

Effect of diet energy density and season on voluntary dry-matter and energy intake in male red deer

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Abstract

Food intake and growth of red deer is lower in winter than in spring and this reduces the efficiency of venison production. Rumen capacity is also lower during winter and this may contribute to the reduced food intake and therefore growth. In the present study, we investigated the ability of deer to regulate food intake during winter and spring by feeding diets of differing energy densities.

Six groups of eight male red deer calves were housed indoors in separate pens. Each group was given, *ad libitum*, a pelleted diet of a different energy density (8.5, 9.0, 9.5, 10.0, 10.5 and 11.0 MJ metabolizable energy (ME) per kg dry matter (DM) for groups 1 to 6 respectively) but the same amount of protein (156 g/kg DM). Food intake of each group was recorded every 2nd day and animals were weighed every 6 days from 17 May to 9 December. For seasonal comparisons, winter was defined as 24 May to 31 August and spring as 1 September to 9 December.

There was no difference ($P > 0.05$) between the mean live weights of the groups at any time during the study. Live-weight gain (LWG) reached a minimum on 4 July and was lower in winter than spring (161 v. 308 g/day, *s.e.d.* = 10.0, $P < 0.001$). LWG was positively related ($P < 0.001$) to diet ME during winter. DM intake (g/kg $M^{0.75}$ per day) and ME intake (MJ ME per kg $M^{0.75}$ per day) decreased until 16 July and increased thereafter. Mean DM intake was lower in winter than spring (83.5 v. 97.2 g/kg $M^{0.75}$ per day, *s.e.d.* = 2.05, $P < 0.001$). DM intake increased as diet energy decreased ($P < 0.001$) in winter and spring with a steeper slope ($P < 0.05$) in spring than winter. ME intake was not related to diet ME ($P > 0.005$) and was lower in winter than spring (0.82 v. 0.95 MJ/kg $M^{0.75}$ per day, *s.e.d.* = 0.25, $P < 0.001$). Maintenance energy requirement (ME_m) across groups and seasons was calculated to be 0.45 (*s.e.* 0.22) MJ ME per kg $M^{0.75}$ and the energy requirement for LWG (ME_p) was 53 (*s.e.* 8.5) MJ/kg LWG. ME_p was related ($P < 0.01$) negatively to diet ME during winter.

In summary, deer consuming diets with a wide range of energy densities, altered their DM intake, resulting in similar energy intakes and growth rates on all diets. Animals seemed less able to achieve this compensation in winter compared with spring when food intake increased to support the natural rise in growth rate at that time. These results indicate that deer have target growth rates and/or energy intakes that change with season, and are defended by adjusting food intake.

Keywords: energy intake, food intake, red deer, seasonality.

Introduction

Food intake in red deer undergoes a seasonal pattern that follows photoperiod even when they are offered a high quality diet *ad libitum* (Suttie *et al.*, 1984). The general pattern consists of a low intake during winter/short photoperiods and a high intake during summer/long photoperiods. Intake level in ruminants on roughage diets is regulated primarily by rumen fill and the rate of digestion, while on highly digestible or concentrate diets it was

suggested that metabolic feedback likely plays a major rôle (Balch and Campling, 1962). The interaction between physical and metabolic regulation of food intake and diet quality has been investigated in sheep (Montgomery and Baumgardt, 1965; Dinius and Baumgardt, 1970), cattle (Conrad *et al.*, 1964) and white-tailed deer (Ammann *et al.*, 1973). These studies provided evidence that ruminants can regulate food intake to control energy intake unless the diet exceeds physical limits. Intake responses to

The time at which DM intake and live weight changed from a linear decrease to a linear increase was identified using change point linear regression (which fitted better than quadratic curves) fitting two lines.

