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Afternoon Session

Chairman: J. ROWSELL ESQ., JP, *Stoke Charity, Near Winchester, Hants.*

Factors affecting the voluntary intake of grass*

By R. C. CAMPLING, *National Institute for Research in Dairying, Shinfield, Reading*

Introduction

Study of the factors controlling the intake of food by ruminants has been neglected for many years and it is only recently that interest among research workers has arisen. There are two good reasons why work is necessary on this subject. First, the most efficient animals are likely to be those that eat most per unit of body-weight (see Kleiber, 1936). Second, economic returns are often limited because the voluntary intake of the animal restricts the amount of cheap foods that can be utilized. Most often the cheap foods are grassland products, and it is with the voluntary intake of such foods by ruminants that this communication is primarily concerned; space permits only a brief discussion of the variation in voluntary intake between animals.

The term voluntary food intake is used to describe the amount of food eaten by an animal when food is offered *ad lib.* The precise conditions under which voluntary food intake is measured must also be described, because many environmental factors can affect voluntary food intake, e.g. time of access to the food (Campbell & Merilan, 1961; Freer, Campling & Balch, 1962). Unfortunately in animal husbandry the term palatability has become equated with voluntary food intake (Ivins, 1955; Garner, 1963) and differences between foods in the extent to which they are eaten have been attributed to differences between the foods in palatability. The voluntary intake of a food depends on the interaction between the animal and its food and, as Blaxter, Wainman & Wilson (1961) have written, to describe a food as palatable and therefore attractive to the animal's palate involves appraisal of the animal's subjective evaluation of its food. I am in complete agreement with Blaxter and his colleagues that the term palatability should not be used in this context at all. This does not mean that the animal's senses of touch, smell and taste are unimportant in determining voluntary food intake, but rather that we know extremely little of these senses in ruminants and almost nothing of how they affect the intake of food. There is evidence that, when a single food only is given (Teitelbaum & Epstein, 1963), taste and smell

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play little or no part in the long-term quantitative regulation of food and water intake in non-ruminant animals such as the rat. It is supposed that taste and smell would be rather more important when a choice of foods is given; nearly all the results reported below have been obtained when the animals were offered only a single food and no choice.

The regulation of food intake

Of the very many factors that have been suggested as affecting voluntary food intake, there is considerable evidence to support the hypothesis that the voluntary intake of roughages by ruminants is determined mainly by the bulkiness of the digesta in, and their rate of disappearance from, the reticulo-rumen (Balch & Campling, 1962; Blaxter, 1962). The regulation of feeding and drinking behaviour in animals was reviewed recently by Brobeck (1960*a*), and voluntary food intake in ruminants by Balch & Campling (1962) and Blaxter (1962). Further discussion, more particularly of possible receptors in the reticulo-rumen sensitive to stretch, was given by Kay (1963) in a review on the physiology of the rumen.

The rate of disappearance of digesta from the reticulo-rumen is determined by the rate of passage of food residues through this compartment and by the rate at which the residues are broken down while they are retained there. A number of factors can accordingly influence the rate of disappearance. For example, the small size of the reticulo-omasal orifice means that particles of roughage have to be reduced in size markedly before they can leave the reticulo-rumen. Reduction in size of particle comes about through chewing during eating and rumination, and the efficiency of chewing must vary with the physical and chemical forms of the roughage and the extent of its degradation by micro-organisms. Most of the digestion of a roughage in the gut occurs within the reticulo-rumen and it is thus possible to understand the close direct relationships recognized recently between voluntary intake of roughages and digestibility. Relationships of this type have been shown at several centres throughout the world in sheep (Crampton, Donefer & Lloyd, 1960; Blaxter *et al.* 1961) and in cattle (Campling, Freer & Balch, 1961; Blaxter & Wilson, 1962; Conrad, Hibbs, Pratt & Davis, 1962; Freer & Campling, 1963; McCullough, 1963). A further component of the rate of disappearance of digesta from the gut is the rate at which the undigested residues pass through the alimentary tract. Because of the importance of the amounts of digesta in the reticulo-rumen in the regulation of the voluntary intake of roughage, the time of retention of food residues in this part of the tract is indirectly linked with the voluntary intake of roughages (Blaxter *et al.* 1961; Campling *et al.* 1961, 1962). Although the digestibility of a food and its time of retention in the gut are generally inversely correlated (i.e. foods of high digestibility have short retention times), the opposite can occur.

