Nutrition* 20:229-243.

Campling, R.C., Freer, M., and **Balch, C.C.** 1963. Factors affecting the voluntary intake of food by cows. 6: A preliminary experiment with ground, pelleted hay. — *British Journal of Nutrition 17:263-272.*

Dauphiné, T.C. Jr. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4: Growth, reproduction and energy reserves. — *Canadian Wildlife Service Report Series No. 38. Ottawa, 71 p.*

Dean, R.E., Thorne, E.T. and **Moore, T.D.** 1980. Passage rate of alfalfa through the digestive tract of elk. — *Journal of Wildlife Management 44:272-273.*

Freer, M. and **Campling, R.C.** 1963. Factors affecting the voluntary intake of food by cows. 5: The relationship between the voluntary intake of food, the amount of digesta in the reticulo-rumen and the rate of disappearance of digesta from the alimentary tract with diets of hay, dried grass or concentrates. — *British Journal of Nutrition 17:79-88.*

Leader-Williams, N. 1979. Age determination of Reindeer introduced into South Georgia. — *Journal of Zoology, London 188:501-515.*

Leader-Williams, N. and **Ricketts, C.** 1981. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. — *Oikos 38:27-39.*

Nilssen, K.J., Sundsfjord, J.A., and **Blix, A.S.** 1984. Regulation of metabolic rate in Svalbard and Norwegian reindeer. — *American Journal of Physiology 247:R837-R841.*

Pearce, G.R. and **Moir, R.J.** 1964. Rumination in sheep. 1: The influence of rumination and grinding upon the passage and digestion of food. — *Australian Journal of Agricultural Research 15:635-644.*

Reimers, E., Ringberg, T. and **Sørumgaard,** 1982. Body composition of Svalbard reindeer. — *Canadian Journal of Zoology 60:1812-1821.*

Siegel, S. 1956. Nonparametric Statistics for the Behavioural Sciences. *McGraw-Hill Kogakusha, Tokyo. 312 p.*

Tyler. N.J.C. 1986. Natural limitation of the abundance of wild reindeer on Spitsbergen. — *PhD thesis, University of Cambridge.*