Equations were developed to model the way $MEI(t)$, ME intake for an animal at time t , is partitioned into maintenance of metabolic live weight ($M^{0.75}$) and energy required for growth over the next day. If ME_m (MJ/kg $M^{0.75}$) is the amount of energy to maintain 1 kg $M^{0.75}$ of metabolic body weight, ME_f (MJ/kg LWG) is the ME required to increase live weight by 1 kg, and $MEI_f(t)$ (MJ) is the daily energy intake available for growth, then

$$MEI(t) = ME_m \times M(t)^{0.75} + MEI_f(t), \quad (1)$$

$$M(t+1) = M(t) + MEI_f(t)/ME_f \quad (2).$$

We can eliminate $MEI_f(t)$ between these equations, and denote change in live weight by $LWG(t+1)$, giving

$$\begin{aligned} LWG(t+1) &= M(t+1) - M(t) \\ &= (MEI(t) - ME_m \times M(t)^{0.75})/ME_f \end{aligned} \quad (3).$$

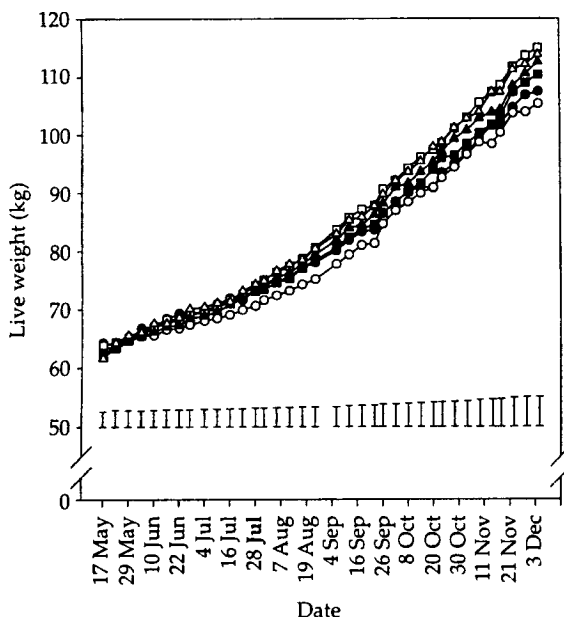


Figure 1 Mean live weight (kg) of groups (no.=8) of male red deer given pelleted diets with energy densities (MJ metabolizable energy per kg dry matter) of 8.5 (●), 9.0 (○), 9.5 (■), 10.0 (□), 10.5 (▲) and 11.0 (△) from 17 May to 9 December. The pooled s.e.d. is shown by the vertical bars at the bottom of the graph.

Equation (3) was fitted by multiple linear regression of $LWG(t+1)$ on $MEI(t)$ and $M(t)^{0.75}$, with the constant set to zero. Seasonal and group differences in ME_m and ME_f were tested within the multiple linear regression model. It was assumed that residuals were uncorrelated in time.

For seasonal comparisons, two parts of the experiment were selected; winter (24 May to 31 August, 100 days) and spring (1 September to 9 December, 100 days), as defined by Fennessy *et al.* (1981).

Results

Live weight

The mean live weights for all groups increased during the experiment (Figure 1). There was no difference ($P > 0.05$) in mean live weight between groups on any sampling date. There was a tendency for the mean group live weights to diverge towards the end of the experiment, however an increase in mean LWG with diet ME (Figure 2) was significant ($P < 0.001$) only during winter. There was a seasonal pattern in mean LWG across all groups (Figure 3) with LWG decreasing during the first part of the