Most of the general relationships between voluntary intake and digestibility have been found with cattle and sheep given conserved grass products—mainly hays and artificially dried grass, and there remains the question of the validity of such relationships when ruminants are grazing or are given foods such as freshly cut herbages, silages, ground pelleted hays, or mixtures of two or more foods.

The intake of herbage

The accurate estimation of the intake of a grazing animal is still difficult and, if selection is exercised by the animal, estimates of the digestibility of 'herbage grazed' by faecal index or cutting techniques may well be incorrect (Tayler & Deriaz, 1963; Minson, 1963*b*). This difficulty must be realized in looking for a relationship between the intake and digestibility of the herbage under grazing conditions. There are reports of grazing cattle showing a decline in the intake of herbage as digestibility declines (Elliott, Fokkema & French, 1961; Corbett, Langlands & Reid, 1963). However, data collected by Hutton (1962*a*,*b*) in New Zealand while offering cows freshly cut herbage *ad lib.* throughout the season showed little, if any, fall in intake of dry matter as the digestibility of the herbage fell rapidly from about 77 to 70%, but below this level intake appeared to decline with decreasing digestibility. On more recent examination Hutton (1963) has claimed that there is little evidence of a causal relationship between the voluntary intake of non-lactating cows and herbage digestibility. Harris & Raymond (1963) found no close relationship between the digestibility of young highly digestible herbage and the voluntary intake of sheep. Also, Armstrong (1960) found with sheep that the voluntary intake of very highly digestible artificially dried grass was below that of slightly less highly digestible material; Crampton *et al.* (1960) reported a similar result with timothy. All these results suggest that the intake of very young, highly digestible herbage is probably not limited by its filling effect in the reticulo-rumen. This may be a situation in which the regulation of voluntary food intake is similar to that which occurs on highly digestible all-concentrate diets (Freer & Campling, 1963), and here the limiting factor(s) is not understood. Possible chemoregulatory and thermoregulatory mechanisms influencing voluntary intake with this type of diet were discussed by Balch & Campling (1962) and Blaxter (1962), but as yet these factors have been little studied experimentally in ruminants. Another approach has been to attempt to isolate chemically from herbage substances responsible for very low intakes of certain types of grass; for example, see the report by Roe & Mottershead (1962) on *Phalaris arundinacea* L.

It seems unlikely that the large amounts of water ingested with grass are the direct cause of low voluntary intakes (MacLusky, 1955; Campling & Balch, 1961; Davies, 1962; Holmes & Lang, 1963), although close relationships have sometimes been observed between the voluntary intake of herbage dry matter by sheep and the percentage of dry matter in the herbage (Arnold, 1962; Davies, 1962).

The effect of height and density of pasture on the herbage intake of grazing animals has recently been examined and discussed by Wheeler, Reardon & Lambourne (1963); they found no significant correlation between the weight of herbage per acre and the intake of digestible organic matter by sheep.

