COMPARATIVE DIGESTIVE PHYSIOLOGY AND METABOLISM OF THE RED DEER AND THE SHEEP

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SUMMARY

Differences between the red deer and the sheep in voluntary intake, digestibility, mean retention time and nitrogen and energy metabolism are outlined. Seasonal changes in the voluntary intake and energy metabolism for red deer are large and the changes in voluntary intake are shown to be related to changes in the amount of digesta in the rumen and in rumen capacity. It is concluded that the differences in digestive physiology and metabolism are unlikely to have a major effect on the biological efficiency with which a pastoral resource would be utliized.

INTRODUCTION

Comparative experimentation on the digestive physiology and metabolism of the sheep and the red deer has been carried out for two major reasons. First, sheep and red deer are potential users of similar types of land resource, and secondly, since the sheep has been widely used as a model for studying the digestive and metabolic functions of the ruminant, it has been used as a reference species in the subsequent study of the red deer. The aim of this paper is to describe those aspects of the digestive physiology and metabolism of the two species which have been investigated recently, and to discuss how any differences between the species may influence the biological efficiency with which a pastoral resource is utilized. The aspects to be considered will be voluntary intake, digestibility and mean retention time of undigested residues in the gut of both species given roughages, and facets of nitrogen and energy metabolism.

INTAKE AND DIGESTION

Valid comparisons between voluntary food intakes by red deer and sheep are difficult to make because of the differences in the mature liveweights of the two species and in physiological maturity at the same chronological age. Voluntary intake is considered to be proportional to $W^{0.75}$ of different mature species (Taylor and Young, 1968), but this may not apply to immature animals.

Most experiments in which voluntary intakes of the two species have been measured have been conducted with immature animals of similar age and physiological condition, but no better means of expressing the voluntary intakes other than on a $W^{0.75}$ basis has been proposed. In this paper all voluntary intakes will be expressed on this basis.

With ground, pelleted and chopped roughages with an organic matter digestibility of approximately 60% or above, the voluntary intake by sheep has been found to be similar to or greater than that by deer (Kay and Goodall, 1976; Milne *et al.*, 1978). With low-quality roughage diets, Milne *et al.* (1978) found that castrated male red deer had considerably greater voluntary intakes than sheep of similar age and physiological condition (Table 1). This apparent interaction between quality of diet and animal species in voluntary intake requires careful consideration. Pronounced seasonal effects on voluntary intake have been observed in red deer (Simpson, 1976; Milne *et al.*, 1978) as well as in other Cervidae (Long *et al.*, 1966; McEwan and Whitehead, 1970), and these are greater than those reported for sheep (Gordon, 1964). Voluntary intakes are lower in winter than summer and these changes have been shown to be related to changes in day-length (Simpson, 1976). This would suggest that, between species, differences among poor-quality roughage diets would be greater in summer than in winter (Table 1), and that consequently there is a need to compare the voluntary intake of diets at more than one time in the year to take account of any interaction between diet quality and species in voluntary intake.

TABLE 1: VOLUNTARY INTAKES OF ORGANIC MATTER BY RED DEER AND SHEEP GIVEN THE SAME POOR-QUALITY ROUGHAGES IN WINTER AND LATE SPRING (g/kg $W^{0.75}$/day)

	Winter		*Late Spring*		*SE of Mean*
	Red Deer	*Sheep*	*Red Deer*	*Sheep*	
Agrostis/Festuca spp.	46.3	23.1	70.0	24.6	3.45
Heather	29.5	17.8	54.9	23.8	2.81

Because of the relationships between voluntary intake, digestibility and mean retention time (MRT), particularly with long medium-quality roughages, comparisons between species in digestibility and MRT are best made at similar intakes. Earlier work (Maloiy *et al.*, 1970; Kay and Goodall, 1976) suggested that red

deer digested food less well than sheep, and this was associated with a shorter MRT in the gut. Results from experiments in which a dried-grass pellet diet was fed support these findings, but with a chopped dried-grass diet no differences were found (Table 2). Fennessy *et al.* (1980) have recently reported higher digestibility values for red deer than for sheep when both were given a high-quality diet and a lower-quality meadow hay. It can thus be concluded that differences between the species in digestibility and MRT at equal intakes are unlikely to be large.

TABLE 2: INTAKES AND DIGESTIBILITIES OF ORGANIC MATTER, RUMEN AND TOTAL GUT MEAN RETENTION TIMES OF ^{103}RuP, IN RED DEER AND SHEEP GIVEN DIETS AT EQUAL INTAKE

	OM Intake (g/day)	*Apparent Digestibility of OM (%)*	*MRT (h)*	
			Rumen	*Total*
Dried grass pellet:				
Red deer	1 764	58.4	12.0	21.1
Sheep	1 612	60.7	12.9	26.3
SE of mean	76.6	0.89	1.99	2.28
Chopped dried grass:				
Red deer	1 070	62.9	25.1	41.1
Sheep	918	63.6	18.3	43.3
SE of mean	76.9	0.65	1.68	2.85

Mean retention times of a particulate-phase marker in the rumen were shorter for the red deer than the sheep when poor-quality roughages were given *ad libitum,* and were associated with lower digestibilitties and higher intakes (Milne *et al.,* 1978). An example is given in Table 3 for an *Agrostis/Festuca* herbage diet offered to both species in winter and late spring. Within any one set of measurements the results are consistent with previously established relationships between intake, digestibility and MRT, with the rumen being considered the most important part of the digestive tract to influence these relationships. However, these relationships do not hold between seasons for the red deer. Voluntary intakes increased but were not associated with a depression in digestibility or MRT (Table 3). The hypothesis that the voluntary intake of long roughages is controlled by the filling effect in the rumen can therefore only hold for the red deer at both times of year if the dimensions of the digestive tract, or some part of it, increase.