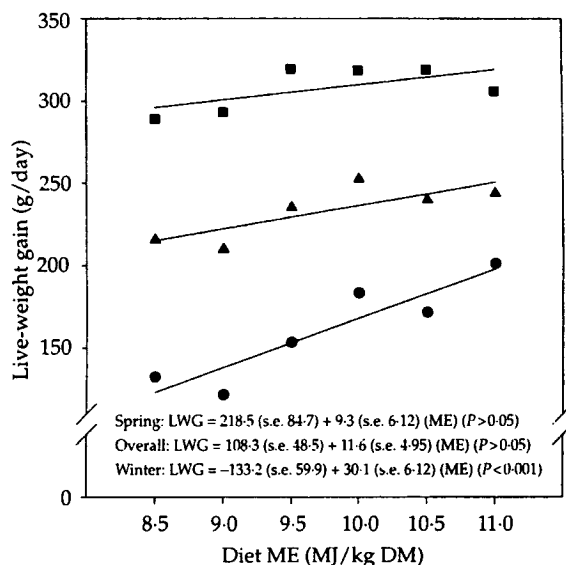


Figure 2 Linear regression of diet metabolizable energy (MJ/kg dry matter) *v* live-weight gain (g/day) for groups (no.=8) of male red deer during winter (24 May to 31 August, ●), spring (1 September to 9 December, ■) and over the entire experimental period (17 May to 9 December, ▲). Equations describing the lines fitted for each of these periods with standard errors for intercepts and slopes and the significance levels of the slopes are at the bottom of the graph.

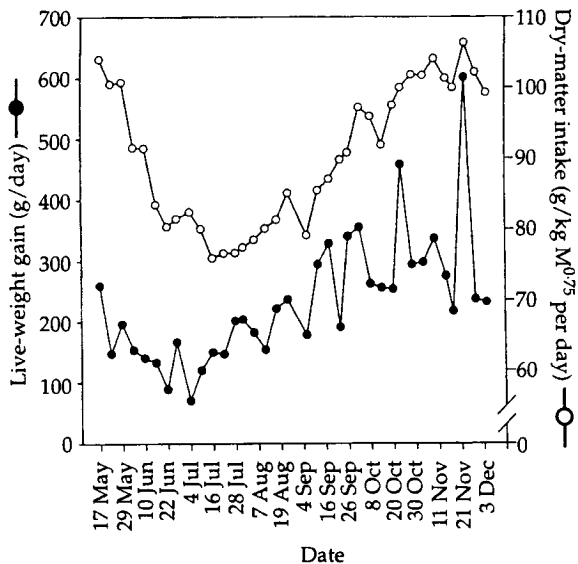


Figure 3 Mean weekly live-weight gain (g/day, ●), and dry-matter intake (g/kg $M^{0.75}$ per day, ○) for groups (no.=8) of male red deer given pelleted diets with a range of energy densities from 8.5 to 11.0 MJ metabolizable energy per kg dry matter, between 17 May and 9 December.

experiment, reaching a minimum on 4 July then increasing after this. LWG between May and December, given in terms of t (days from 4 July) was predicted by the following equations:

$$\text{LWG} = 14.4 \times (\text{ME}) - 26.1 + \begin{cases} -1.20 \times t (t < 4 \text{ July}) \\ 1.46 \times t (t \geq 4 \text{ July}). \end{cases}$$

Mean LWG for all groups was lower in winter (161 g/day) than in spring (308 g/day) (s.e.d. = 10.0, $P < 0.001$).

Dry-matter intake

DM intake had two clear phases, a decrease during the first part of the experiment followed by an increase over the remainder (Figure 3). The time at which DM intake reached a minimum was 16 July. DM intake (g/kg $M^{0.75}$) between May and December was predicted by the following equations:

$$\text{DM intake} = -8.96 \times (\text{ME}) - 159.4 + \begin{cases} -0.46 \times t (t < 16 \text{ July}) \\ 0.22 \times t (t \geq 16 \text{ July}). \end{cases}$$

DM intake for all diets averaged 83.5 g/kg $M^{0.75}$ and 97.2 g/kg $M^{0.75}$ (s.e.d. = 2.05, $P < 0.001$) during winter and spring, respectively.

There was a significant ($P < 0.001$) linear relationship between DM intake (g/kg $M^{0.75}$ per day) and diet ME