The intake of silage

Cattle given silage seldom consume as much dry matter as when they are offered hay (Sykes, Converse & Moore, 1955; Nicholson & Parent, 1957; Moore, Thomas & Sykes, 1960; Brown, Hillman, Lassiter & Huffman, 1963; McCarrick, 1963;

Murdoch & Rook, 1963; Everett, 1963). My own unpublished results of comparisons of silage and hay prepared from similar herbage confirm this finding and show that when grass silage was given without choice about 20% less dry matter was eaten than of hay made from similar herbage. Harris & Raymond (1963) found that the voluntary intakes of silages by sheep were on average only half those of the corresponding herbages. These workers also reported that there was no relationship between the voluntary intake of the silages and their digestibilities. The reason for the low intake of silage is unknown. The water contained in the silage is probably not directly a limiting factor (Moore *et al.* 1960; Brown *et al.* 1963) although, within limits, the drier the silage the more of it will be eaten (Dodsworth, 1954; Danasoury, 1954; Moore *et al.* 1960; Thomas, Moore, Okamoto & Sykes, 1961), and prewilting herbage is an effective way of increasing the intake of silage (Murdoch, 1960; Harris & Raymond, 1963). The digestibility of the silage is generally equal to that of the hay prepared from similar herbage (Harris & Raymond, 1963; McCarrick, 1963). Substances having marked pharmacological effects and present in silage in very small quantities (e.g. histamine) have been suggested as a possible cause of the low intake; however giving histamine orally to sheep has not affected their voluntary intakes of silage (McDonald, Macpherson & Watt, 1963). Many other substances (e.g. urea, tyramine, sucrose, lactic acid and the liquid effluent from a silo) have been tested for their effect on voluntary intake of lucerne silage by adding them directly to the rumen of dairy heifers (Thomas *et al.* 1961). Although several of these substances depressed intake (e.g. urea, large quantities of lactic acid and the liquid effluent from a silo), there is little evidence to show that any of them is the normal cause of the low intake of silage. A few clues from work in this Institute indicate that the rate of disappearance from the rumen of digesta derived from silage may be slower than that of hay. Study of the eating and ruminating behaviour of cattle given silage showed that per unit of dry matter silage was eaten at a slower rate than hay. Also, more time was spent ruminating per kg silage than per kg hay, on a dry-matter basis.

The intake of ground, pelleted roughages

Grinding and pelleting roughages is practised on a fairly wide scale in the USA and because of this and its great theoretical interest there have been several studies of its effect on voluntary food intake and animal production. Much of the work has been summarized by Minson (1962, 1963*a*). Contrary to popular opinion, it is by no means certain that grinding and pelleting a roughage will be associated with an increased voluntary intake of food (see Campling *et al.* 1963). A major factor determining whether an increase will be obtained is the quality of the roughage. It has been found at Shinfield that cows derive little or no benefit from grinding and pelleting a medium-quality hay or an artificially dried grass, but a considerable increase in intake was observed when oat straw was so treated. Recent results from Canada with sheep also show the importance of the stage of maturity of the roughage in determining the response in intake on grinding and pelleting (Heaney, Pigden, Minson & Pritchard, 1963) although here considerable increases in voluntary intake were

found associated with the grinding and pelleting of even the youngest, highly digestible roughage.

The effect of concentrates on the intake of roughage

Another factor that can influence greatly the voluntary intake of roughage is the amount and type of concentrates given. It is well known that marked increases in voluntary intake of low-quality roughages can occur when concentrates containing nitrogen are given (Clark & Quin, 1951; Coombe, 1959; Campling *et al.* 1962; Hemsley & Moir, 1963). The increased intake appears to occur because of an accelerated rate of disappearance of digesta from the reticulo-rumen (Campling *et al.* 1962; Coombe & Tribe, 1963; Hemsley & Moir, 1963). The important role of higher volatile fatty acids in effecting the utilization of urea and the subsequent increase in intake of low-quality roughages was demonstrated recently by Hemsley & Moir (1963).

