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The relationship between the control of meal size and the control of daily intake in ruminants

M. Gill*, D. Romney

Natural Resources Institute, Chatham Maritime, Kent ME4 4TB, UK

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Abstract

The relationship between factors which determine meal size and the determinants of daily intake is examined with the aim of assessing whether daily intake can be predicted by simulating the control of individual meals. The hypothesis that factors limiting the size of the first meal dominate the control of daily intake is discounted, based on eating patterns for forages. The potential for predicting intake using models which simulate the within-day pattern of eating is considered, but observations that meal size can change with restricted access to feed suggests that "set points" for factors ending meals vary in response to a control operating on a longer time scale. It is widely accepted that the intake "drive" is somehow related to the energy/oxygen metabolism of the animal, and meal size and pattern may be controlled to minimise the production of waste products. Alternatively, the degree of "discomfort" accepted by an animal may be greater the further the animal is from meeting its "target". It is concluded that there is a need to understand better the relationship between factors controlling the size of individual meals and the control of daily intake to improve our ability to characterize feeds on the basis of their intake potential.

Key words: Ruminant; Voluntary intake; Meal size

1. Introduction

Intake over a 24 h period is equal to the sum of the amount eaten in individual meals. However, there is increasing evidence, at least for ruminants, that different factors may predominate in ending meals during any one 24 h period (Thiago et al., 1992b) and further, that more than one factor may contribute simultaneously to limiting ingestion over short periods (Mbanya et al., 1993). These findings raise the question as to whether the representation within a model of the effect of these varied factors which control meal size can be used to predict the daily intake of particular feeds.

This paper considers two hypothesis: (a) that the primary factor limiting daily intake is the one which dominates in ending the first (main) meal; (b) that daily intake can be predicted by integrating the effects of the factors limiting the size of each meal; and then discusses how the factors controlling meal size might relate to the animal's "drive" to eat.

2. Control of the size of the first meal

Even when offered feed ad lib., ruminants restrict their intake to a number of discrete periods (meals) per day, with the first meal after fresh feed is offered, generally being the largest. Many intake studies have con-

*Corresponding author.

centrated on understanding the factors controlling the size of this meal as an indicator of factors controlling daily intake.

Studies by Campling and colleagues in the sixties measured the weight of digesta in the reticulo-rumen before and after a main meal (e.g. Freer and Campling, 1963) and these authors concluded that with low digestibility dry feeds (but not silage), the amount of digesta in the rumen signalled the end of the meal. Data such as these were interpreted as supporting the theory that rumen "fill" was a dominant factor in limiting the intake of forages by ruminants. This theory was widely accepted as dogma until the mid eighties when the original data were re-analysed (Grovmum, 1987) and the weight of digesta in the rumen at different times of day was recorded. Grovmum's re-analysis raised doubts regarding the interpretation of the original data, while the rumen data demonstrated considerable variation in digesta weight, even in animals with ad lib. access to feed. The greatest weight of digesta is frequently recorded in the early evening for sheep (Cruickshank et al., 1987), beef (Thiago, 1988) and dairy cattle (Gasa et al., 1991) i.e. disputing the claim that ruminants eat to maintain a fairly constant weight of rumen digesta. These results could be interpreted as demonstrating that the weight of digesta does not equate with rumen fill (which would then be difficult to represent mathematically) that rumen fill is not the sole factor limiting intake and/or that the factor(s) which terminates the first meal is not dominant in controlling daily intake.

To examine this latter hypothesis further, the weights of digesta in the rumen at the end of the first/main meal in cattle offered grass hay and silage (made from the

same sward), at a restricted level of 20 gDM/kg LW (Thiago et al., 1992 a,b), and grass and clover hay offered at 17.6 gDM/kg LW, (Gill and England, unpublished observations) are presented in Table 1, together with the voluntary intake for the same feeds when offered ad lib. The cattle offered the grass hays stopped eating at a higher weight of digesta in the rumen than for clover hay or grass silage. This suggests that the size of this first meal for clover hay and grass silage was not restricted by rumen fill. Alternatively, stimulation of chemo-receptors in the rumen by the end-products of fermentation either in the rumen or after absorption (Forbes, 1986) could have made a significant contribution to the signals ending the meal. More rapid release of fermentation products would be expected from the faster digestion (as measured in dacron bags) of grass silage compared to hay (Thiago et al., 1992a) and clover compared to grass hays (Aitchison et al., 1986). However, although similar factors may have ended the first meal the daily intake of the clover when offered ad lib. was greater than for the grass hay, while the intake of the grass silage was less than for the grass hay (Table 1). Thiago et al. (1992b) suggested that physical factors probably limited the intake of both hay and silage later in the day, since the fractional rate of passage of silage out of the rumen was similar to that for the hay as was total digestibility (Thiago et al., 1992a). It has been suggested that ruminants eat more clover than grass hay before physical factors become limiting due to either a faster rate of passage of clover particles compared to grass (Moseley and Jones, 1984) or to a faster rate of digestion (Beever et al., 1986). These comparisons provide further argument against the suggestion that the control of daily intake is likely to be dominated by the factor limiting the size of the first meal.