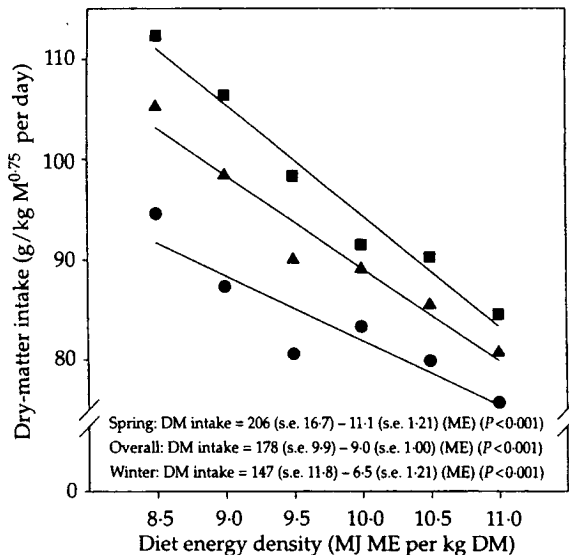


Figure 4 Linear regression of diet metabolizable energy (MJ/kg dry matter (DM) *v.* intake (g/kg $M^{0.75}$ per day) for groups (no.=8) of male red deer during winter (24 May to 31 August, ●), spring (1 September to 9 December, ■) and over the entire experimental period (17 May to 9 December, ▲). Equations describing the lines fitted for each of these periods with standard errors for intercepts and slopes and the significance levels of the slopes are at the bottom of the graph.

(MJ/kg DM) over the whole experiment (Figure 4). A decrease in DM intake with increasing diet energy was significant in winter and spring ($P < 0.001$) with a steeper slope ($P < 0.05$) in spring than winter (-11.1 *v.* -6.5 (s.e.d. 1.71) g/kg $M^{0.75}$ per day for every MJ ME per kg DM increase in diet energy).

Metabolizable energy intake

ME intake (MJ ME per kg $M^{0.75}$ per day) followed a very similar biphasic pattern to DM intake (g/kg $M^{0.75}$ per day) that was characterized by a decline to reach a minimum on 16 July, followed by an increase thereafter. The change in ME intake between May and December could be explained by the following equations with a negative slope prior to 16 July and a positive slope after this date:

$$\text{ME intake} = 0.00415 \times (\text{ME}) - 0.583 + \begin{cases} -0.00622 \times t (t < 16 \text{ July}) \\ 0.00186 \times t (t \geq 16 \text{ July}). \end{cases}$$

There were no significant ($P > 0.05$) relationships between ME intake and diet ME (Figure 5). ME intake across all groups averaged 0.82 and 0.95 MJ/kg $M^{0.75}$ per day (s.e.d. = 0.25, $P < 0.001$) in winter and spring, respectively.

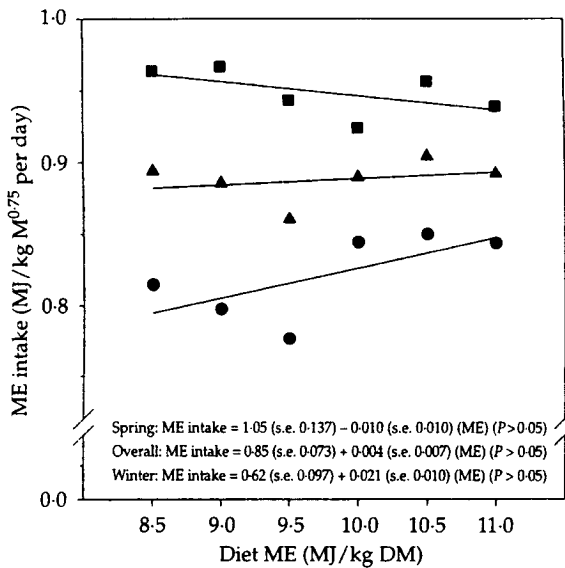


Figure 5 Linear regression of diet metabolizable energy (ME) (MJ/kg dry matter) *v.* ME intake (MJ/kg M^{0.75} per day) for groups (no.=8) of male red deer during winter (24 May to 31 August, ●), spring (1 September to 9 December, ■) and over the entire experimental period (17 May to 9 December, ▲). Equations describing the lines fitted for each of these periods with standard errors for intercepts and slopes and the significance levels of the slopes are at the bottom of the graph.