TABLE 3: INTAKES AND DIGESTIBILITIES OF ORGANIC MATTER, RUMEN AND TOTAL MEAN RETENTION TIMES OF ^{103}RuP, IN RED DEER AND SHEEP GIVEN *AGROSTIS/FESTUCA* SPP. *AD LIBITUM*

	OM Intake ($g/kg\ W^{0.75}/day$)	*Apparent Digestibility of OM (%)*	*MRT (h)* *Rumen*	*Total*
Winter:				
Red deer	46.3	43.3	17.0	27.4
Sheep	23.1	52.4	25.2	56.1
Late spring:				
Red deer	70.0	46.0	23.4	32.5
Sheep	24.6	52.0	28.0	53.4
SE of mean	3.45	1.81	2.41	3.09

In an experiment conducted to examine this hypothesis, twelve 4-year-old castrated male deer were given a medium-quality grass hay *ad libitum* in the winter. A representative group of six animals was slaughtered (after measurements of voluntary intake, digestibility and rumen marker MRT had been made) to determine the weight of gut components and contents. The remaining animals were offered the same hay in late spring and the same procedures adopted as for the winter period. Table 4 (Spence and Milne, unpublished data) shows that, in agreement with the previous finding, an increase in intake between winter and late spring was not associated with any change in digestibility and rumen or total marker MRT. However, the dry weight of rumen contents was significantly ($P < 0.05$) higher in late spring than in the winter, and the amount of liquid in the rumen was also

TABLE 4: CHANGES IN SOME DIGESTION PARAMETERS ASSOCIATED WITH SEASONAL CHANGES IN INTAKE IN RED DEER GIVEN A GRASS HAY

	Winter	*Late Spring*	*SE of Mean*
Voluntary intake of OM (g/day)	1 436	1 938	110.9
Apparent digestibiliy of OM (%)	57.1	57.0	0.75
Rumen mean retention time (h)	21.1	20.9	0.88
DM weight of rumen contents (kg)	1.40	2.37	0.211
Liquid content of rumen (kg)	10.6	13.1	1.13
Rumen capacity (litres)	16.3	19.9	0.71

higher. Rumen capacity, as measured by the method described by Tulloh (1966), was also significantly ($P < 0.05$) greater in late spring.

These findings are interpreted as indicating that the control of voluntary intake can still be exerted by a filling effect in the rumen provided that a higher threshold limit is postulated in the late spring to accommodate the additional weight of dry matter found in the rumen. Levels of the hormone prolactin have been found to increase with increasing day-length in the red deer (Suttie, 1980), and it is possible that the effect of increased prolactin levels may directly or indirectly alter the response of stretch receptors in the rumen wall, allowing greater distention of the rumen and the setting of a higher threshold to the amount of rumen contents. If such a mechanism does not operate, then the filling-effect theory of voluntary intake control for medium-quality long roughage would be difficult to sustain as an explanation for the seasonal changes in the voluntary intake of the red deer.

NITROGEN AND ENERGY METABOLISM

There is little evidence of differences between the two species in the aspects of nitrogen (N) digestion and metabolism studied. At the same N intakes, the two species have not been found to differ in apparent N digestibility or the amount of N excreted in the urine (Maloiy *et al.*, 1970; Milne *et al.*, 1978; Simpson *et al.*, 1978). Maloiy *et al.* (1970) also concluded from an examination of the concentrations of urea in plasma and ammonia in rumen fluid over a range of N intakes that sheep and red deer were similar in their ability to recycle N between blood plasma and the rumen.

Further experimentation with sheep (MacRae *et al.*, 1979) and red deer (MacRae, Milne, Spence and Lamb, unpublished data) given similar poor-quality *Agrostis/Festuca* diets has provided corroborative evidence. Three red deer were given *Agrostis/Festuca* diets in winter and late spring over a range of intakes, and measurements were made of urea entry rates and amounts of urea transferred from plasma to the rumen using the methods described by MacRae *et al.* (1979). When the results from both experiments are expressed on a similar N intake basis, urea entry rates (sheep 0.43, red deer 0.49 g urea-C/day/g N intake) and urea transfer from plasma to rumen (sheep 0.060, red deer 0.068 g urea-C/day/g N intake) were similar for both species.