The results also suggest that the type of correlations between digestion parameters from dacron bag incubation and intake found by Ørskov et al. (1988) and Hovell et al. (1986) for hays may not apply to silages, since the higher solubility of the silage (Thiago et al., 1992a) did not result in higher intake. Another potential predictor, at least of animal preference, is initial rate of eating (Kenney and Black, 1984). Interestingly, the clover hay of Gill and England (quoted by Gill et al., 1987b) was eaten faster than the grass hay when offered ad lib. (17.9 vs. 13.8 gDM/minute) and the grass hay of Thiago was eaten faster than the silage (29

Table 1

Parameters associated with the first meal (after fresh feed offered) of grass and clover hay (Gill and England, unpublished observations) and grass hay and silage (Thiago et al., 1992 a&b) offered to young (3–6 months) beef cattle

Parameters of first meal	Hay		Sig	Grass		Sig
	Grass	Clover		Hay	Silage	
Wt rumen contents (gDM/kg LW)	18.5	14.5	$P < 0.01$	25.	4.2	$P < 0.001$
Voluntary intake (gDM/kg LW)	22.8	29.8	$P < 0.0$	18.6	24.4	$P < 0.001$

Table 2

Short term (over 4 min) rate of intake (g/min) and ad libitum intake (kg/day) for 3 hays offered to goats (Romney, unpublished observations)

Type of hay	Short term intake rate (g/min)	Ad lib intake (kgDM/day)
Clover	25.8	1.574
Ryegrass	21.9	1.301
Meadow	23.2	1.467
S.E. (pooled)	2.96	0.163

vs. 5.8 gDM/minute). Further, Romney (unpublished observations) obtained a significant ($P < 0.001$) correlation between ad lib. intake and rate of eating measured over a 4 minute period after 4 h of fasting for three different hays (Table 2). However, such relationships are unlikely on their own to be accurate predictors of intake over a wider range of feeds. Improved evaluation of the intake potential of feeds requires a better understanding of the mechanisms underlying such relationships.

3. Integration of meal control

Much of the research on the mechanisms of intake control in the last few decades has concentrated on elucidating the factors controlling the size of individual meals. Forbes (1980) developed a "minute by minute" model of intake based on existing knowledge of threshold levels of physical and metabolic factors initiating and ending meals. This model simulated patterns of consumption of a range of feeds, even though it was based on single factors limiting the size of each meal. More recently the concept of additivity (Forbes, 1986), i.e. that different factors operate simultaneously to end a meal is gaining acceptance. Mbanya et al. (1993) showed that combinations of treatments may have a greater effect when given together than when given separately (Table 3). However, given the variation in rumen volume within a day (Gasa et al., 1991) and evidence which suggests that even fractional outflow rate from the rumen may vary within a day (Gill, 1990), the accuracy of prediction of rumen VFA concentrations and the degree of rumen fill at different times of day, is likely to be limited. Indeed the inability

Table 3

Depression of intake during treatment (0–3 h) and for the 2 h following treatment (3–5 h), expressed as a percentage of the control (no treatment) for lactating cows offered grass silage + 3 h infusions of 9 mol acetate and/or distension of 101 of balloon inflation (Mbanya et al., 1993)

	Silage intake as % control	
	0–3 h	3–5 h
Acetate	85.7	57.1*
Distension	89.3	109.1
Acetate + Distension	66.4*	56.4*

* $P < 0.05$ relative to control.

of current rumen models to predict these parameters accurately even for steady state conditions was highlighted recently by Neal et al., (1992).

Another problem with the prediction of intake through models of feeding behaviour within a day is the assumption that total intake is a function of eating rate and the time during which feeding is not inhibited by physical (e.g. rumen fill) or other factors (e.g. rumen VFA concentrations) or time spent ruminating, i.e. the time during which the animal is prepared to eat. However, eating rate is not necessarily constant within a day. Higher rates can be observed in fasted animals (Greenwood and Demment, 1988) and unpublished results by Romney and Sendalo showed significant differences ($P < 0.001$) in rates of herbage intake by goats determined in the first (4.62 gDM/minute) and fourth or eighth hours (av. 2.16 g DM/minute) of 4 or 8 hour grazing periods. Further, the threshold or "set-point" at which animals stop eating in response to inhibitory factors (and hence the time available for eating) may also vary. For example, Romney et al. (1993) observed that goats allowed to graze for only 4 h adapted their grazing behaviour such that intake was the same as goats with access to grazing for 8 h (Fig. 1). This suggests that an additional control mechanism (related to daily intake) was modifying the set-points for initiating and ending meals. Until we understand the form of this control, we are unlikely to be able to predict daily intake from feeding behaviour.