There was a tendency for ME intake per kg LWG to decrease with increasing diet ME concentration however this was significant ($P < 0.001$) only during winter. There was no evidence of significant variation in ME_m with either diet energy or season and ME_m over the entire experimental period was calculated to be 0.45 ± 0.22 MJ ME per kg M^{0.75}. Using this value of 0.45 for ME_m , ME_f was calculated by group and season (Figure 6) and produced a significant ($P < 0.01$) relationship with diet energy during winter only. There was no evidence of a difference in ME_f between winter (59) and spring (51, s.e.d. = 0.43, $P > 0.05$). The mean value for ME_f overall was 53 (s.e. 8.5) MJ/kg LWG.

Discussion

This study has shown that male red deer regulate DM intake in order to achieve a certain energy intake and growth rate. The deer were able to alter DM intake and achieve similar growth rates over the range of diet energy densities used in this study, in both winter and spring. This suggests that lower growth rates during winter than spring were not caused by limitations to DM intake and supports the concept that appetite is a consequence of the seasonal

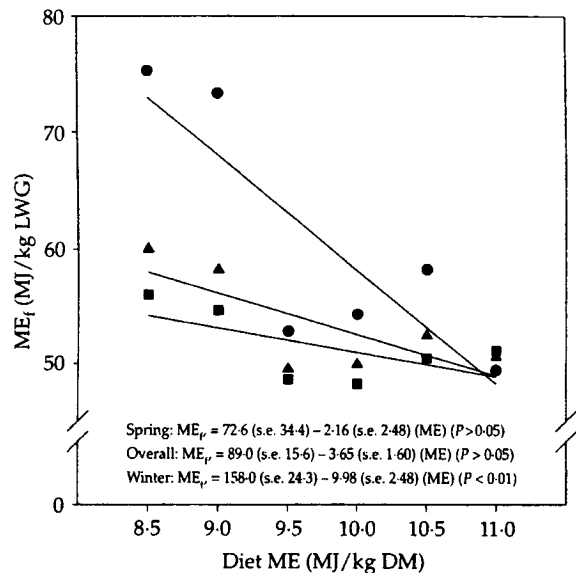


Figure 6 Linear regression of diet metabolizable energy (ME) (MJ/kg dry matter) *v.* energy requirement per kg of live-weight gain (ME_f , MJ/kg LWG) for groups (no.=8) of male red deer during winter (24 May to 31 August, ●), spring (1 September to 9 December, ■) and over the entire experimental period (17 May to 9 December, ▲). Equations describing the lines fitted for each of these periods with standard errors for intercepts and slopes and the significance levels of the slopes are at the bottom of the graph.

changes in growth rate, rather than its cause (Kay, 1988). Further evidence that the seasonal growth cycle drives appetite was found in the present study when the seasonal increase in growth rate on the 4 July was followed by the increase in food and energy intake on the 16 July.

Ruminants have evolved a digestive system that is able to cope with poor quality forages but a slow rate of digestion of this material means that rumen capacity may limit intake (Forbes and France, 1993). With food of a higher quality, intake may be determined by metabolic feedback before the physical constraints can apply (Illius and Jessop, 1996). Food intake is therefore a result of the integration of a complex set of signals (Forbes, 1996). The net result is a general increase in intake as energy content or digestibility of the diet decreases (Conrad *et al.*, 1964; Dinius and Baumgardt, 1970; Ammann *et al.*, 1973). We have found a similar situation exists in red deer with a clear increase in DM intake as diet energy density decreased. While intake may also be reduced on a high barley, low roughage diet due to acidosis (Elam, 1976), there were no signs of this in the present study.

Red deer are an interesting species in which to study food intake regulation because they undergo a sudden increase in growth rate in spring. If the appetite cycle reflects the sum of nutrient demands from other seasonal cycles rather than a primary response (Barry *et al.*, 1991), then food intake must increase for the faster growth to occur. It may be predicted that if deer were given a poor diet in spring the increased metabolic demand for energy would exceed the capacity of the digestive system to process the dietary intake. However, evidence from the present study, such as the decrease in LWG and ME_f with diet energy, which was significant only in winter and the steeper slope of the DM intake *v.* diet energy relationship in spring suggest that it was more difficult to compensate for lower diet energy in winter than in spring. This may be because the reported increases in digestive capacity from winter to spring (Domingue *et al.*, 1991; Sibbald and Milne, 1993; Freudenberger *et al.*, 1994) more than compensates for the increased intake required on the low energy diet. This mechanism would enable an increase in growth rate in spring even if food quality does not improve.