In Britain concentrates prepared from several ingredients and balanced for milk production are frequently given to cows receiving hay or silage with or without other roughages. Although the total intake of dry matter generally increases when restricted amounts of concentrates are given, the intake of roughage often drops and considerable variation in the extent of the decline in the voluntary intake of roughage per unit of concentrates has been reported (Danasoury, 1954; Holmes, Reid, MacLusky, Waite & Watson, 1957; Holmes, Arnold & Provan, 1960). This effect is possibly due in part to the varying quality of the roughages that have been given, for Blaxter *et al.* (1961) and Blaxter & Wilson (1963) showed in sheep that the extent of the depression in voluntary intake of roughage, when restricted amounts of concentrates were given, varied inversely with the quality of the roughage: the more digestible the roughage the greater the depression of roughage intake. Perhaps these results have some relevance to the results obtained when grazing cows are given concentrates. Results from work in progress at Shinfield suggest that the depression in hay intake observed when concentrates are given may be due to a depression in the rate of disappearance from the rumen of hay digesta: it is well known that additions of starch depress the digestibility of the cellulose of hay (Head, 1953). This effect in turn is possibly due to the less efficient cellulolytic activity of the rumen microflora. Very little is known of the effect of the type of concentrate on voluntary intake of roughage. Murdoch (1962) described the results of a trial in which a mixture of barley and 16% decorticated groundnut cake was superior to barley alone in increasing the voluntary intake of cows offered grass silage *ad lib.* Also, in one experiment sheep given silage *ad lib.* showed no depression in silage intake when given 1 lb of dairy cubes but when given hay *ad lib.* and a similar amount of concentrates there was an appreciable depression in intake of hay (Murdoch, 1963), and Clifton, Miller & Cameron (1963) reported that the depressing effect of concentrates on the roughage intake of milking cows was less with silage than with hay. Clearly there is still much to be learnt of the interaction between concentrates and roughages.

The voluntary intakes of completely ground and pelleted mixtures of roughage and cereals may show trends very different from those observed when concentrates are given in restricted amounts to animals receiving long roughage *ad lib.*; Donefer, Lloyd & Crampton (1963) found marked decreases in total food intake as the amount of cereals was increased.

None of the foods discussed above fit the relationships between voluntary intake and digestibility found with hays and artificially dried grass given singly. The intakes of very highly digestible grass and of silage are lower than would be predicted on the basis of their digestibility, whereas those of ground pelleted roughages, and mixed diets of hay given *ad lib.* with restricted amounts of concentrates, are higher than expected.

The kind of animal

The quantity of food eaten will, of course, depend on the kind of animal. For example a cow may eat eight to ten times the amount eaten by a ewe; comparative studies of the voluntary intake of food by different species and breeds of ruminants are scarce. Among apparently similar animals there may be variation in voluntary food intake even when expressed per unit of metabolic body size (usually $W^{0.73}$); coefficients of variation of voluntary food intake of between 10 and 13% have been recorded by Greenhalgh & Runcie (1962) and Corbett *et al.* (1963) among grazing cows and in stall-fed steers and sheep by Blaxter & Wilson (1962). Although it is often convenient to express food intake per unit of size or body-weight (or some function of it) when comparing different animals of the same species (cf. Blaxter *et al.* 1961) or different species (Blaxter & Wilson, 1962; Ingalls, Thomas & Tesar, 1963; Buchman & Hemken, 1963), it must be remembered that these are statistical relationships between body-weight and voluntary food intake calculated between animals. It seems that the fatter an adult animal becomes the smaller will be its voluntary food intake (Ferguson, 1956; Mather, 1959).

The causes of variation in voluntary intake of roughage among animals of apparently similar size are not known (see Balch & Campling, 1962). Part of the variation may be genetic in origin (Mather, 1959; England, 1962; Rimm, 1963). Differences in digestibility between animals of the same species are small (Weston, 1959), and Campling *et al.* (1961) suggested that cows with a characteristically longer mean retention time of food in the gut might have smaller voluntary intakes than those with characteristically shorter retention times. Differences between animals in retention time might be due to variation in the efficiency of chewing or in the propulsive action of the musculature of the gut or in both; information on these factors is lacking.