4. The "Drive" to eat

It is usually assumed that animals eat to satisfy their requirements for production (e.g. Forbes, 1986). This

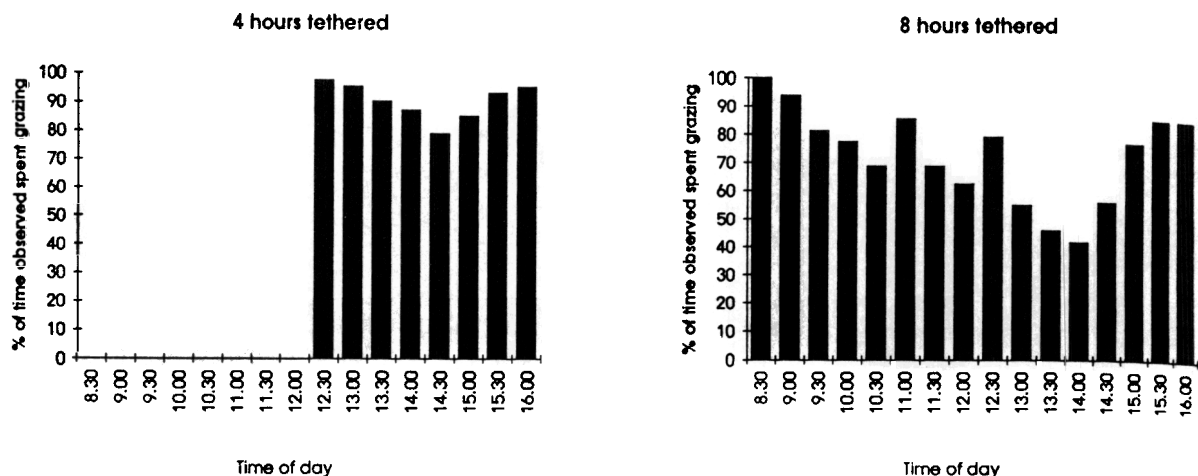


Fig. 1. Proportion of each half hour at grass spent grazing, for goats tethered on tropical pasture for 4 or 8 hours, estimated from 5 minute observations of behaviour (Romney et al. 1993).

assumption is supported by results from pigs which appear to select diets according to their requirements (Kyriazakis et al., 1990). Recent evidence suggests that sheep also select higher or lower protein diets according to their requirements (Kyriazakis and Oldham, 1993), but the receptors which participate in this response have not been identified. Leng (1990) re-emphasized the hypothesis of Egan (1977) that the ratio of protein:energy supplied to the tissues, relative to that required for maximum production could play a major role in controlling daily intake. Leng (1990) hypothesized that when protein is deficient, the rate at which the animal has to lose heat from the body (generated by the oxidation of acetogenic substrates which cannot be used for synthesis of protein) would be increased and could form the basis of intake control at least at high ambient temperatures. There is less evidence for excess protein limiting intake, although a trend in this direction was observed by Gill et al. (1987a) in response to fishmeal supplementation in silage. However, the patterns of protein and energy supply within a day will vary independently, related to the pattern of feed consumption and digestion (see Gill, 1990 for examples), and the consequences of short-term asynchrony of protein and energy supply on the inefficiency of energy utilization (i.e. daily heat production) are not yet understood. Further calculations are required to determine the time scale over which such a mechanism could operate.

The concept of animals controlling feed intake to maximize their rate of growth or milk production is not, however, universally accepted; Ketelaars and Tolkamp (1993) have recently questioned this basic feeding “drive”. In a companion paper (Tolkamp and Ketelaars, 1992), they suggested that animals consume feed in such a way as to maximize the efficiency of oxygen utilization i.e. to maximise the intake of net energy per litre of oxygen produced from the feed consumed.

It is very difficult to “prove” any theories of intake control, although they can be tested by considering whether they apply to a range of experimental observations. However, such a task is not within the scope of this paper and hence the following speculation as to how the control of meal size might relate to an overall control of daily intake simply assumes that a control at this level exists. One possibility which could be investigated is that the stretch- or chemo-receptors function to control the size and pattern of meals of specific feeds such that the imbalance of nutrients absorbed, the amount of heat produced, the inefficiency of oxygen utilization or whatever negative factor controls daily intake, is minimized per kg of feed. Another possibility is that these receptors serve to minimise “discomfort” and that the degree of “discomfort” accepted by an animal is related to how far the animal is from meeting its production or oxygen utilization “targets”.

5. Conclusions

The long held belief that physical bulk is the major factor limiting the daily intake of forages has been increasingly challenged during the last 8–10 years, although stimulation of the stretch receptors in the reticulo-rumen does send inhibitory signals to the satiety centre in the brain. This is one example of the lack of understanding of the relationship between the control of feeding behaviour and the control of daily intake. Better understanding of this relationship would help to improve our ability to characterize feeds on the basis of their intake potential

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