There was no evidence of food intake reaching a plateau on the lower energy density diets in this study, indicating that the physical limit to food intake was not reached. This plateau has been found to occur on diet energy densities of 7.35 (Ammann *et al.*, 1973) and 8.4 (Dinius and Baumgardt, 1970) MJ ME per kg DM in white-tailed deer and sheep respectively. It is therefore likely that in the present study, the energy content of diet 1 was not low enough to cause the deer to reach this physical limit. This suggests that intake was limited by metabolic factors on diets 2 to 6 as these animals physically could have eaten as much DM as those on diet 1. In fact during winter, if animals on diet 6 had eaten the equivalent DM as animals on diet 1, it could have supported an improved growth rate of around 100 g/day in these animals. This leads to the question, why do ruminants not exploit this capacity to increase food intake? (Ketelaars and Tolkamp, 1992). This would have obviously enabled animals on the higher energy diets to grow faster. However, it has been suggested that it is unlikely that animals actually try to grow as fast as they can and instead aim for an optimum, rather than a maximum (Ketelaars and Tolkamp, 1992). One possible reason for this would be that the consequences might be severe if food quantity and quality cannot supply the energy demand of a maximum growth rate. The results of the present study suggest that seasonal changes in the deer digestive system may allow it to cope with the increased metabolic demand in spring even on a unchanging diet of relatively poor quality.

The marked increase in DM intake with decreasing diet energy density suggests that the animals were compensating in order to reach some target. It is not clear from the present study whether this target was a particular live weight or growth rate, for the given season, a particular energy intake or some combination of these. Evidence that such a target may exist was seen when fallow deer given restricted amounts of food during spring were forced below the growth path of control animals given food *ad libitum*. The restricted animals then compensated by maintaining a higher food intake than their controls during the rut (Jopson *et al.*, 1997). It is likely that various nutrient-related signals act together to determine intake in relation to rates of nutrient utilization and that certain rates of nutrient utilization or fuel oxidation are defended in relation to the animals seasonal growth state. In this way, the seasonal change in the drive to grow may cause a change in energy homeostasis, and in the integration of signals about the animal's metabolic state by the central nervous system. In the present study, the alteration in energy homeostasis was seen when there was a shift from a decreasing rate of LWG to an increasing rate of LWG on 4 July. This was followed on 16 July by an appetite response from a decreasing to an increasing DM intake and ME intake.

A gradual divergence in live weights occurred between the groups, with animals on the lower diet energies tending to grow more slowly, however this effect was only significant in winter. One possible explanation for this may be a reduction in digestive efficiency as a physical limit to gut fill is approached and failure to achieve the calculated ME from the diets with higher straw contents. A high ME_f with low diet energy in winter may indicate poor energy yield from those diets. No change in digestibility of forage with either season or intake level has been found however (Freudenberger *et al.*, 1994).

The calculated maintenance energy value of 0.45 MJ ME per kg $M^{0.75}$ is similar to values found previously for male red deer indoors of 0.45 to 0.5 MJ ME per kg $M^{0.75}$ (Simpson *et al.*, 1978; Milne *et al.*, 1987) and 0.57 MJ ME per kg $M^{0.75}$ (Fennessy *et al.*, 1981). It is also close to the value for wapiti and moose of 0.57 MJ ME per kg $M^{0.75}$ (Cool and Hudson, 1996). The ME_f of 53 MJ/kg live-weight gain found in the present study, is higher than that reported for male red deer by Fennessy *et al.* (1981) of 37 MJ/kg live-weight gain. However, it is similar to the value obtained for red deer hinds of 55 MJ/kg live-weight gain (Suttie *et al.*, 1987) and that calculated for mixed sex calves indoors in winter of 53 to 57 MJ/kg live-weight gain (Milne *et al.*, 1987). The probable reason for the higher value for hinds than stags was