Metabolic heat production in the red deer appears to be considerably higher than in the sheep (Brockway and Maloiy, 1968). Basal metabolic rate for other species of deer (Silver *et al.*, 1969) has also been found to be higher than the interspecies mean. Simpson *et al.* (1978) estimated that the metabolizable energy (ME) requirements for maintenance for red deer were 464 kJ/kg $W^{0.75}$/day, 38% higher than those found for sheep. Seasonal differences in ME requirementts for maintenance for the red deer were also found by these authors, with an increase in requirement in the summer of 10% over the winter values. Even greater seasonal differences have been reported for other species of deer (Holter *et al.*, 1976). The magnitude of the difference in ME requirements for maintenance of the two species may not be as great as the results of these experiments would suggest. Red deer are more difficult to accustom to the measurement procedures than the sheep, and this may lead to elevated heat production associated with stress (Knox *et al.*, 1974). However, the ME requirements for maintenance found for red deer are not very different from those suggested for cattle (MAFF, 1975). A similar comparison between the voluntary intake of cattle and red deer was also made by Milne *et al.* (1978).

From the small amount of evidence available there is little to suggest that the metabolizability of diets or the utilization of ME for growth differs between the red deer and the sheep.

BIOLOGICAL EFFICIENCY

The principal differences so far identified between the two species in nutritional parameters are in the intakes of lower-quality roughages and in maintenance requirements. In the UK, low-quality roughage is likely to be ingested by both species in winter in most pastoral systems. On the basis of the results of Milne *et al.* (1978), the red deer would ingest twice as much digestible energy as the sheep. However, the red deer would have an approximately 30% greater ME requirement for maintenance at this time. Moreover, red deer are considered to be less well adapted to cold-weather stress than the sheep (Simpson, 1976), although this has not yet been adequately quantified. Consequently there may be only a small effect of these combined sets of nutritional parameters on the biological efficiency with which pastoral resources are converted to agriculturally useful output by the two species. Differences in behaviour between the species could modify this interpretation of the nutritional results, but

there is a dearth of quantitative evidence on such factors as shelter-seeking and ranging ability which may influence energy expenditure, or on the mechanics of grazing which may affect voluntary intake. There is also little evidence that the efficiency with which summer pasture is used would be influenced by any differences in the digestive or metabolic function of the two species not associated with differences in date of parturition.

It is thus concluded that the differences so far identified between the two species in digestive physiology and metabolism are unlikely to lead to large differences in the biological efficiency with which they use pastoral resources, Such differences in biological efficiency are unlikely to be as large as those arising, for example, from the different reproductive rates, dates of parturition and carcass fat contents of the red deer and sheep.

REFERENCES

Brockway, J. M.; Maloiy, G. M. O., 1968. *J. Physiol., Lond., 194*: 22.
Fennessy, P. F.; Greer, G. J.; Forss, D. A., 1980. *Proc. N.Z. Soc. Anim. Prod., 40*: 158.
Gordon, J. G., 1964. *Nature, Lond., 204*: 798.
Holter, J. B.; Hayes, H. H.; Wiley, J., 1976. In *Proc. 7th Symp. Energy Metabolism of Farm Animals* (Ed. M. Vermorel). EAAP Publ. No. 19. p. 307.
Kay, R. N. B.; Goodall, E. D., 1976. *Proc. Nutr. Soc., 35*: 98A.
Knox, K. L.; Wesley, D.; Crownover, J. C.; Nagy, J., 1974. In *Energy Metabolism of Farm Animals* (Eds. K. H. Menke, J. H. Lantzch, J. R. Reichl). University of Hohenheim Press, Hohenheim. p. 229.
Long, T. A.; Gowan, R. L.; Strawn, G. D.; Wetzel, R. S.; Miller, R. C., 1966. *PA agric. exp. Stn Prog. Rep. No. 262.*
McEwan, E. H.; Whitehead, P. E., 1970. *Can. J. Zoo., 48*: 905.
MacRae, J. C.; Milne, J. A.; Wilson, S.; Spence, A. M., 1979. *Br. J. Nutr., 42*: 525.
Maloiy, G. M. O.; Kay, R. N. B.; Goodall, E. D.; Topps, J. H., 1970. *Br. J. Nutr., 24*: 843.
Ministry of Agriculture, Fisheries and Food, 1975. *Tech. Bull. No. 33.* HMSO, London.
Milne, J. A.; MacRae, J. C.; Spence, A. M.; Wilson, S., 1978. *Br. J. Nutr., 40*: 347.
Silver, H.; Colovos, N. F.; Holter, J. B.; Hayes, H. H., 1969. *J. Wildl. Mgmt, 44* (3): 490.
Simpson, A. M., 1976. PhD Thesis, University of Aberdeen.
Simpson, A. M.; Webster, A. J. F.; Smith, J. S.; Simpson, C. A., 1978. *Comp. Biochem. Physiol., 59A*: 95.
Suttie, J. M., 1980. *Proc. 2nd Reindeer Symp., Roros, Norway* (September, 1979). In press.
Taylor, St. C. S.; Young, G. B., 1968. *Anim. Prod., 10*: 393.
Tulloh, N. M., 1966. *N.Z. Jl agric. Res., 9*: 999.