Variation in voluntary food intake associated with sex, age or with physiological changes such as growth, fattening, pregnancy and lactation are not well documented for ruminants. To take one important example, the effect of lactation is reported as being associated with a marked rise in voluntary intake in sheep (Cook, Mattox & Harris, 1961; Davies, 1962), but for the cow there are extremely few valid observations on this subject. Hutton (1962*a*, 1963) in New Zealand, using monozygous

twin cows and freshly cut herbage, found that the lactating cows ate 47% more gross energy than their dry twin-mates. My unpublished results, again with stall-fed monozygous twin cows, show considerable variation between pairs of twins in the changes in voluntary food intake that occurred with the onset of lactation. Also, there is very little information on the effect of these physiological changes on eating and ruminating behaviour, on rates of breakdown and digestion, and on retention time of food in the gut. Graham & Williams (1962) recently observed in sheep given a constant amount of food that the retention time of residues in the gut increased as pregnancy advanced. Reid & Hinks (1962) studied the marked depression in voluntary food intake in late pregnancy of fat, twin-bearing ewes. It appears that the depression in intake was not simply a consequence of reduction in abdominal space due to the large volume occupied by twin foetuses or abdominal fat, but probably involved metabolic changes associated with pregnancy and fattening. It will be most interesting to see what modifications need to be made to the gut-fill hypothesis to make it comprehensive enough to explain the effect on voluntary food intake of these physiological changes.

Environmental factors

Changes in the climatic environment of the ruminant can also influence intake (Ragsdale, Thompson, Worstell & Brody, 1950; Winchester & Morris, 1956; MacDonald & Bell, 1958); a rise in ambient temperature leads to a decrease in hay intake, and Wayman, Johnson, Merilan & Berry (1962) suggested that part of this effect may be due to a decreased rate of passage of digesta through the rumen. Conversely, a decrease in temperature is associated with an increase in hay intake. With sheep, shearing is often associated with an increase in food intake, which, it was suggested, may be due to cold stress (Wheeler *et al.* 1963). Although the existence of a 'thermostatic' mechanism in the hypothalamus affecting food and water intake has been demonstrated in the ruminant (Andersson & Larsson, 1961), Andersson and his colleagues recently concluded that it may serve mainly as an emergency mechanism when body temperature reaches a critically high level (Andersson, Gale & Sundsten, 1963). Thus it would be unwise to think that environmental temperature exerts its effect on food intake only through a relatively simple type of mechanism as outlined by Brobeck (1960*b*).

Conclusion

There are, of course, many problems still to be solved: our knowledge of the factors governing the selection of foods by ruminants is extremely meagre. Although we know something of certain simple associative effects on voluntary intake of two foods given together, we are ignorant of the effect of allowing the animal a choice of two or more foods given *ad lib.* Further experimentation similar to that of Weir (1962) who examined the selective intake of sheep offered a choice of five ground, pelleted diets would be well worth while. Nor is much understood of the reasons why one animal eats more food than another apparently similar animal or of how environmental conditions, growth, fattening, pregnancy and lactation affect voluntary intake.

Though the hypothesis for the regulation of roughage intake based on the amount of contents in the reticulo-rumen is useful, it is extremely crude and not capable of explaining the voluntary intakes of all the diets ruminants will eat. It is particularly important to study the factors that control the intake of young, highly digestible herbage by ruminants. Further knowledge of the biochemical and physiological changes that occur concurrently with eating will help the understanding of this important factor in animal production.

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The efficiency of utilization of fresh grass*

By W. HOLMES and J. G. W. JONES, *Wye College (University of London), Ashford, Kent*

Grass is a major crop in this country and grassland a cheap source of feed. But unless the produce is effectively utilized it is an unprofitable way of using land, particularly where conditions suit the growing of other crops. Grass is of course the only way of utilizing land which by reason of topography or rainfall is unsuitable for other crops. Moreover, in arable areas a grass ley is considered to confer some benefits on succeeding crops. Nevertheless grassland and especially grazing is probably one of the farming resources which in general is least well exploited. This is not difficult to explain in view of the technical complexities of grassland management, and it should be appreciated that improving grazing efficiency is not necessarily the best thing a farmer can do with his available time and resources. However, grass efficiently used can compete in economic terms with many other

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