suggested as being a difference in the composition of live-weight gain (Suttie *et al.*, 1987). Seasonal differences in ME_f have been found when a constant ME_m value was used (Milne *et al.*, 1987). However, in the present study, there was no difference in ME_f between seasons, suggesting there is little change in the composition of LWG in animals between these two periods. There is very little compositional data available for animals in their first year of life to support this, however extrapolation from older animals suggests that fat deposition only begins above 85 to 90 kg live weight (Suttie *et al.*, 1983). There was however, a tendency for a lower ME_f in spring when growth was fastest and when a faster glucose clearance rate may facilitate tissue growth (McMahon *et al.*, 1997). The results of the present study would suggest that maintenance energy requirements could be used with increasing confidence, while energy requirements for gain should be used with more caution until further work is carried out.

In conclusion, this study has demonstrated that red deer will compensate for lower diet energy by increasing intake, and thereby regulate energy intake and growth rate at different levels in winter from those in spring.

References

- Ammann, A. P., Cowan, R. L., Mothershead, C. L. and Baumgardt, B. R. 1973. Dry matter and energy intake in relation to digestibility in white-tailed deer. *Journal of Wildlife Management* 37: 195-201.
- Baile, C. A. and Forbes, J. M. 1974. Control of feed intake and regulation of energy balance in ruminants. *Physiology Reviews* 54: 160-214.
- Balch, C. C. and Campling, R. C. 1962. Regulation of voluntary food intake in ruminants. *Nutrition Abstracts and Reviews* 32: 669-686.
- Barry, T. N., Suttie, J. M., Milne, J. A. and Kay, R. N. B. 1991. Control of food intake in domesticated deer. In *Physiological aspects of digestion and metabolism in ruminants* (ed. T. Tsuda, Y. Sasaki and R. Kawashima) *proceedings of the seventh international symposium on ruminant physiology*, pp. 385-401. Academic Press, San Diego.
- Blaxter, K. L., Kay, R. N. B., Sharman, G. A. M., Cunningham, J. M. M. and Hamilton, W. J. 1974. *Farming the red deer*. The first report of an investigation by the Rowett Research Institute and the Hill Farming Research Organisation. Her Majesty's Stationery Office, Edinburgh.
- Conrad, H. R., Pratt, A. D. and Hibbs, J. W. 1964. Regulation of feed intake in dairy cows. I. Change in importance of physical and physiological factors with increasing digestibility. *Journal of Dairy Science* 47: 54-62.
- Cool, N. and Hudson, R. J. 1996. Requirements for maintenance and live weight gain of moose and wapiti calves during winter. *Rangifer* 16: 41-45.
- Dinius, D. A. and Baumgardt, B. R. 1970. Regulation of food intake in ruminants. 6. Influence of caloric density of pelleted rations. *Journal of Dairy Science* 53: 311-316.
- Domingue, B. M. F., Dellow, D. W., Wilson, P. R. and Barry, T. N. 1991. Comparative digestion in deer, goats, and sheep. *New Zealand Journal of Agricultural Research* 34: 45-53.
- Elam, C. J. 1976. Acidosis in feedlot cattle: practical observations. *Journal of Animal Science* 43: 898-901.
- Fennessy, P. F. 1982. Growth and nutrition. In *The farming of deer. World trends and modern techniques* (ed. D. Yerex), pp. 105-114. Agricultural Promotion Associates Ltd, Wellington, New Zealand.
- Fennessy, P. F., Moore, G. H. and Corson, I. D. 1981. Energy requirements of red deer. *Proceedings of the New Zealand Society of Animal Production* 41: 167-173.
- Fennessy, P. F. and Thompson, J. M. 1989. Biological efficiency for venison production in red deer. *Proceedings of the New Zealand Society of Animal Production* 49: 5-10.
- Forbes, J. M. 1996. Integration of regulatory signals controlling forage intake in ruminants. *Journal of Animal Science* 74: 3029-3035.
- Forbes, J. M. and France, J. 1993. Introduction. In *Quantitative aspects of ruminant digestion and metabolism* (ed. J. M. Forbes and J. France), pp. 1-10. University Press, Cambridge.
- Freudenberger, D. O., Toyokawa, K., Barry, T. N., Ball, A. J. and Suttie, J. M. 1994. Seasonality in digestion and rumen metabolism in red deer (*Cervus elaphus*) fed on a forage diet. *British Journal of Nutrition* 71: 489-499.
- Friedman, M. I. 1991. Metabolic control of calorie intake. In *Chemical senses* (ed. M. I. Friedman, M. G. Tordoff and M. R. Kare), pp. 19-37. M. Dekker, New York.
- Illius, A. W. and Jessop, N. S. 1996. Metabolic constraints on voluntary intake in ruminants. *Journal of Animal Science* 74: 3052-3062.
- Jopson, N. B., Thompson, J. M. and Fennessy, P. F. 1997. Tissue mobilization rates in male fallow deer (*Dama dama*) as determined by computed tomography: the effects of natural and enforced food restriction. *Animal Science* 65: 311-320.
- Kay, R. N. B. 1988. Seasonal variation of appetite in ruminants. In *Recent developments in ruminant nutrition 2* (ed. W. Haresign and D. J. A. Cole), pp. 34-45. Butterworths, London.
- Kenward, M. G. 1987. A method for comparing profiles of repeated measurements. *Applied Statistics* 36: 296-308.
- Ketelaars, J. J. M. H. and Tolkamp, B. J. 1992. Toward a new theory of feed intake regulation in ruminants. 1. Causes of differences in voluntary feed intake: critique of current views. *Livestock Production Science* 30: 269-296.
- McMahon, C. D., Corson, I. D., Littlejohn, R. P., Stuart, S. K., Veenvliet, B. A. and Suttie, J. M. 1997. Effects of season, protein and nutritional state on glucose tolerance during an annual cycle of growth in young red deer. *Journal of Endocrinology* 154: 275-283.
- Milne, J. A., MacRae, J. C., Spence, A. M. and Wilson, S. 1978. A comparison of the voluntary intake and digestion of a range of forages at different times of the year by the sheep

- and the red deer (*Cervus elaphus*). *British Journal of Nutrition* **40**: 347-357.
- Milne, J. A., Sibbald, A. M., McCormack, H. A. and Loudon, A. S. I. 1987. The influences of nutrition and management on the growth of red deer calves from weaning to 16 months of age. *Animal Production* **45**: 511-522.
- Montgomery, M. J. and Baumgardt, B. R. 1965. Regulation of food intake in ruminants. 1. Pelleted rations varying in energy concentration. *Journal of Dairy Science* **48**: 569-574.
- Sibbald, A. M. and Milne, J. A. 1993. Physical characteristics of the alimentary tract in relation to seasonal changes in voluntary food intake by the red deer (*Cervus elaphus*). *Journal of Agricultural Science, Cambridge* **120**: 99-102.
- Simpson, A. M., Webster, A. J. F., Smith, J. S. and Simpson, C. A. 1978. The efficiency of utilization of dietary energy for growth in sheep (*Ovis ovis*) and red deer (*Cervus elaphus*). *Comparative Biochemistry and Physiology, A: Comparative Physiology* **59**: 95-99.
- Suttie, J. M., Corson, I. D. and Fennessy, P. F. 1984. Voluntary intake, testis development and antler growth patterns of male red deer under a manipulated photoperiod. *Proceedings of the New Zealand Society of Animal Production* **44**: 167-170.
- Suttie, J. M., Fennessy, P. F., Veenvliet, B. A., Littlejohn, R. P., Fisher, M. W., Corson, I. D. and Labes, R. E. 1987. Energy nutrition of young red deer (*Cervus elaphus*) hinds and a comparison with young stags. *Proceedings of the New Zealand Society of Animal Production* **47**: 111-113.
- Suttie, J. M., Goodall, E. D., Pennie, K. and Kay, R. N. B. 1983. Winter food restriction and summer compensation in red deer stags (*Cervus elaphus*). *British Journal of Nutrition* **50**: 737-747.

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